Norwegian University
of Life Sciences

Master's Thesis 2017 60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Factors Affecting Prey Choice and Diel Activity in Ospreys (*Pandion haliaetus*) Nesting in SE Norway

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Acknowledgements

This thesis is my final project as a master student in biology at the Norwegian University of Life Sciences (NMBU). First, I owe my greatest gratitude to my main supervisor Geir A. Sonerud, for good guidance and help throughout the year, and to my co – supervisor Ronny Steen, for technical support, and help with statistics. Big thanks also go to Thrond O. Haugen for help with prey species identification, and to Ole Jørgen Hanssen, Tellef Kjellesvig, Per Ivar Aleksandersen, and Rune Aae for help with localizing nest sites, climbing trees, installation of video equipment, swapping SD cards and help with dirty camera lenses and cameras out of position. A special thanks to Rune Aae, who frequently climbed the tall pine at Skjeberg, when problems occurred. I also would like to thank the photographer Jørn Bøhmer Olsen, for stating hatching date for the nestlings at Isnes, and for his general interest in the nestling's development and well – being during the season.

I would also thank my fellow students, Tuva Flor Lien, who was my partner in crime, Kim Daniel Hansen, with help and cooperation during the field season, and Jonas Olseng Vik and Peter Valkeneer for cooperation and support in the working process. I would also thank one of my best friends, Silje S. Amundsen for motivation and proofreading (#siljepower). Great thanks also go to Silje Bjørgeengen, for going up the trail, and answering questions during the year.

The person helping me the most is nevertheless my boyfriend Roger Johansen Bjørvik, who deserves it all for helping me with all the aspects of this thesis, while writing his own. We made it.

For this project, I received financial support from the Norwegian Environment Agency (wildlife fund), and the Østfold county governor.

Ås, 11 May 2017

Silje Klo Hansen

Abstract

Prey deliveries and prey handling were video recorded at two ospreys (*Pandion haliaetus*) nests in Sarpsborg municipality, south – eastern (SE) Norway, during the nestling period in May – August 2016. The males delivered most prey while the female did the brooding and most of the feeding. The female at one of the nests disappeared in early July, most likely due to an accident, leaving the male with both hunting and feeding the dependent nestlings. All 379 prey items recorded delivered to the nests, 271 at one (Isnes) and 108 at the other (Skjeberg), were identified as fish. Among the prey, 39.6% were carps (Cyprinidae sp.), 20.3% were perches (Percidae sp.), 15.8% were flounders (Pleuronectidae sp.), 11.6% were pikes (Esocidae sp.), while 2.4% were needlefishes (Belonidae sp.). Freshwater bream (*Abramis brama*), European perch (*Perca fluviatilis*), northern pike (*Esox lucius*) and European flounder (*Platichytus flesus*) was the most frequently delivered prey at species level with 36.7%, 19.5%, 11.9% and 4.7%, respectively, while 6% could not be identified as anything but fish. Mean prey body mass for delivered prey to the nests was estimated to be 318.5 g. Freshwater bream was the most likely prey species to be decapitated prior to delivery, while perch was least likely to be decapitated prior to delivery. Larger prey was more likely to be decapitated than smaller prey. For both nests (Isnes and Skjeberg), the probability of assisted feeding decreased with nestling age. The nestlings started to feed unassisted at day 47 for one nest (Skjeberg) and at day 51 at the other (Isnes). Prey deliveries were frequent during daylight, with especially high peaks at 05:00 – 07:00, 12:00 – 13:00, and 18:00 – 19:00 at one nest (Isnes), and at 05:00 – 07:00 and 18:00 – 20:00 at the other (Skjeberg). Neither tide nor wind speed affected the probability of prey deliveries. The diel pattern of deliveries of the different prey types also had peaks in the morning and evening, except for delivery of pikes, which peaked at midday. This is most likely due to other prey species being less abundant at this time. The estimated prey mass that each nestling received per day increased during the season at one nest (Isnes), but not at the other (Skjeberg). Carps and perches were delivered uniformly throughout the season, while there was a decrease for delivered pikes and flounders. For garfish (*Belone belone*), there was a trend for an increase. Video monitoring has been shown to be an accurate method to investigate prey composition and prey handling during nestling season.

Sammendrag

Byttedyrleveringer og håndtering ble filmet i to fiskeørnreir gjennom hekkesesongen i perioden mai – august 2016, i Sarpsborg kommune, Sør – Øst (SE) Norge. Som forventet leverte hannen flest byttedyr, mens hunnen sto for rugingen og det meste av fôringen. Hunnen ved det ene reiret (Skjeberg) forsvant i starten av juli, mest sannsynlig på grunn av en ulykke, og hannen måtte dermed stå for både jakt og fôring av ungene. Alle de 379 byttedyrene som ble levert til reirene, 271 ved det ene (Isnes) og 108 ved det andre (Skjeberg) ble identifisert som fisk. Blant byttedyrene var 39,6% karpefisk (Cyprinidae sp.), 20,3% var abborfisker (Percidae sp.), 15,8% var flyndrefisker (Pleuronectidae sp.), 11,6% var gjedde (Esocidae sp.) mens 2,4% var horngjel (Belonidae sp.). Brasme (*Abramis brama*), abbor (*Perca fluviatilis*), gjedde (*Esox lucius*) og skrubbe (*Platichytus flesus*) var de mest leverte byttedyrene på artsnivå med 36,7%, 19,5%, 11,9% og 4,7%, mens 6% ikke kunne bli identifisert som noe annet enn fisk. Gjennomsnittlig vekt for levert byttedyr ble estimert til å være 318.5 g. Brasme var den arten som hadde høyest sannsynlighet for å være dekapitert før levering til reiret, mens abbor hadde minst sannsynlighet for å være dekapitert før levering. Større byttedyr var mer sannsynlig å være dekapiterte enn mindre byttedyr. Ved begge reirene (Isnes og Skjeberg) gikk sannsynligheten for assistert fôring ned med økende alder på ungene. Ungene begynte å spise selvstendig når de var 47 dager gamle ved det ene reiret (Skjeberg) og 51 dager gamle ved det andre reiret (Isnes). Det var jevnlige leveringer av byttedyr mens det var dagslys, med spesielt høy aktivitet mellom kl. 05:00 – 07:00, 12:00 – 13:00 og 18:00 – 19:00 ved det ene reiret (Isnes), og kl. 05:00 – 07:00 og 18:00 – 20:00 ved det andre reiret (Skjeberg). Verken tidevann eller vindhastighet påvirket sannsynligheten for byttedyrlevering. De ulike byttedyrene hadde også høyere aktivitet om morgenen og om kvelden, bortsett fra gjedde som hadde høyest aktivitet midt på dagen. Dette er mest sannsynlig en konsekvens av at de andre byttedyrene er mer utilgjengelige i denne perioden. Estimert byttedyrmasse hver unge mottok hver dag gjennom sesongen, økte ved det ene reiret (Isnes), men ikke ved det andre (Skjeberg). Karpefisk og abborfisk ble jevnt levert gjennom sesongen, mens det var en nedgang i levering av gjedde og flyndrefisk. Det var en tendens til økning for horngjel. Videoovervåkning har vist seg å være en nøyaktig metode for å undersøke byttedyrsammensetningen og byttedyrhåndtering gjennom hekkesesongen.

Contents

Introduction

The osprey (*Pandion haliaetus*) is a summer visitor from Africa to Norway and West Palearctic (Cramp & Simmons, 1979). It is widespread across large parts of the world, and nests in all continents except South – America and Antarctica. In Norway, it is mainly distributed east of the mountains, from Sørlandet up to Trøndelag and Finnmark. It was nearly gone in the 1930 - 1940s due to extensive hunting, and was therefore totally protected in 1962. In the last 30 years, the population have increased to 150 - 200 breeding individuals (Syvertsen, 2009), but is still listed as nearly threatened (NT) in the Red list of species 2015 (Norwegian Biodiversity Information Centre, 2015). Nowadays, the ospreys face new threats as acidification of river systems, pollution from industry, agriculture, household and emissions of pollutants, such as pesticides and heavy metals (Bierregaard, 2014). The increasing focus on wind mills (Dahl et al., 2012), increased recreational use and human intervention in nature may also be a source for mortality and disruption in breeding season, although they are adaptable to some level (Cramp & Simmons, 1979). Because of this, it is important to monitor the populations, and to do food chain analysis to be aware of changes in the ecosystem(s). Since the osprey is a top – town predator, it is a great model species for this purpose (Häkkinen, 1978; Lewis et al., 2004; Clancy, 2005).

The osprey is a diurnal, medium sized (body mass 1400 - 2000 g) bird of prey where the female is larger than the male (5 - 10%). It is both solitary and loosely social, and normally form monogamous bonds in breeding season. The osprey has asymmetrical parenting roles where the male usually has the sole role as food provider for the female and the nestlings during incubation and nestling period, while the female does the main part of the brooding and feeding (Cramp & Simmons, 1979).

The osprey´s diet and foraging behavior is quite well studied in Europe and America (Häkkinen, 1978; Swenson, 1978, 1979; Nordbakke, 1980; Edwards, 1988; Edwards, 1989; Hagan III & Walters, 1990; Flemming & Smith, 1990; McLean & Byrd, 1991; Francour & Thibault, 1996; Cartron & Molles, 2002; Clancy, 2005; Marquiss et al., 2007; Glass & Watts, 2009; Martins et al., 2011; Bjørgeengen, 2016). The osprey may be regarded as a generalized specialist (Bierregaard et al., 2014), preying on a variety of fish species. Because the osprey is a single prey loader and central place forager it is expected to prey on relatively large prey to minimize the costs of transportation from the hunting site to the nest (Sonerud, 1992). The providing parent needs to make decisions based upon which prey is most profitable to maximize the overall net gain per time unit. The optimal choice of prey depends therefore both on search time, handling time and energy content of prey (Davies, 2012), while the osprey's choice of diet basically reflects the abundance and availability of prey near the water surface (Cramp & Simmons, 1979; Edwards, 1988). The osprey usually fishes in shallow bays of lakes, and the fishing site is often several km (up to 20 km) away from the nest (Cramp & Simmons, 1979), with some exceptions (Häkkinen, 1978; Bjørgeengen, 2016). Because the osprey localize prey by vision, it hunts during daytime due to better visibility through the water surface, and the foraging is most frequent at dusk and dawn (Flemming & Smith, 1990; Bjørgeengen, 2016). North of the arctic circle on the other hand, where the sun does not set in summer, the white – tailed eagle (*Haliaeetus albicilla*) also foraged at night (Eriksen, 2016), which also may be the case for northern populations of the osprey. In poorer light conditions, visibility is less important if the prey is close to the surface (Grubb, 1977), while in extreme poor weather the osprey stops hunting completely (Cramp & Simmons, 1979).

The hunting efficiency and dive success of ospreys has been found to be affected by time of day (Stinson, 1978; Boshoff & Palmer, 1983; Flemming & Smith, 1990; Bjørgeengen, 2016), tidal (Ueoka, 1974; Planque et al., 2011), weather variables (Grubb, 1977; Machmer & Ydenberg, 1990), water clarity, although weak influences (Flemming & Smith, 1990), and thus prey behavior and dispersion (Swenson, 1979). The spatial distribution of fish is not random, and the suitability of fish habitats is affected by external drivers, such as environmental factors, but also internal drivers like population size, age structure, fish diversity, condition and behavior. These internal drivers would modulate the spatial distribution of fish through density dependence, age– or stage – dependent habitat preference, and differential migration capacities (Planque et al., 2011). Swenson (1979), for instance, found that ospreys had higher dive success when they preyed on benthic – feeding fish than on piscivorous fishes. With respect to tide, flatfish was most frequently delivered to the nest as the tide was falling, while mullet (Mugilidae), garfish (*Belone belone*) and sea bass (*Dicentrarchus labrax*) was delivered more frequently as tide was rising (Marquiss et al., 2007). Flemming and Smith (1990) found that the frequency of foraging ospreys, and their dive success, increased at mid – tide in contrast to when the tide was high or low, and that cloud cover did not affect diving success, but affected the number of foraging ospreys.

The studies conducted on the osprey's diet is mostly based upon prey remains and carcasses at the nest (Häkkinen, 1978; Swenson, 1978; Francour & Thibault, 1996; Martins et al., 2011;). This method, however, may lead to overestimation of the profitability of large prey and avian prey, and underestimation of smaller prey and mammalian prey, because the birds occasionally do not consume all parts of the prey for various reasons (Slagsvold et al., 2010), and the same may apply to fish eating species, like the osprey (Häkkinen, 1978).

The method used in my study resembles with other successful studies on birds of prey based on monitoring prey delivery using video equipment (Steen et al., 2010; Steen et al., 2012; Sonerud et al., 2014a; Sonerud et al., 2014b; Dihle, 2015; Moen, 2015; Nygård, 2015; Bjørgeengen, 2016; Eriksen, 2016), and is a modified version of the method described by Steen (2009). The benefits and disadvantages of video monitoring is illuminated in the article by Lewis et al. (2004), but basically, video monitoring enables seeing and measuring prey handling more accurate than is possible by direct observation in the field, and to replay the recorded session until confidence to the data is obtained. Video recordings is particularly a good method to avoid disturbance of the study subject(s), but also a cost – efficient method that do not require the presence of observers.

In this study, I evaluated the prey composition, prey handling, and diel activity of two breeding pairs of the osprey in SE Norway. The research questions of this study were as follows: 1) How is the diet composition at the two nests during nestling season, and because one nest is inland and the other coastal, would the diet differ between the two nests? 2) Which factors affected whether the female dismember the prey item, or the nestlings ingest the prey item independently? 3) Which factors affected whether a prey is decapitated prior to delivery at the nests? 4) Which factors affected the amount of prey mass delivered to the nestlings? 5) Would the female capture larger prey than the male because she is larger or due to family conflicts (Sonerud et al., 2013)? 6) Which factors (e.g. prey availability, time of day, wind speed and tide) affected choice of prey delivered to the nestlings?

Methods

Study area

The field work for this study was conducted during June, July and August in 2016, at two osprey nests in Sarpsborg municipality, Østfold county, Norway, termed Isnes (59°20´4.69N, 11°2´6.67E) and Skjeberg (59°10´53.95N, 11°6´4.37E), situated 20 km apart (figure 1). The sites were chosen based on previous studies conducted at Isnes, and observations made by local collaborators from the local ornithological association. The nest at Isnes had been video recorded the previous season (2015), as one of four nests in the study of Bjørgeengen (2016), while the nest at Skjeberg had not. Both nests are located at the top of a scots pine (*Pinus sylvestris*), and the surrounding area consists of mixed coniferous forests and deciduous forests, dominated by spruce (*Picea abies*) and scots pine. The nest at Isnes is closest to freshwater and brackish water, while the nest at Skjeberg is closest to salt water.

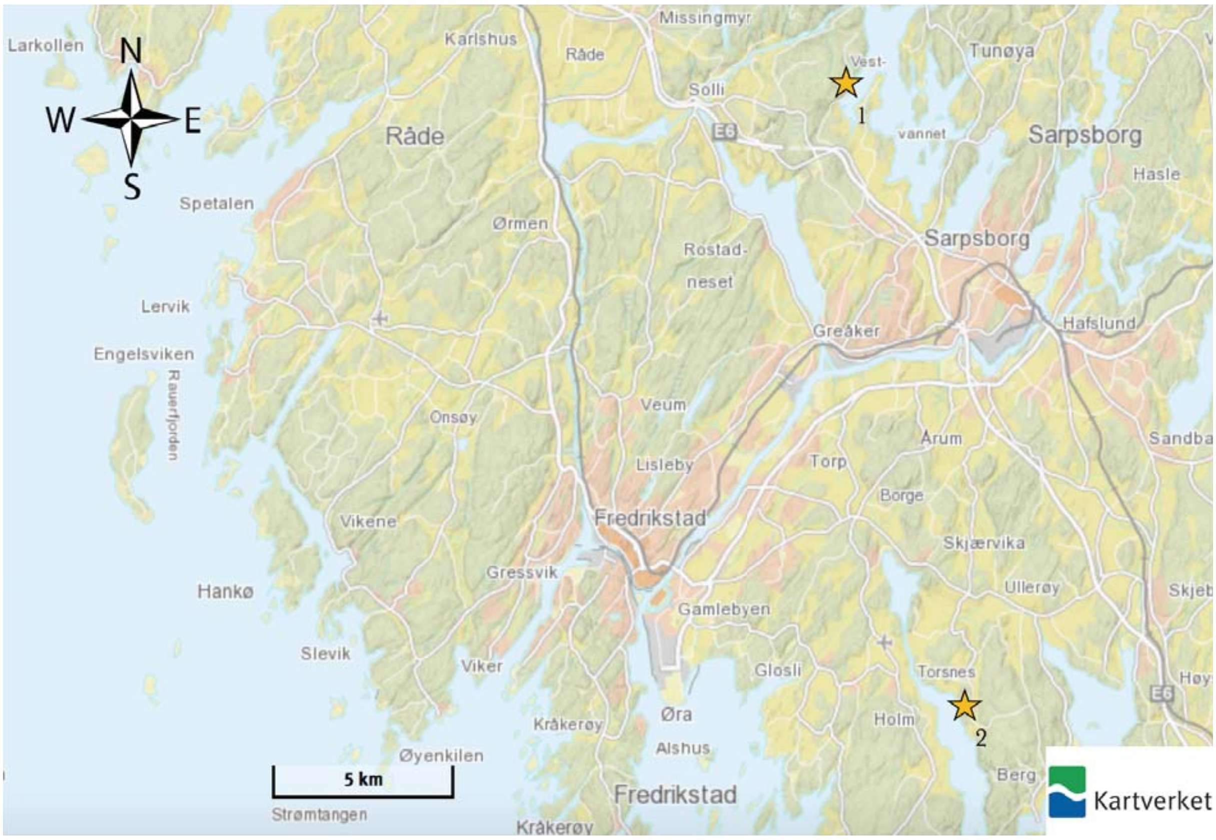

Figure 1. The location of the two osprey nests video recorded: (1) Isnes and (2) Skjeberg (The map is taken from The Norwegian Mapping Authority).

The nest at Isnes is close to Glomma, which runs through the associated area (figure 2), and thereafter southwards by Fredrikstad, into the Oslo fjord (Thorsnæs, 2015). The southern part of Glomma contains brackish water, but the ospreys at Isnes also have access to salt water within a range of 14 km. The access to freshwater (Vestvannet) is in immediate vicinity to the nest. Other larger freshwater localities in the area is Tunevannet, Vansjø and Isesjøen (table 2).

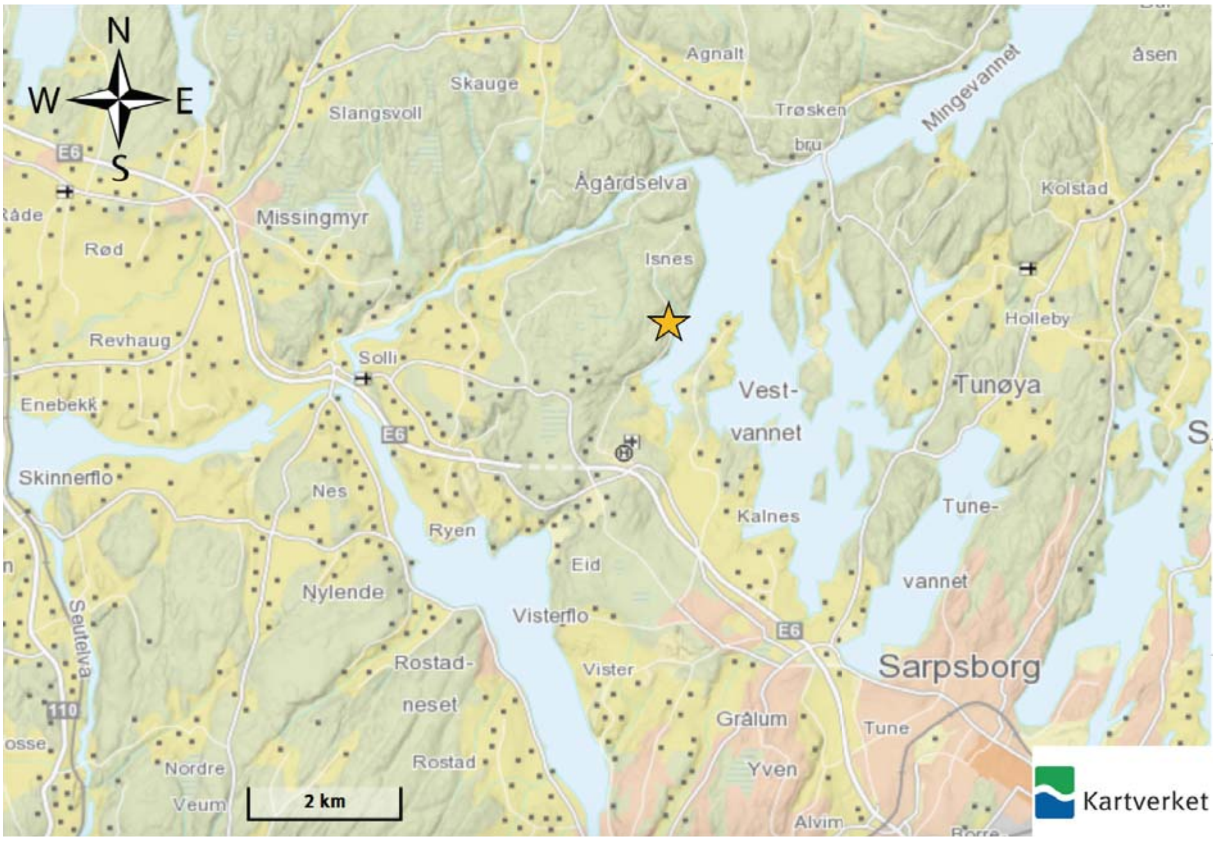

Figure 2. The location of the osprey nest video recorded at Isnes (The map is taken from The Norwegian Mapping Authority).

The nest at Skjeberg is located near the fjord Tosekilen, which forms the border between Fredrikstad and Sarpsborg municipality. Tosekilen expands to the fjord Hunnebunnen on the north side. The distance from the nest to salt water localities is 0.2 km, and the nearest freshwater locality is Isesjøen 10.3 km away, while the distance to the river Glomma is 9 km (table 2). Both nests are located close to human settlement, respectively 0.6 km at Isnes and 0.2 km at Skjeberg. During monitoring, there was little human activity in the immediate area of the nests, but sounds from traffic on land and water, and other human activities, were heard when visiting the nest sites.

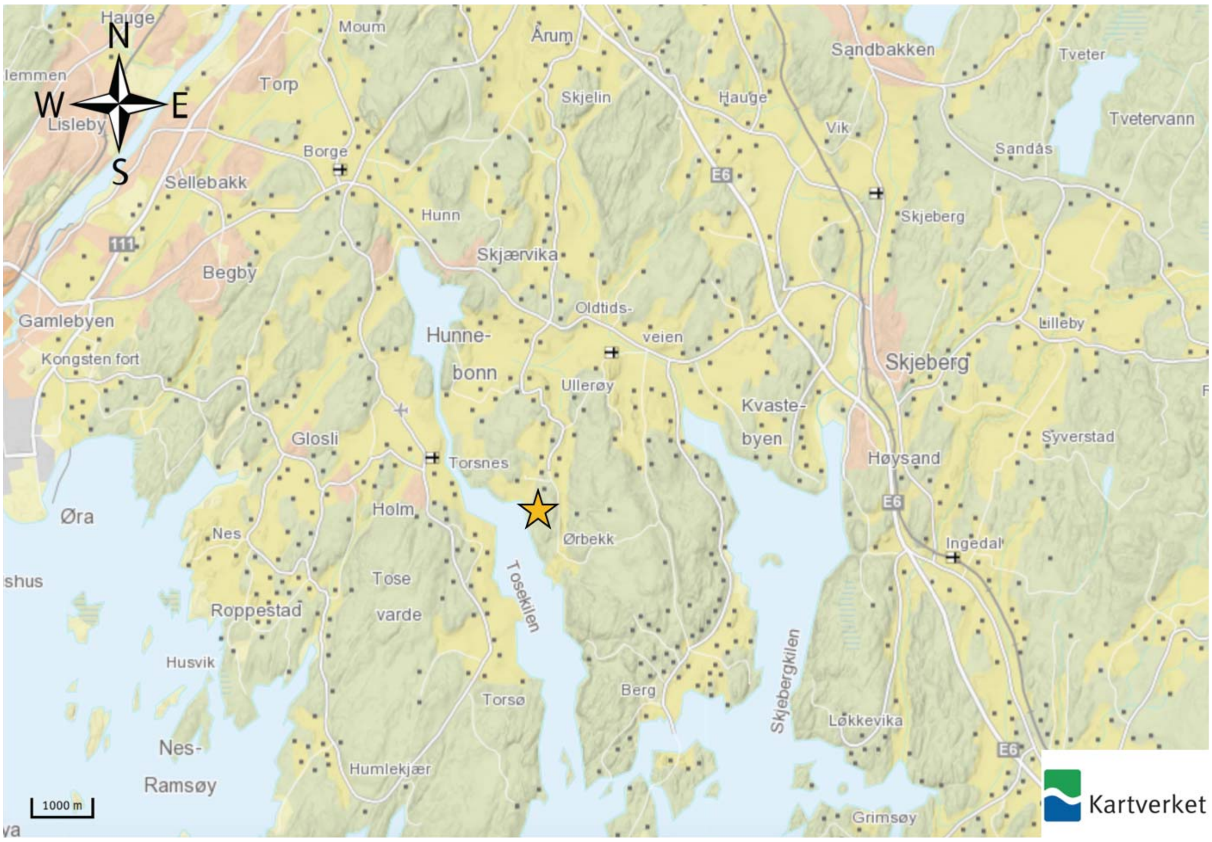

Figure 3. The location of the osprey nest video recorded at Skjeberg (The map is taken from The Norwegian Mapping Authority).

No less than 22 species of freshwater fish has been recorded in the study area (table 1). The nest at Skjeberg is located farther from the major freshwater entities than the nest at Isnes (table 2).

Table 1. The fish species recorded in rivers and freshwater lakes around the osprey nest sites Isnes and Skjeberg (table after Bjørgeengen, 2016).

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

Table 2. Approximate distances (km) from the two osprey nest locations at Isnes and Skjeberg to the river and lakes in the study area (Turkart, 2016).

Rivers and lakes	Isnes	Skjeberg
Vestvannet	0	18
Glomma	9	28
Åsgårdselva	2	20
Seutelva	8	11
Visterflo	3	12
Skinnerflo	4	19
Tunevannet	1	14
Mingevannet	3	22
Vansjø	9	25

Video recordings

Video monitoring started on 17 June at Isnes and on 21 June at Skjeberg when the nestling ages ranged from 14 to approximately 27 days. The three nestlings at Isnes hatched on 3 June and was then two weeks of age at the start of video recording, while the three nestlings at Skjeberg were approximately four weeks of age at the start of video recording. To determine nestling age at Skjeberg, we compared the size of the nestlings with the ones at Isnes, where the age was known. All the nestlings were ringed by local collaborators from the local ornithological association prior to monitoring. The adult birds at both locations were unringed. The female at Skjeberg disappeared early July, for unknown reasons, but all the nestlings developed normally, and survived despite this incident.

The nests were monitored until 12 August at Isnes and 1 August at Skjeberg, with some pauses due to technical and logistic difficulties. The camera at Isnes were installed before the nesting season in 2015, while the camera at Skjeberg were installed in June 2016. A wide angled camera lens were mounted on a branch using screws, cable ties, duct tape and camo tape, and installed approximately 1 m over the nest, pointing down towards the nest. To avoid disturbance of the ospreys, the camera was connected to a remote recording device of the type Secumate H.264, by an approximately 100 m long video cable that was hidden on the ground.

There was thus no need to enter the nest tree to operate the video recorder and to change SD cards. The cameras and the recording devices was supplied with power from 12V deep cycle marine batteries, which was changed weekly. At Isnes, the ospreys did not always notice our arrival and we could therefore often change SD cards and battery without disturbing the birds. This was not the case at Skjeberg, where the ospreys always noticed our presence.

The method described in the next section is a modified version of the one described in Steen (2009). The mini DVR is triggered by pixel changes within the successive images recorded by the camera, this feature is called video motion detection (VMD). The VMD sensitivity was set to 9 (highest sensitivity) and the VMD area was concentrated at the center of the nest. When there was movements in the nest, a 10 second video was recorded. The recordings were stored as .avi-files, which was saved on a 32 GB SD card. To avoid loss of important data on prey deliveries 5 s of pre-recordings (before movements) was also stored on the SD cards for each event (i.e. video were buffered continuously and 5 s was only kept when there was events). The VMD area was changed during the field season based on the size and movements of the nestlings. The recordings started immediately after the installation of the video equipment, and the parents arrived at the nest shortly after. The SD cards were changed each day until the nestlings fledged. Due to signal interference, the SD cards at Isnes often filled up faster than every 24 hours, so the cards were changed at different hours to avoid consistent gaps in the recordings. After the nestlings fledged, the VMD sensitivity was set lower (2), and the SD cards were changed approximately every 2 – 3 day.

At Isnes there were two incidents of stools on the camera lens which made the vision poorer. At Skjeberg there were one incident of loosened camo tape which fluttered in front of the camera. At both nests, there were incidents of cameras out of position because the ospreys occasionally perched on top of the cameras. All these incidents were sorted out within a few days, except when the camera went out of position in the last part of the monitoring period, when the nestlings had fledged.

Video analysis

Identification of prey

The recordings were analyzed retrospectively using a computer screen and VLC Version 2.2.4 Weatherwax (Intel 64bit). First, the video clips that showed prey deliveries were found, and the time the delivering parent landed on the nest with the prey were noted. Each prey was, if possible, identified to class, order, family and species by use of a fish handbook (Muus & Nielsen, 2012), and with help from Thrond Haugen (pers. comm.). The species identification was done by using the shape of body, fins and tails, and by using color and patterning of the skin, fin and flesh. Some prey items could not be identified to any taxonomic level due to difficulties in seeing the prey properly, and was classified as “unidentified”. This was in case of stools or dew on the lens, camera out of position, only parts of prey or that prey were hidden from the camera view.

Estimation of prey length and prey mass

Predicted prey length was estimated both for captured and delivered prey, because prey often was decapitated or further eaten at prior to delivery to the nests. To estimate prey length, a metal grid (figure I, appendix 1) was temporarily put on top of the nest at Isnes, after the nestlings had fledged. Still pictures and video clips were then taken, before the grid was removed. The whole grid measured 1 m x 1 m, and each square of the grid measured 7.5 cm x 7.5 cm. A simulated grid (figure II, appendix 2) was created for the nest at Skjeberg, by using a folding ruler at different spots in the nest. This was due to difficulties with the grid and the cameras position at the nest, which was different between the original video recordings and the recordings when the grid was present. The simulated grid measured 1 m x 1 m, and each square of the grid measured 10 cm x 10 cm. The nest at Skjeberg was quite hollow, so the measurements could not be done with complete accuracy.

To estimate prey length, I used still pictures of the metal grid in the nests displayed on a computer screen, and drew the grid on to transparent plastic sheets. These sheets was later put on top of the computer screen again for each prey delivery, and it therefore functioned as a size reference. To estimate the length of each prey, I determined the number of square sides each fish covered, to the closest quarter. When the fish did not cover a whole quarter square length, the length was rounded up or down to the closest quarter square length. If the fish laid askew in relation to the grid, I used Pythagoras $a^2 + b^2 = c^2$.

When the fish was decapitated or further eaten at prior to delivery at the nest, the length of the missing part was added to the estimated net prey length, which gives estimated gross prey length. This was done by using reference images from Muus & Nielsen (2012), and the length of the delivered prey item was divided by its proportion of a whole fish to find the gross prey length.

As far as it was possible, the missing length was found by comparing the shapes and proportions on the delivered fish with the illustrations in Muus & Nielsen (2012). Otherwise, the prey was only registered as decapitated.

At both nests some prey items could not be measured due to irregularities in the cameras position. Nevertheless, it was still possible to measure some prey items at Isnes because there were recordings of the nest with the metal grid also when the camera was out of position.

Prey mass for each delivered prey item was determined by using length - weight coefficients for each prey species (table 3). The formulas used to estimate prey mass is $W = a \times L^b$, where W is weight (g), L is length (cm), and a and b are species – specific coefficients (Froese, 2016a). When the fish was decapitated or more eaten at prior to delivery, weight was estimated both for captured prey (gross mass) and delivered prey (net mass). Estimated prey body mass may be both over– or underestimated due to small changes in the cameras position during monitoring, and due to the position of the fish in the nest.

Table 3. Species - specific coefficients used in the length - weight model. The values are collected from Fishbase.org (Froese, 2016a).

Species	a	b
Freshwater bream (*Abramis brama*)	0.00871	3.14
Northern pike (*Esox Lucius*)	0.00437	3.09
Atlantic cod (*Gadus morhua*)	0.00741	3.06
Roach (*Rutilus rutilus*)	0.00794	3.15
Zander (*Sander lucioperca*)	0.00692	3.10
European flounder (*Platichthys flesus*)	0.00776	3.07
Garfish (*Belone belone*)	0.00100	3.04
European perch (*Perca fluviatilis*)	0.01000	3.08
Common dace (*Leuciscus leuciscus*)	0.00676	3.11
Atlantic mackerel (*Scomber scombrus*)	0.00759	3.03
Trout (*Salmo trutta*)	0.00851	3.03
Seabass (*Dicentrarchus labrax*)	0.00891	3.05
Ide (*Leuciscus idus*)	0.00794	3.13

Weather and tide

In the middle of the monitoring period, i.e. on 15 July the sun rose at 04:26 and set at 22:16, with solar midday at 13:22 in Sarpsborg municipality (Time and date AS, 2017). These times are used as reference in the illustrations for diel activity. Data on wind speed (m/s) were received from the Norwegian Meteorological Institute (eKlima, 2017) for the entire period of monitoring. Data from Rygge weather station (station number 17150), approximately 23 km away from the nest at Isnes and 32 km away from the nest at Skjeberg, was used for both the nests. More accurate data were difficult to obtain due to incomplete filings at weather stations closer located to the nests.

Data on tide was collected from the Norwegian Mapping Authority (2017), and the station used was Viker. The reference level used is chart datum, and hourly data are given in cm, and is a deviation from the lowest astronomical tide (LAT). These data, and the data from eKlima has not taken into account Norwegian summer time (UTC + 2). In the analysis therefore, data on observed tide was adjusted back one hour (UTC + 1) to match recorded prey delivering times.

Observation in field

The osprey nest at Isnes was observed by one or two observers for a total of eleven times (approximately 35 hours) to monitor the foraging behavior between 28 June – 11 August 2016, mostly after the nestlings had fledged. For that purpose, binoculars, telescope lens and field sheets were used. The distance from the observation site at Sandtangneset and over the bay to the nest were approximately 500 m, allowing observations without disturbing the ospreys. During observation, it was noted at what time the male was observed with prey and if possible, which direction he came from and went to after delivering prey to the nest, to get an idea of fishing site. Temperature and weather variables were also noted. Also, it was noted whether the male handed over prey to the female or the nestlings outside the nest.

Statistical analyses

Statistical analyses were conducted in JMP Pro 13.0 (SAS Institute Inc., 2017) for the data in general and R version 3.3.3 (R Development Core Team, 2017) for the diel activity analysis. All the statistics were done separately for the two nests due to major differences in prey species and parental behavior. Chi – square-values stated in all tests is from Pearson – test and backward elimination is at significance level 0.05. Estimates are given as average ± SE.

Differences in delivered prey species and prey mass between the nests

To test for differences between the two nests regarding prey species delivered, I used a contingency analysis. This analysis was first based on all the prey species and second on the five most common prey species in total delivered to both the nests.

To test for differences between the two nests in estimated mean prey body mass (net) delivered, I used a one – way analysis of variation, both for all prey species delivered and for the five most common prey species. For tests regarding prey mass, I used the species –

specific coefficients for European flounder (*Platichthys flesus*) for all the unidentified flounders sp. to obtain more data points.

I also ran a nominal logistic regression to test if mean prey body mass captured and delivered by each sex at Isnes differed between the sexes. Delivering sex were set as explanatory variable, while both gross prey body mass and net prey body mass were set as response.

Prey handling

The delivering parent (M/F), handler (parent = 1 or nestling = 0), and whether a prey item was decapitated (yes/no), were determined for each prey item delivered to the nest, except when the delivering sex could not be identified. Nominal logistic tests were created for two analyses for each of the two nests separately (see model specifications in table 4). All prey were included in the models, except for unidentified prey and for prey items where prey body mass could not be estimated. For the tests with decapitation as response, those with small numbers (< 5) are excluded from the model, leaving us with three prey families at Isnes and two prey families at Skjeberg.

Table 4. Models in nominal logistic tests used in the analyses of prey handling at the osprey nests Isnes and Skjeberg, where model 1 had handler (nestling or parent) as response and model 2 had decapitation (yes/no) as response. x_1 is prey family, x_2 is nestling age and x_3 is prey body mass (net prey body mass for model 1, and gross prey body mass for model 2. ε = random effect (nest ID).

Model no.	Variables in model
1)	$f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_1 x_1 * \beta_2 x_2 + \beta_1 x_1 * \beta_3 x_3 + \beta_2 x_2 * \beta_3 x_3 + \varepsilon$
2)	$f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_1 x_1 * \beta_2 x_2 + \beta_1 x_1 * \beta_3 x_3 + \beta_2 x_2 * \beta_3 x_3 + \varepsilon$

Diel activity

The method used for analyses regarding diel activity was the COSINOR method explained by Pita et al. (2011). This method was used both for all prey deliveries at Isnes and Skjeberg, and for the most commonly delivered prey families Cyprinidae, Percidae, Pleuronectidae and Esocidae. Only Pleuronectidae was investigated for the nest at Skjeberg. The packages used to create mixed effect models and model selections in R was lme4 (Bates et al. 2014) for mixed effect models, and AICcmodavg (Mazerolle, 2016) for model selections. The response variable was whether there was at least one prey delivery within a given hour block (yes/no), while the explanatory variables were time of day (hour blocks), wind speed (m/s) and tide (cm) (See model specifications in table 5). In total, there were data from 940 hour blocks at Isnes and 645 hour blocks at Skjeberg.

The best models were found by using Akaike information criterion values. The models with the best fit to the data was the ones with ΔAICc below 2.0 and few variables. Models with p-values ≤ 0.001 were assessed further.

Table 5. 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), FF = wind speed (m/s), tide = lowest astronomical tide (cm) and ε = random effect (nest ID).

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

10	$$f(x) = a_0 + \left(a_1\cos\frac{2\pi x}{24} + b_1\sin\frac{2\pi x}{24}\right) + \left(a_2\cos\frac{2*2\pi x}{24} + b_2\sin\frac{2*2\pi x}{24}\right) + \left(a_3\cos\frac{3*2\pi x}{24} + b_3\sin\frac{3*2\pi x}{24}\right) + \text{Tide} + \varepsilon$$
11	$$f(x) = a_0 + \text{Tide} + \varepsilon$$
12	$$f(x) = a_0 + \left(a_1\cos\frac{2\pi x}{24} + b_1\sin\frac{2\pi x}{24}\right) + \text{Tide} + \text{FF} + \varepsilon$$
13	$$f(x) = a_0 + \left(a_1\cos\frac{2\pi x}{24} + b_1\sin\frac{2\pi x}{24}\right) + \left(a_2\cos\frac{2*2\pi x}{24} + b_2\sin\frac{2*2\pi x}{24}\right) + \text{Tide} + \text{FF} + \varepsilon$$
14	$$f(x) = a_0 + \left(a_1\cos\frac{2\pi x}{24} + b_1\sin\frac{2\pi x}{24}\right) + \left(a_2\cos\frac{2*2\pi x}{24} + b_2\sin\frac{2*2\pi x}{24}\right) + \left(a_3\cos\frac{3*2\pi x}{24} + b_3\sin\frac{3*2\pi x}{24}\right) + \text{Tide} + \text{FF} + \varepsilon$$
15	$$f(x) = a_0 + \text{Tide} + \text{FF} + \varepsilon$$

Distribution of prey mass during the nesting season

Prey body mass (net) delivered for each day were added together and divided on number of nestlings and number of monitored hours the specific day, which gives the average prey body mass that each nestling received per monitored hour/day. The earliest prey delivery occurred at 3:40, and the latest prey delivery occurred at 11:07, so the five hours in between are excluded from the hours a day, which gives maximum 19 hours monitored per day. Also, when there was pauses in monitoring due to logistic difficulties, the missing hours were also excluded from the number of monitored hours/day.

Standard least squares regression was used to test if delivered prey mass varied during nestling season. Prey mass received per nestling per day was set as response, and explanatory factor were number of days after 1 June.

Seasonal distribution of prey species

To test if there were any seasonal changes in deliveries of prey, the number of each prey species delivered each day was added to the data set. For the statistics, I used generalized linear model (Poisson regression). The most delivered prey types (carps, perches, pikes, flounders and garfish) were used as response, and days after 1 June were the explanatory variable. Nest ID were set as random effect.

Results

Prey selection

In total, 379 prey deliveries were recorded, 271 at Isnes and 108 at Skjeberg. All of them were identified as fish. Of these, 358 were identified to order, 356 to family level and 310 to species level. Of prey deliveries, 23 prey items (5.5%) could not be identified as anything but fish. The prey types which were delivered most frequently to both nests were carps (Cyprinidae) with 39.6%, followed by perches (Percidae) with 20.3%, flounders (Pleuronectidae) with 15.8%, pikes (Esocidae) with 11.6%, and needlefishes (Belonidae) with 2.4%. Freshwater bream (*Abramis brama*) was the most frequent prey type delivered at species level (36.7%), followed by European perch (*Perca fluviatilis*) (19.5%) and Northern pike (*Esox lucius*) (11.9%) (table 6).

Table 6. Distribution of prey species video recorded and delivered at the two osprey nests Isnes and Skjeberg.

Prey Species	N Isnes	% Isnes	N Skjeberg	% Skjeberg
Freshwater bream (*Abramis brama*)	139	51.3	0	0.0
Unidentified carp sp.	1	0.0	0	0.0
European perch (*Perca fluviatilis*)	59	21.8	15	13.9
Northern pike (*Esox lucius*)	44	16.2	1	0.9
European flounder (*Platichthys flesus*)	0	0.0	18	16.7
Unidentified flounder sp.	0	0.0	42	39.0
Atlantic mackerel (*Scomber scombrus*)	0	0.0	5	4.6
Garfish (*Belone belone*)	0	0.0	9	8.3
Trout (*Salmo trutta*)	0	0.0	6	5.6
Atlantic cod (*Gadus morhua*)	0	0.0	1	0.9
Common dace (*Leuciscus leuciscus*)	3	1.1	0	0.0
Roach (*Rutilus rutilus*)	5	1.8	0	0.0
Ide (*Leuciscus idus*)	0	0.0	2	1.9
Seabass (*Dicentrarchus labrax*)	0	0.0	1	0.9
Zander (*Sander lucioperca*)	2	0.7	0	0.0
Unidentified fish	18	7.0	8	7.4
Total prey species	271	100.0	108	100.0

Prey delivery and handling at the nest

At Isnes, the male delivered 76% of the recorded prey items while the female delivered 22%. The delivering parent could not be determined in the last 2% of the cases. At Skjeberg, the male delivered all the recorded prey items, except in one case when the delivering parent could not be determined. The female at Skjeberg disappeared in early July, when the nestlings were 42 days old.

At Isnes, the female had the main role in handling and dismembering the prey to the nestlings (59%), but the male contributed in 4% of the cases. The nestlings ate by themselves in 27% of the cases, while the handler could not be determined in 10% of the cases. The nestlings handled prey for the first time at an age of 33 days at Isnes. At Skjeberg, the female dismembered the prey in 38% of the cases, the male in 20%, and the nestlings in 27% of the cases. The handler could not be determined in 15% of the cases. The nestlings handled prey for the first time at an age of 42 days at Skjeberg. The predicted nestling age where the nestlings became more likely to ingest the prey item unassisted, than to be fed by the female or the male, was 50 days for Isnes and 47 days for Skjeberg.

Isnes

The probability that the nestlings ingested the prey item unassisted rather than to be fed by the female, was significantly affected by nestling age, but not by prey family, net prey body mass or their interaction (table 7). The parent was less likely to dismember prey as the nestlings grew older (figure 4).

Table 7. Parameter estimates for a model explaining whether the nestlings ingested prey items unassisted rather than being fed by the female, for the osprey nest at Isnes as a function of nestling age (n =173).

Variable	Estimate	SE	x^2	P
Intercept	14.3385279	2.715176	27.89	0.0001
Nestling age (days)	-0.2832234	0.0520204	29.64	0.0001

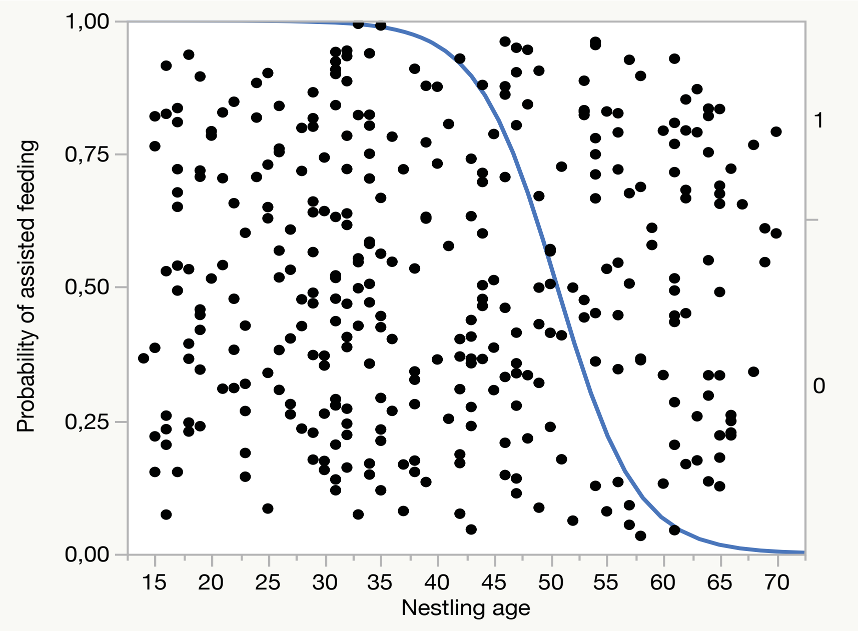

Figure 4. The predicted probability that the parent at the osprey nest at Isnes dismembered the prey rather than the nestlings feeding independently as a function of nestling age based on all prey families (n =173, 0 = parent, 1 = nestling).

Skjeberg

The probability that the nestlings ingested the prey item unassisted rather than to be fed by the female, was significantly affected by nestling age, but not by prey family, net prey body mass or their interaction (table 8). The parent was less likely to dismember prey as the nestlings grew older (figure 5).

Table 8. Parameter estimates for a model explaining whether the nestlings ingested prey items unassisted rather than being fed by the female/male, for the osprey nest at Skjeberg as a function of nestling age (n = 64).

Variable	Estimate	SE	x^2	P
Intercept	14.8834204	4.2644271	12.18	0.0005
Nestling age (days)	-0.3109972	0.0909332	11.70	0.0005

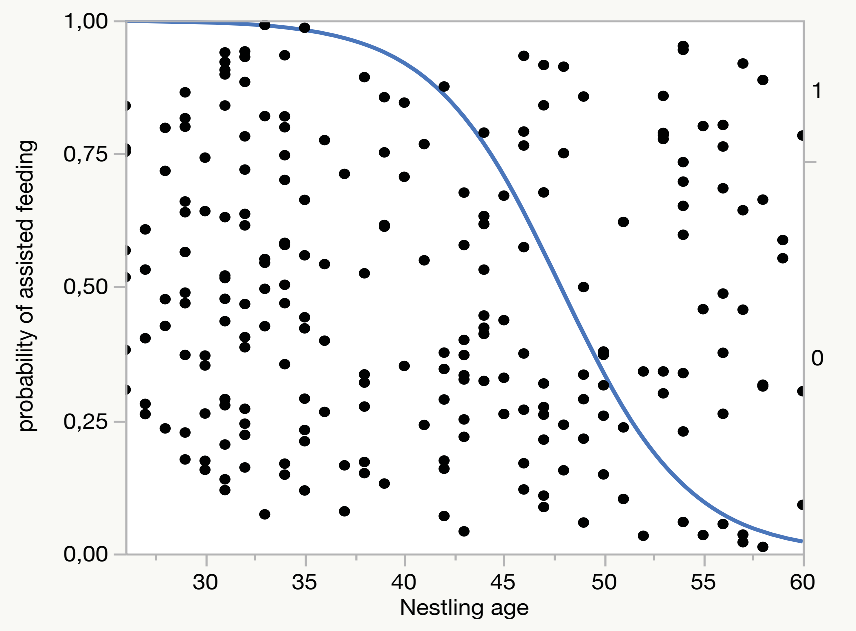

Figure 5. The predicted probability that the parent at the osprey nest at Skjeberg dismembered the prey rather than the nestlings feeding independently as a function of nestling age based on all prey families (n = 64, 0 = parent, 1= nestling).

Mass of prey

Prey body mass could be estimated for 260 prey items delivered (all flounders were registered as European flounder for weight estimates). Freshwater bream, European perch and northern pike accounted for 59.8%, 11.1% and 5.8% of the total body mass of captured prey, respectively. Estimated mean prey body mass (gross body mass) at capture was 482.0 $\pm$ 32.5 g for all prey in general (range 12.6 – 3153.3 g), while it was 740.6 $\pm$ 67.3 g for freshwater bream (range 17.4 – 3153.3 g), 257.3 $\pm$ 32.1 g for European perch (range 17.3 – 1368.8 g) and 222.5 $\pm$ 42.3 g for northern pike (range 26.6 – 1087.2 g) (table 9). Estimated length of captured prey ranged from 10.6 – 86.5 cm, with average of 30.5 $\pm$ 0.68 cm.

Table 9. Gross prey body mass (g) of prey recorded delivered at the two osprey nests Isnes and Skjeberg.

Prey species	Mean ± SE mass per item	n	Total mass	%
Freshwater bream (*Abramis brama*)	740.6 ± 67.3	139	102943	59.8
European perch (*Perca fluviatilis*)	257.3 ± 32.1	74	19040	11.1
Northern pike (*Esox lucius*)	222.5 ± 42.3	45	10013	5.8
Flounders (Pleuronectidae)	474.5 ±60.44	61	28944	16.8
Atlantic mackerel (*Scomber scombrus*)	444.1 ±111.6	5	2221	1.3
Garfish (*Belone belone*)	373.2 ±145.7	9	3359	1.9
Trout (*Salmo trutta*)	168.8 ± 28.7	6	1013	0.6
Atlantic cod (*Gadus morhua*)	204.9 ± 0.0	1	205	0.1
Common dace (*Leuciscus leuciscus*)	83.0 ± 70.4	3	249	0.1
Roach (*Rutilus rutilus*)	49.0 ± 0.6	5	245	0.1
Ide (*Leuciscus idus*)	732.6 ± 28.9	2	1465	0.9
Seabass (*Dicentrarchus labrax*)	874.5 ± 0.0	1	875	0.5
Zander (*Sander lucioperca*)	843.3 ±384.4	2	1687	1.0
Total	482.0 ± 32.5	353	172259	100.0

For Isnes, there also was a significant difference between prey body mass captured and delivered to the nest by the two sexes (table 10 and table 11). The mean prey body mass captured by the female (n = 46) was 886.9 ± 79.3 g, while the mean prey body mass captured by the male (n = 134) was 343.8 ± 46.5 g. The mean prey body mass delivered by the female was 593.2 ± 42.7 g, while the mean prey body mass delivered by the male was 213.0 ± 25.0 g. The proportion of decapitated prey was not significantly different between the female (37%) and the male (33%) (n = 255, df = 1, $x^2 = 0.06$, p = 0.8143).

Table 10. Parameter estimates for a model explaining whether the two sexes captured markedly different amount of prey body mass (g) at the osprey nest monitored at Isnes (n =180).

Variable	Estimate	SE	x^2	P
Intercept	-1.9129649	0.2646954	52.23	0.0001
Gross prey body mass	0.00153318	0.0003333	21.16	0.0001

Table 11. Parameter estimates for a model explaining whether the two sexes delivered markedly different amount of prey body mass (g) at the osprey nest monitored at Isnes (n =180).

Variable	Estimate	SE	x^2	P
Intercept	-2.4033366	0.3193321	56.64	0.0001
Net prey body mass	0.00377545	0.0006928	29.70	0.0001

Prior to delivery to the nestlings, 39% of the prey items was decapitated or further eaten at. Estimated average prey body mass at delivery (net body mass) was 318.5 ± 20.1 g for all prey in general (range 12.6 – 1936.6 g), while it was 445.6 ± 38.0 g for freshwater bream (range 17.4 – 1936.6 g), 213.7 ± 25.2 g for European perch (range 17.3 – 1052.8 g) and 165.0 ± 36.9 g for northern pike (range 18.8 – 1087.2 g), respectively (table 12). The body mass of pikes were probably underestimated due to difficulties in estimating the length of the largest individuals.

Table 12. Net prey body mass (g) of prey recorded delivered at the two osprey nests Isnes and Skjeberg.

Prey species	Mean ± SE mass per item	n	Total mass	%
Freshwater bream (*Abramis brama*)	445.6 ± 38.0	139	61938	54.6
European perch (*Perca fluviatilis*)	213.7 ± 25.2	74	15814	13.9
Northern pike (*Esox lucius*)	165.0 ± 36.9	45	7425	6.5
European flounder (*Platichthys flesus*)	342.6 ± 54.7	61	20899	18.4
Atlantic mackerel (*Scomber scombrus*)	286.8 ± 121.6	5	1434	1.3
Garfish (*Belone belone*)	238.6 ± 75.1	9	2147	1.9
Trout (*Salmo trutta*)	121.3 ± 44.4	6	728	0.6
Atlantic cod (*Gadus morhua*)	85.0 ± 0.0	1	85	0.1
Common dace (*Leuciscus leuciscus*)	83.0 ± 70.4	3	249	0.2
Roach (*Rutilus rutilus*)	42.0 ± 6.5	5	210	0.2
Ide (*Leuciscus idus*)	732.6 ± 28.9	2	1465	1.3
Seabass (*Dicentrarchus labrax*)	334.9 ± 0.0	1	335	0.3
Zander (*Sander lucioperca*)	360.2 ± 164.2	2	720	0.6
Total	318.5 ± 20.1	353	113449	100.0

Differences between prey composition at the two nests

At Isnes, 51.2% of all delivered prey was freshwater bream, while European perch (21.8%) and northern pike (16.2%) were the second and third most delivered species, respectively (figure 6). At Skjeberg, 16.7% of the delivered prey were identified as European flounder, while the second and third most delivered species were European perch with 13.9% and garfish with 8.3%, respectively (figure 6). There was a significant difference in prey species composition delivered between the two nests when prey species with less than 6 items delivered were excluded from the analysis ($n = 285$, $x^2 = 184.0$, $df = 4$, $p<0.0001$).

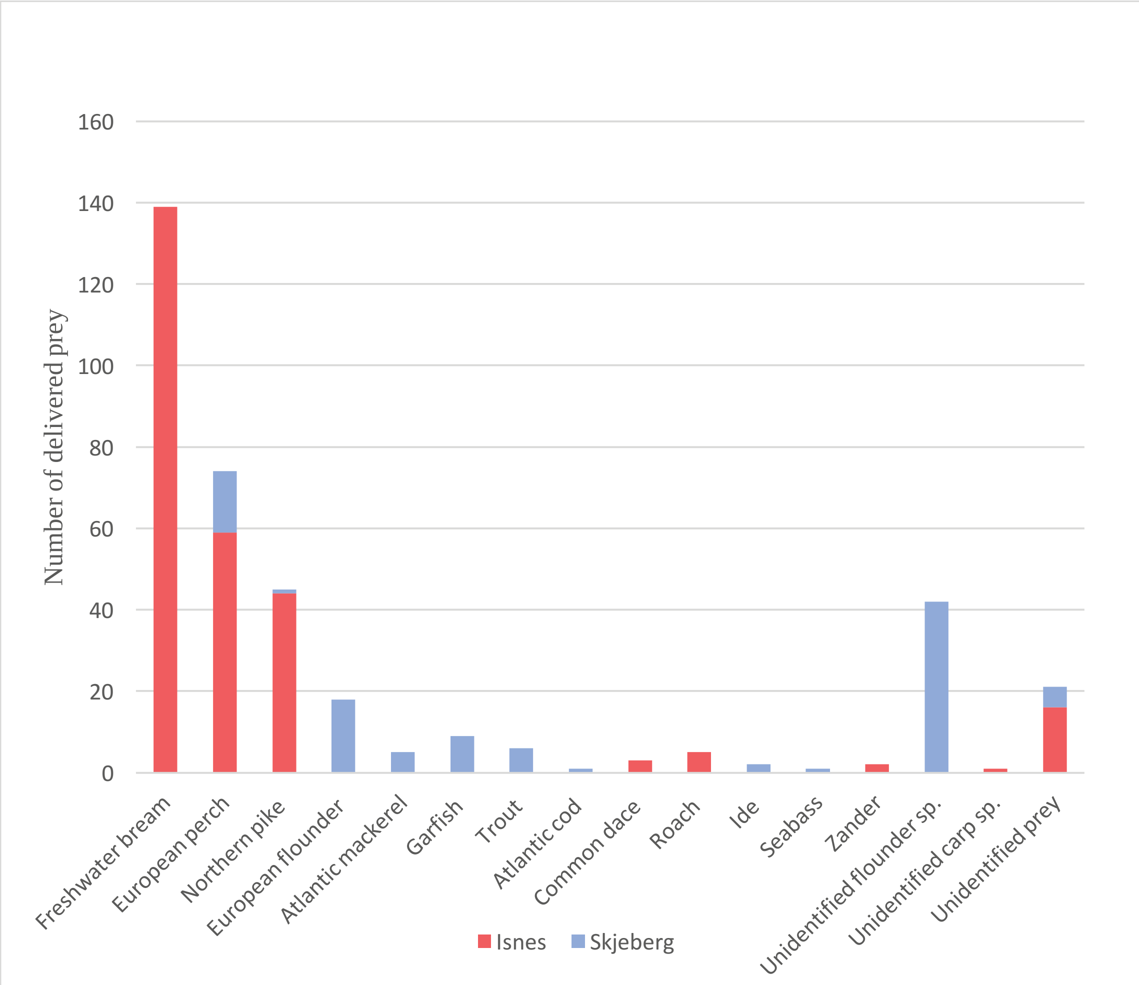

Figure 6. The proportion of all prey species delivered at the two osprey nests Isnes and Skjeberg (n = 379).

For delivered prey, the estimated mean prey body mass (net) was 310.4 ± 24.1 g (range 12.6 g – 1936.6 g) at Isnes, and 339.9 ± 36.2 g (range 31.7 g – 1601.9 g) at Skjeberg. For the five most commonly delivered prey species at both nests pooled, the estimated mean prey body mass was 324.9 ± 21.3 g. A one – w ay analysis showed no significant difference in net prey body mass between the two nests for all prey species (n = 260, df = 1, p = 0.51) or for the five most commonly prey species delivered (n = 240, df = 1, p = 0.50).

Decapitation of prey

At Isnes, the probability that a prey item was decapitated prior to delivery was significantly affected by prey body mass at capture, and the interaction between nestling age and prey family (table 13). Prey was less likely to be decapitated as the nestlings grew older, and larger prey were more likely to be decapitated prior to delivery (figure 7). The interaction between prey family and nestling age were also significant for both Cyprinidae and Esocidae. Carps were more likely to be decapitated prior to delivery as the nestlings grew older (figure 8), while pikes were less likely to be decapitated prior to delivery as the nestlings grew older (figure 9), compared to perches (table 13). At Skjeberg, neither nestling age, prey family, prey mass or their interaction were significant on the probability that prey was decapitated prior to delivery.

Table. 13. Parameter estimates for a model explaining whether prey recorded at Isnes was decapitated prior to delivery. Percidae used as reference level (n = 189).

Variable	Estimate	SE	x^2	P
Intercept	3.16468994	0.7557505	17.53	0.0001
Prey family [Cyprinidae]	-0.1110595	0.3198558	0.12	0.7282
Prey family [Esocidae]	-0.5087858	0.4940363	1.06	0.3031
Prey body mass (gross)	-0.0019781	0.0004612	18.39	0.0001
Nestling age (days)	-0.0421782	0.0182666	5.33	0.0209
Prey family [Cyprinidae] x nestling age	0.04758085	0.0200423	5.64	0.0176
Prey family [Esocidae] x nestling age	-0.0939623	0.0334404	7.90	0.0050

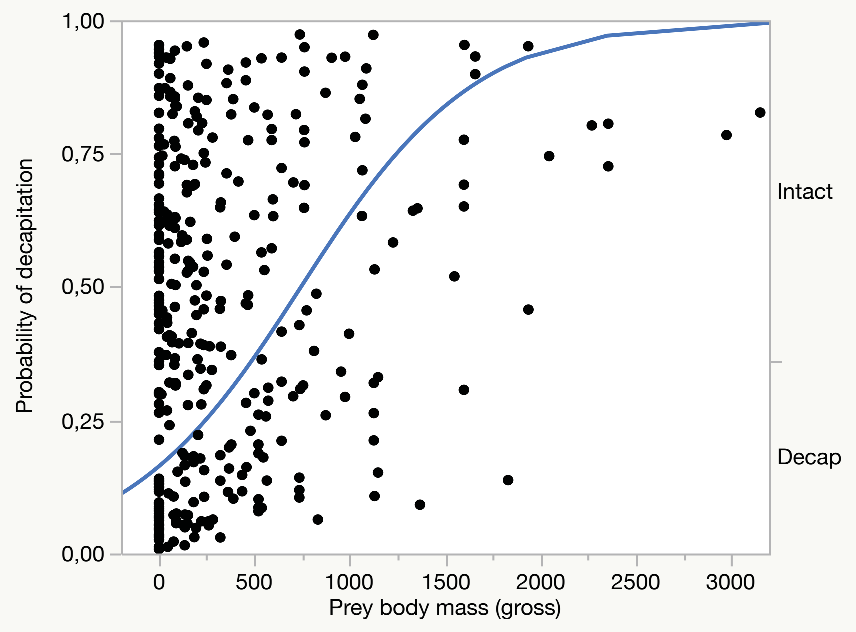

Figure 7. The probability that a prey item was decapitated prior to delivery as a function of prey body mass at capture for the osprey nest video monitored at Isnes (n = 189, x^2 = 27.5, df = 1, p<0.0001).

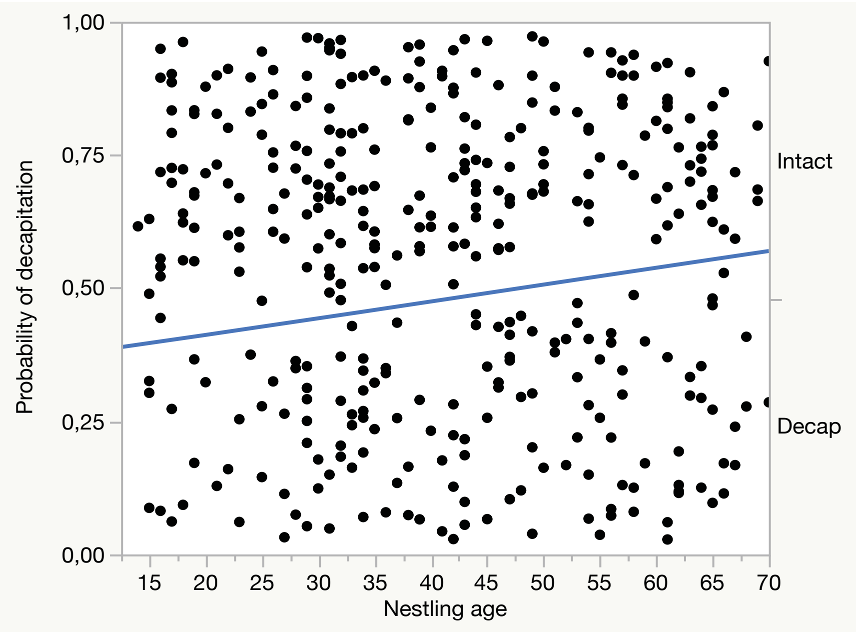

Figure 8. The probability that carps was decapitated prior to delivery as a function of nestling age for the osprey nest video monitored at Isnes (n = 148, df = 1, x^2 = 1.39, p = 0.24).

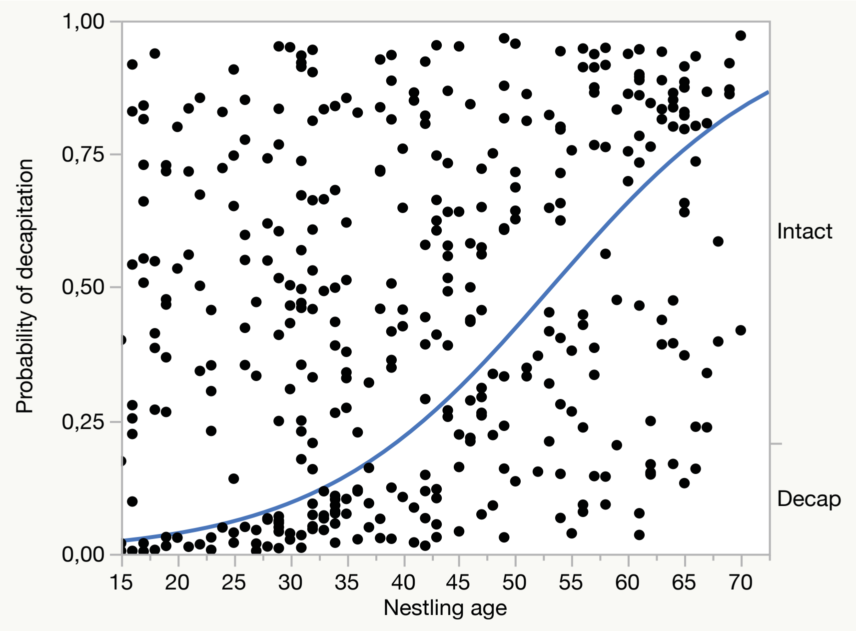

Figure 9. The probability that pikes was decapitated prior to delivery as a function of nestling age for the osprey nest video monitored at Isnes (n = 43, df = 1, x^2 = 15.4, p<0.0011).

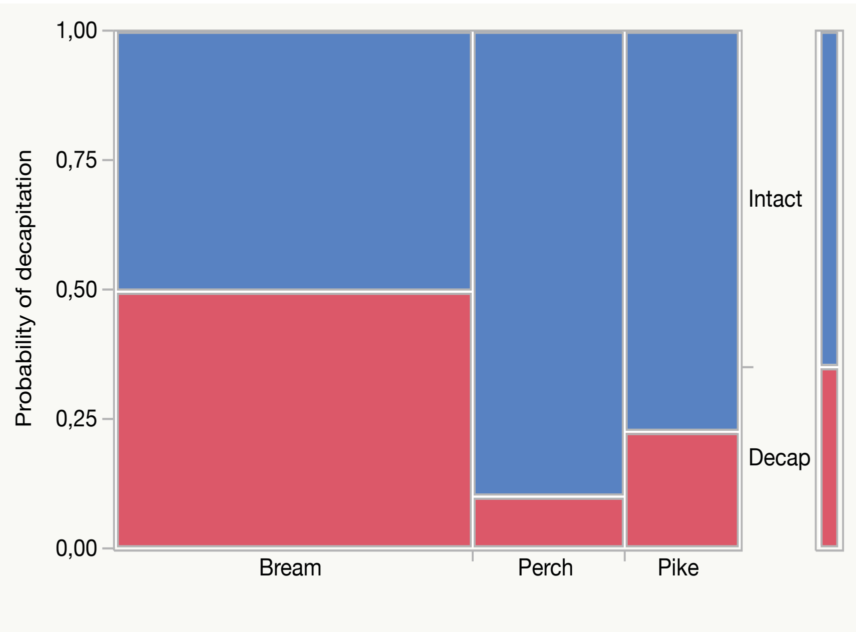

Figure 10. The probability that a prey item was decapitated prior to delivery of the three most common prey species at the osprey nest at Isnes. Species with < 5 deliveries are excluded. There was a significant difference in decapitation between the species (n = 242, x^2 = 31.9, df = 2, p<0.0001).

Diel Activity

The definition of high diel activity is that the predicted activity curve is above the overall modelled activity curve (MESOR), and the definition of low activity is that the predicted activity curve is below MESOR.

Isnes

During the day, the earliest delivery occurred at 03:40 and the latest one at 22:58. The ospreys had periods when they were more likely to deliver prey to the nest, although there were deliveries during the whole day from sunrise to sunset. The best model to explain diel activity was the one which included hour as explanatory variables (model 3), with 7 variables (table II, appendix 2). The second – best model was model 10, which included hour and observed tide as explanatory variables (ΔAICc = 0.96) (table III, appendix 2), although tide was not significant. Wind speed was not significant neither. Both models showed that time of day was a significant predictor for the probability that a prey was delivered during a specific hour block, while tide was not a significant predictor. There was a pattern in diel activity for the ospreys at Isnes, with activity peaks at 05:00 – 07:00, 12:00 – 13:00 and 18:00 – 19:00 (figure 11). Only the first peak was significantly different from random, and there was no activity between dusk and dawn.

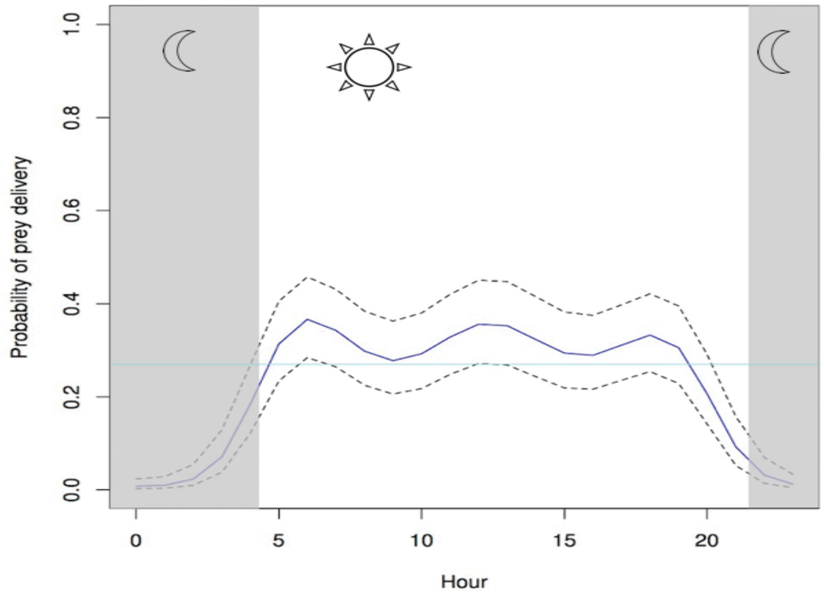

Figure 11. The probability of prey delivery within an hour block at the osprey nest at Isnes as a function of time of day based on model 3 (p<0.0001). The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI), and the light blue line is MESOR (overall mean). The grey shaded areas denote the time between sunset and sunrise.

Skjeberg

During the day, the earliest delivery occurred at 04:45, and the latest one at 23:07. Also for Skjeberg, there was activity during the whole day from sunrise to sunset. As for Isnes, the best model to explain diel activity were model 3 with hour as explanatory variable, and with 7 variables (table V, appendix 2). The best model show that time of day was a significant predictor for the probability that a prey was delivered during a specific hour block. There was a pattern in diel activity for the ospreys at Skjeberg, with activity peaks at 05:00 – 07:00 and 18:00 – 20:00, but there was also a smaller peak at 12:00 – 15:00, although not significant. There was no activity between dusk and dawn (figure 12).

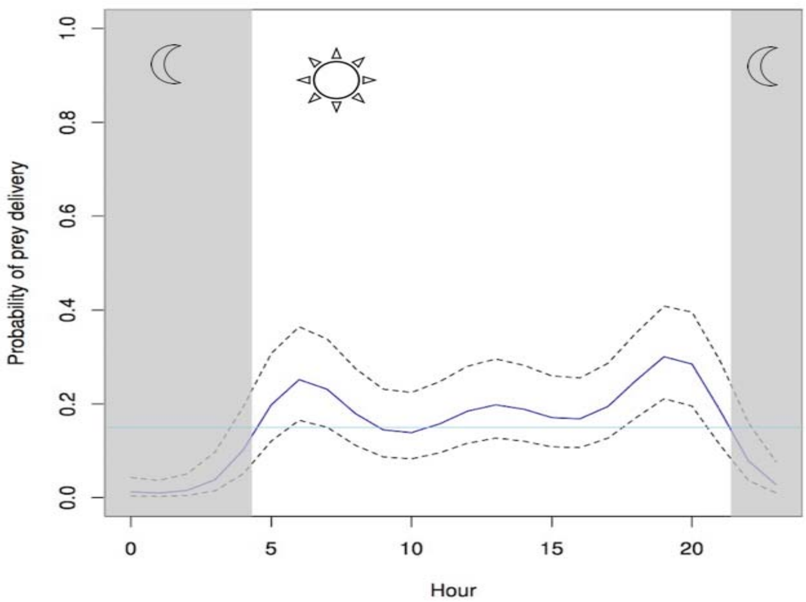

Figure 12. The probability of prey delivery within an hour block at the osprey nest at Skjeberg as a function of time of day based on model 3. The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI) and the light blue line is MESOR (overall mean). The grey shaded areas denote the time between sunset and sunrise.

Carps

During the day, the earliest delivery of carps occurred at 03:40 and the latest one at 22:58. There were deliveries of carps during the whole day from sunrise to sunset. The best model was the one which included hour as explanatory variable (model 3), with 7 variables (table VII, appendix 2). The second – best model was model 10, which included hour and observed tide as explanatory variables (ΔAIC = 0.00) (table VIII, appendix 2), although the latter was not significant. There was a pattern in deliveries of carps, with activity peaks at 18:00 – 19:00 and 18:00 – 19:00, and a smaller peak at midday at 12:00 – 13:00, although not significant (figure 13).

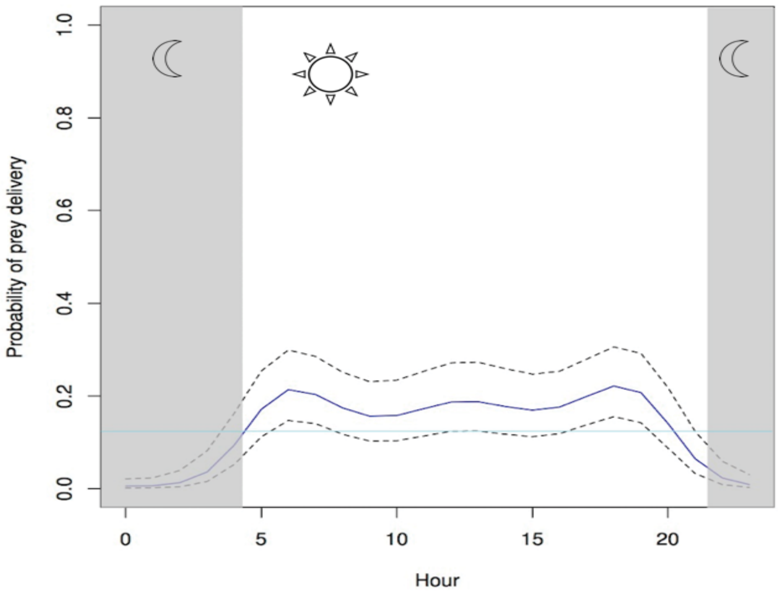

Figure 13. The probability of delivery of carps at the osprey nest at Isnes within an hour block as a function of time of day based on model 3. The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI) and the light blue line is MESOR (overall mean). The grey shaded areas denote the time between sunset and sunrise.

Perches

During the day, the earliest delivery of perches occurred at 04:39 and the latest one at 21:31. There were deliveries of perches during the whole day from sunrise to sunset. The best model was the one which included hour as explanatory variable (model 2), with 5 variables (table X, appendix 2). The second – best model was model 9, which included hour and observed tide as explanatory variables (ΔAIC = 1.24) (table XI, appendix 2), although the latter was not significant. There was a pattern in deliveries of perches, with activity peaks at 18:00 – 20:00 and at 16:00 – 18:00 (figure 14).

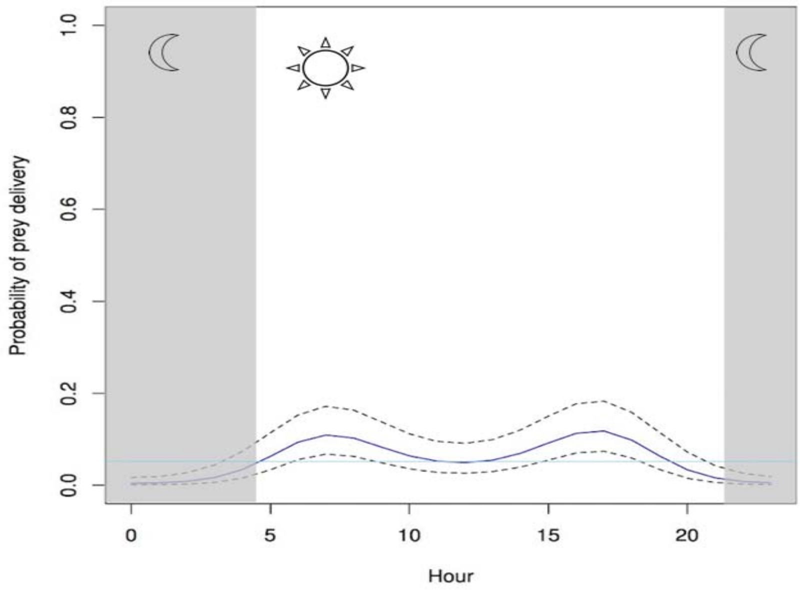

Figure 14. The probability of delivery of perches at the osprey nest at Isnes within an hour as a function of time of day based on model 2. The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI) and the light blue line is MESOR (overall mean). The grey shaded areas denote the time between sunset and sunrise.

Pikes

During the day, the earliest delivery of pikes occurred at 04:41 and the latest one at 22:16. There were deliveries of pikes during the whole day from sunrise to sunset. The best model was the one which included hour as explanatory variable (model 1), with 3 variables (table XII, appendix 2). The second – best models were model 8 and model 4 which included hour, observed tide and wind speed as explanatory variables (ΔAIC =1.94 and ΔAIC =1.98) (table XIV and table XV, appendix 2), although tide and wind speed was not significant. There was a pattern in deliveries of pikes, with activity peaks at midday from 10:00 – 13:00 (figure 15).

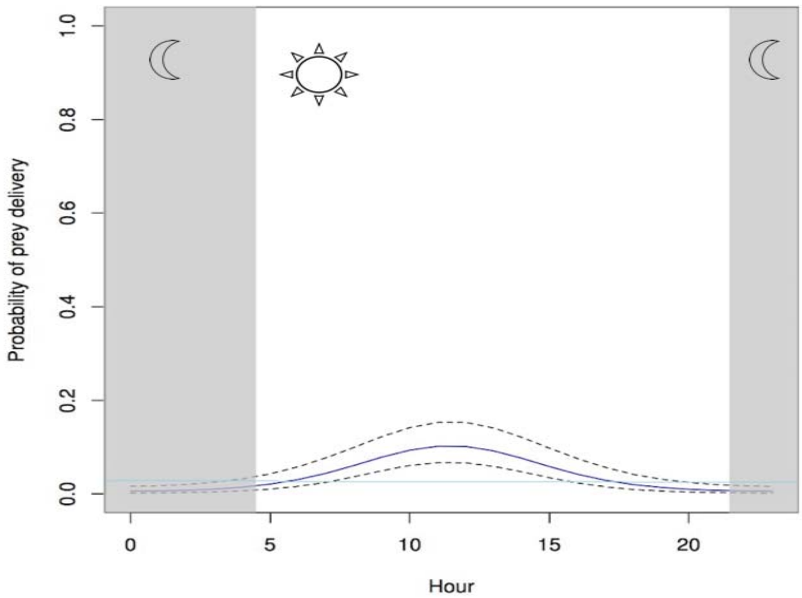

Figure 15. The probability of delivery of pikes at the osprey nest at Isnes within an hour block as a function of time of day based on model 1. The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI) and the light blue line is MESOR (overall mean). The grey shaded areas denote time between sunset and sunrise.

Flounders

During the day, the earliest delivery of flounders occurred at 04:45 and the latest one at 23:07. There were deliveries of flounders during the whole day from sunrise to sunset. The best model was the one which included hour as explanatory variable (model 2), with 5 variables (table XVII, appendix 2). The second – best model was model 5, which included hour and wind speed as explanatory variables (ΔAIC = 0.85) (table XVIII, appendix 2), although the latter was not significant. There was a pattern in deliveries of flounders, with activity peaks at 07:00 – 08:00 and at 18:00 – 20:00 (figure 16).

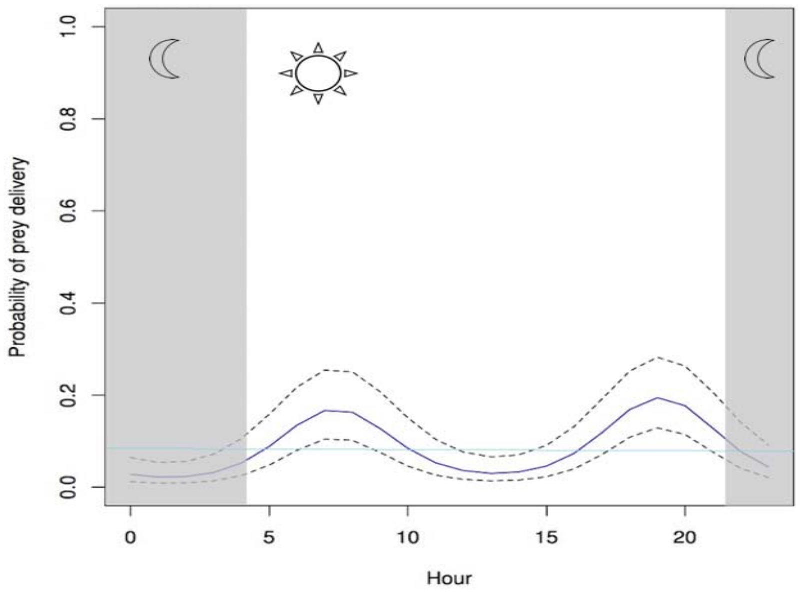

Figure 16. The probability of delivery of flounders at the osprey nest at Skjeberg within an hour block as a function of time of day based on model 2. The dark blue line is the model prediction, the dotted lines are the 95% confidence interval (CI) and the light blue line is MESOR (overall mean). The grey shaded areas denote the time between sunset and sunrise.

Distribution of prey mass during the nesting season

At Isnes, the estimated amount of prey mass that each nestling received per day increased during the season, although the increase was marginally non – significant (n = 57, r^2 = 0.06, p = 0.057) (figure 17). For Skjeberg, there was a non – significant decrease in estimated prey mass each nestling received per day during period of monitoring (n = 42, r^2 = 0.04, p = 0.20) (figure 18).

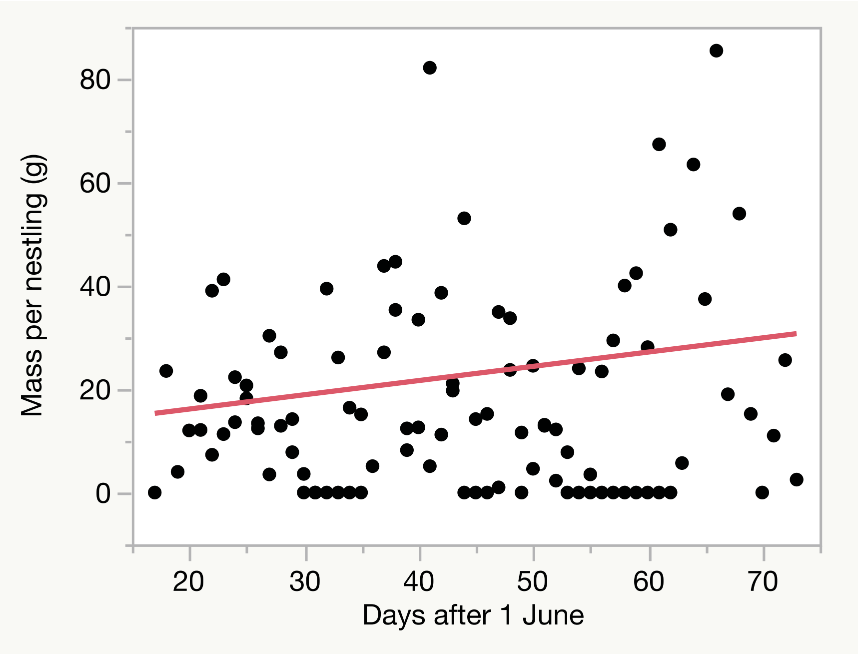

Figure 17. Prey mass received per nestling per hour monitored at the osprey nest at Isnes as a function of days after 1 June.

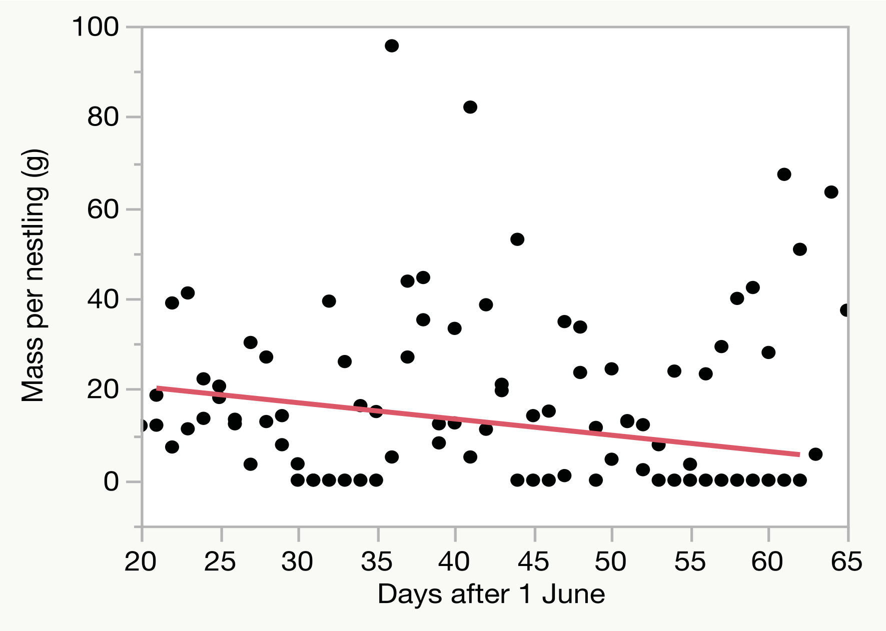

Figure 18. Prey mass received per nestling per hour monitored at the osprey nest at Skjeberg as a function of days after 1 June.

Seasonal distribution of prey species

By using Poisson regression, I found that carps were delivered throughout the nestling period, with no significant change in daily number of deliveries (figure 19). For pikes, there was a significant decrease in the daily number of deliveries (figure 20), while for perches, there was no significant change in daily number throughout the nestling season (figure 21). I found that for flounders, there was a significant decrease in daily number delivered during the period of monitoring (figure 22). For garfish, the first prey item was delivered as late as 12 July, and it was a marginally non – significant increase in daily number of deliveries after that (figure 23).

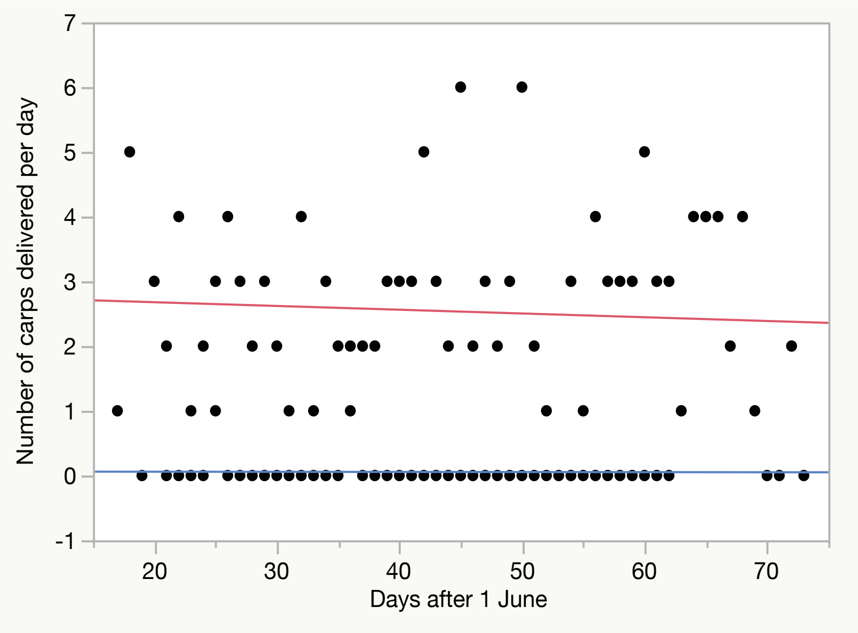

Figure 19. Seasonal distribution of the number of carps delivered at Isnes (red line) and Skjeberg (blue line) per day modelled as Poisson regression (n = 54, df = 1, p = 0.65). The tests were corrected for nest ID.

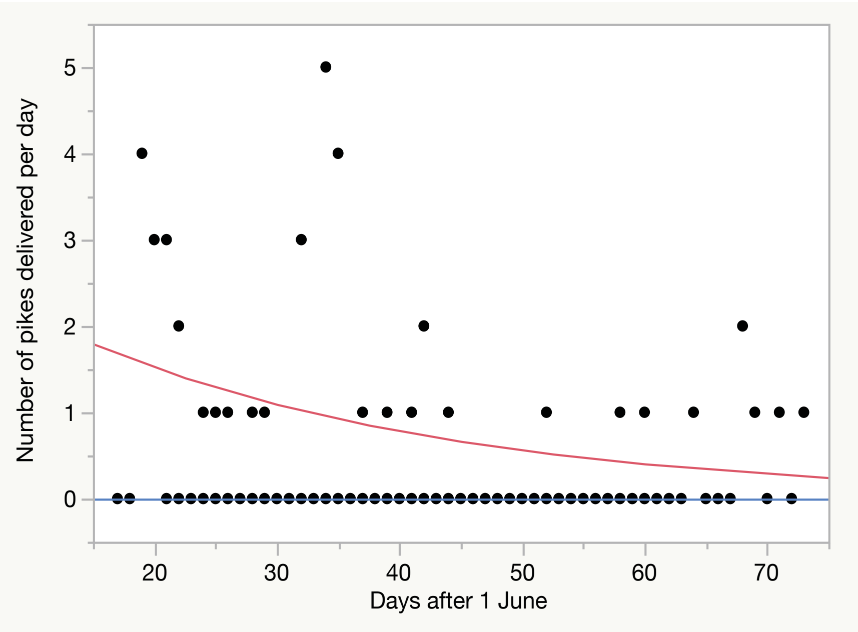

Figure 20. Seasonal distribution of the number of pikes delivered at Isnes (red line) and Skjeberg (blue line) per day modelled as Poisson regression (n = 25, df = 1, p = 0.0006). The tests were corrected for nest ID.

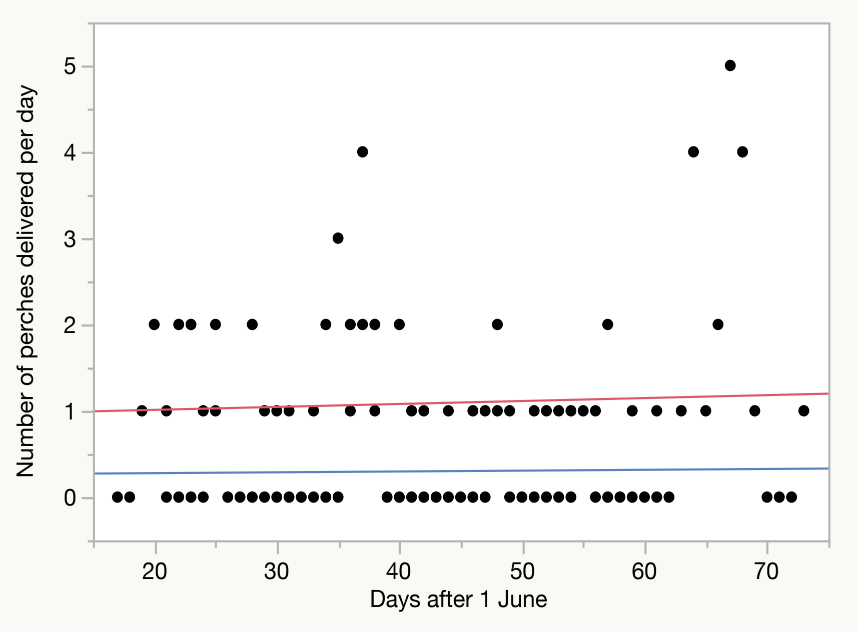

Figure 21. Seasonal distribution of the number of perches delivered at Isnes (red line) and Skjeberg (blue line) per day modelled as Poisson regression (n = 48, df = 1, p = 0.67). The tests were corrected for nest ID.

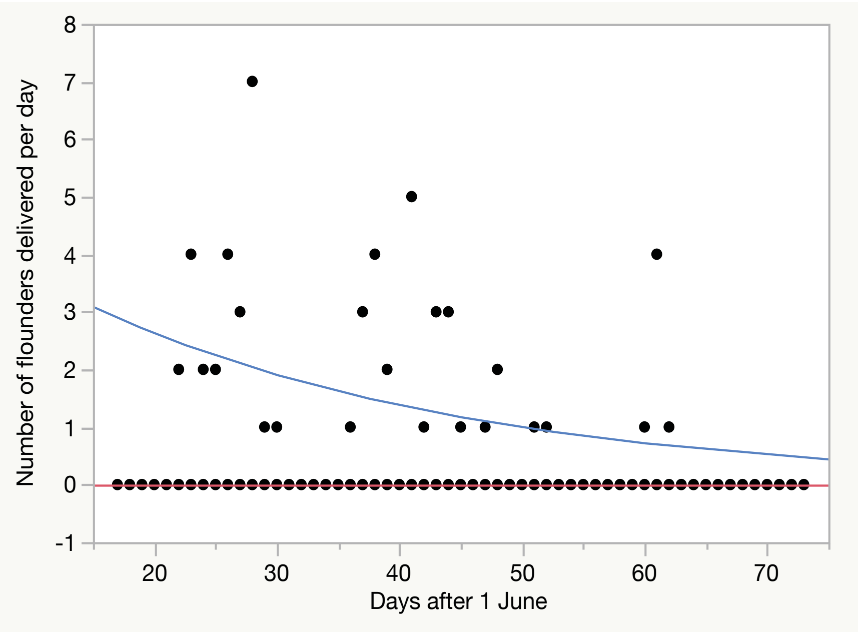

Figure 22. Seasonal distribution of the number of flounders delivered at Isnes (red line) and Skjeberg (blue line) per day modelled as Poisson regression (n = 25, df = 1, p = 0.0033). The tests were corrected for nest ID.

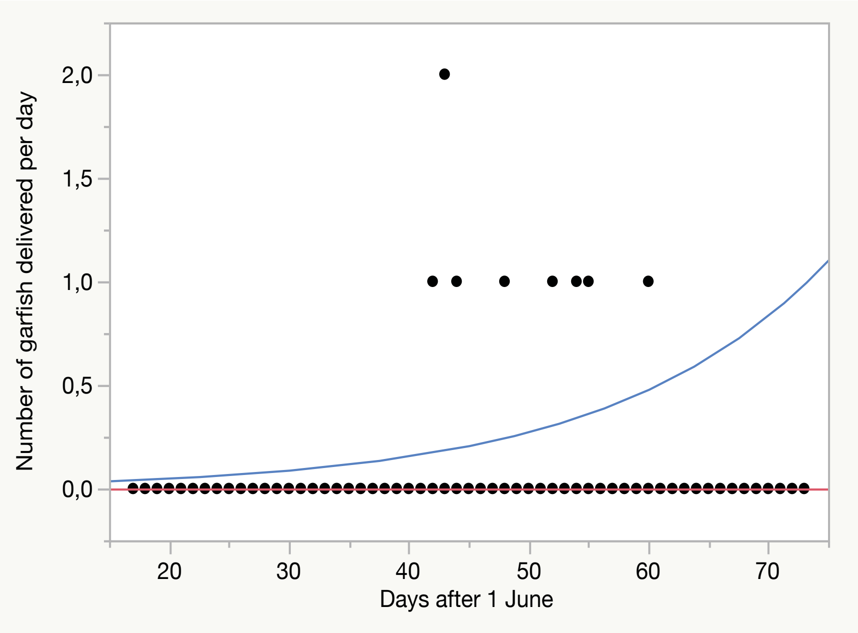

Figure 23. Seasonal distribution of the number of garfish delivered at Isnes (red line) and Skjeberg (blue line) per day modelled as Poisson regression. (n = 8, df = 1, p = 0.058). The tests were corrected for nest ID.

Discussion

Prey selection

The most commonly delivered prey types overall to the two nests were carps (Cyprinidae), perches (Percidae), pikes (Esocidae), flounders (Pleuronectidae) and garfish (Belone). A similar pattern was found by Bjørgeengen (2016), for 4 nests in the same area in 2015, where Isnes was the same, also for 2016. In 2015, more flatfish were identified as European flounder, and Atlantic mackerel (*Scomber scombrus*) was more frequently delivered to the nests than in 2016. The unidentified flatfish in my study was also assumed to be European flounder, although it could not be registered as that due to small insecurities. Alternatively, it may have been lemon sole (*Microstomus kitt*), but only one lemon sole was identified in 2015, and one in 2016, so it is unlikely that the unidentified flatfish would have been anything else than European flounder. Atlantic mackerel was an unexpected prey species in 2015, but was delivered to the coastal nest (Elinborg) in large numbers (Bjørgeengen, 2016). According to Iversen (2002), the mackerel population in the North Sea suffered from overexploitation in the 1960 – 1970s. However, it has expanded over the last 10 – 15 years (Berge et al., 2015), making it more abundant. In my study, five Atlantic mackerels were delivered to the nest at Skjeberg, marked less than in the study of Bjørgeengen (2016). The reason for this may be that the nests were at different locations, where the nest at Skjeberg was located in a small cove, while the nest at Elinborg was located closer to the open sea in the Oslo fjord. Flounders also may have been more abundant in Skjeberg, and more easily preyed on than mackerel, which are fast and vigorous fishes (Bjørgeengen, 2016). Another marine prey species delivered at the nest at Skjeberg, was garfish, which is a schooling surface – dwelling fish, and therefore vulnerable to predation from air. It was also delivered in a similar amount last season (Bjørgeengen, 2016), and was also captured by non – breeding ospreys in the study of Long (1968) in the UK.

Freshwater bream, northern pike, European perch and European flounder dominated as prey also in the studies of Moll (1962), Nordbakke (1974, 1980), Häkkinen (1978) and Marquiss et al. (2007), where freshwater bream seemed to be the most delivered prey species overall. Breams occurs in warm and shallow lakes, also brackish water, and was therefore expected as prey for the ospreys at Isnes. Breams travel in shoals, making them locally abundant, but also easier to spot from air in still and slow – running waters (Froese, 2016b). Benthic-feeding fish also seems to be more vulnerable to capture than limnetic – feeding fish, because their attention is directed against the bottom, compared to predatory piscivorous fishes (Swenson, 1979). Even so, European perch were also frequently delivered to the nest at Isnes, and as for bream, smaller perches travel in shoals, making them more easily seen and more locally abundant (Craig, 1974).

Prey delivery and handling at the nest

The males were the main providers of prey at both nests, while the females did the brooding and mostly of the feeding, as expected (Cramp & Simmons, 1979; Bjørgeengen, 2016). The female at Isnes also delivered a considerably amount of prey to the nest, most likely because of the short distance to fishing grounds in Vestvannet. She may have been able to spot fishes while perching on the nest or on a perching branch, before plunging into the water. In this way, she spent little energy contributing with prey. According to Eldegard and Sonerud (2010), females of Tengmalm´s owl (*Aegolius funereus*) adjusted their provisioning effort based on the provisioning rate of the male, which also may have been the case for the female at Isnes.

The female at Skjeberg disappeared in early July for unknown reasons and the male had to do the feeding of the young as well. This was after the most crucial period when the nestlings were dependent on the female`s brooding, and one can only speculate whether she deserted or died. It is although interesting that this happened just at the time for the nestlings to survive without the female`s care. The male provided the nestlings with prey, and started to feed them when the female was not returning, although at a lower feeding rate. Despite this, the nestlings developed and gained weight normally. Also, they started to ingest prey independently earlier than the nestlings at Isnes, most likely because the male did not feed them sufficiently. The male often delivered prey which piled up in the nest, so the nestlings were most likely forced to try to feed independently at an earlier stage.

Mate desertion is not uncommon in raptors, as documented by Beissinger and Snyder (1987), Kelly and Kennedy (1993), Eldegard et al. (2003), Eldegard and Sonerud (2009), Eldegard and Sonerud (2012). This is regardless not common before the nestlings are able to maintain thermic independence and ingest prey unassisted (Beissinger & Snyder, 1987; Roulin & Marti, 2002; Wiebe, 2005; Sonerud et al., 2014a). In this case, it is therefore more likely that the female deceased than deserted.

At both nests, the parents were less likely to dismember prey as the nestlings grew older. This corresponds well with earlier studies on other raptors and owls like white – tailed eagle, northern goshawk (*Accipiter gentilis*), Eurasian kestrel (*Falco tinnunculus*), European sparrowhawk (*Accipiter nisus*), Eurasian pygmy owl (*Glaucidium passerinum*), Tengmalm´s owl and golden eagle (*Aquila chryaetos*) (Steen et al., 2010; Sonerud et al., 2014a; Sonerud et al., 2014b; Eriksen, 2016). The nestlings ingested more than 50% of the prey items by themselves when they become older than 50 days at Isnes and 47 days at Skjeberg. This is late compared to other raptors preying on mammalian and avian prey. The reason may be that fish prey is bonier, potentially larger, may have thicker skin and stickier flesh than mammals and birds.

Mass of prey

In my study, freshwater bream, European flounder, European perch and northern pike accounted for 54.8%, 18.5%, 14.0% and 6.6% of the total prey body mass of delivered prey, respectively, while Bjørgeengen (2016) reported 48.6%, 12.0%, 9.7% and 5.8% for the same prey species. Freshwater bream accounted for most of the prey mass delivered in both studies, while Nordbakke (1974, 1980) found that bream accounted for 5.3% only. This was even though freshwater bream was present in all three study areas. The same was the case for European flounder, which only accounted for 1.7% of the total estimated prey body mass in the study of Nordbakke (1974, 1980). He found that ide (*Leuciscus idus*) was the most delivered prey, while ide only accounted for 1.3% in my study and 1.7% in the study of Bjørgeengen (2016). Both Nordbakke (1974, 1980), Häkkinen (1978) and Bjørgeengen (2016) found that perches and pikes were important contributions to the osprey’s diet.

In my study, mean prey body mass at capture was 482.0 g for all prey in general, markedly heavier than the mean prey body mass of 380 g found by Bjørgeengen (2016). Average length in my study was estimated to 30.5 cm, which coincides well with findings from Scotland (Cramp & Simmons, 1979), who found an average of 34.7 cm. Prey body mass at delivery to the nest was 318.5 g in my study while it was 293 g in 2015 (Bjørgeengen, 2016). My findings fit well with estimates made by Nordbakke (1974, 1980) and Häkkinen (1978). Since the latter estimates are based on prey remains, potential differences may be due to the methods, differences in prey abundancy, distribution of prey, and/or size range in the prey populations. The fact that the female at Isnes also hunted, may have driven the estimated mean prey body mass up, due to size differences between the sexes. One possibility is also that the female received prey from the male outside the range of the camera, although they sometimes both arrived with prey within a short time frame, making it unlikely that this happened often. At Isnes, the heaviest prey item delivered to the nest, was a freshwater bream with estimated prey mass slightly above 3 kg at capture, although it was further eaten at prior to delivery to the nest. This is not an unlikely body mass for bream, which can be up to 6 kg (Muss & Nielsen, 2012), but for the ospreys with body mass at 1.5 – 2 kg, it may be a difficult task to bring the prey to the nest. Ospreys are nevertheless observed with prey over 3 kg, including carps (Cramp & Simmons, 1979), and it is known that big bream occur in the area around Glomma (Norsk meiteunion, 2017).

Due to possible inaccuracies, the interpretation of prey mass in my study must be done with caution. Prey have most likely been both under- and overestimated due to large variation in the perception of prey length, and therefore prey mass, after where the prey had been placed in the nest. The same method was used by Bjørgeengen (2016), and I can assume that the results are more accurate and alike than those from the other studies (Häkkinen, 1978; Nordbakke, 1974, 1980) which are based on prey remains.

Decapitation of prey

When eating, ospreys starts with the fish head (Cramp & Simmons, 1979), as this is the easiest and most natural part to get a grip on. Some prey species were more likely to be decapitated than others. Freshwater bream was more likely to be decapitated while perch were less likely to be decapitated prior to delivery to the nest. Larger prey was also more likely to be decapitated than smaller prey, and the same was found by Bjørgeengen (2016). Many freshwater breams delivered to the nest were large, and decapitation was therefore expected. Decapitated prey is easier to handle for the nestlings, as the head often is heavy and hard. With the head off, the flesh is exposed and made more available to the nestlings. The head is also a good resource to exploit by the male. This will reduce his search time for new prey to self – feed on (Ydenberg, 1994), and the male will have an energy – rich meal, since I assume that the brain has a higher energy – value than the rest of the fish body (Tremblay, 2011) Decapitation of prey may also reduce prey body mass prior to transport to the nest, and then energy cost (Rands et al., 2000), although Bjørgeengen (2016) found this unlikely. Decapitation also leave the male to allocate prey between him, the female and the nestlings prior to delivery to the nest (Sonerud et al., 2013).

Perches were seldom decapitated, and this was also expected as they often were smaller than other prey. They are also not as bony as other fish (Froese, 2016c), and the head may therefore be easier to handle for the nestlings, although it is spiky. Since most of the perches delivered were quite small, the nestlings were most likely in need for the whole prey item by themselves. The male may have made a trade – off between whether he should feed on the small prey prior to delivery, or go hunting for larger prey to self – feed. If he chooses to feed on the small prey before delivery to the nestlings, they are sooner in need for more energy, than if he provides them with the whole prey.

Diel activity

For both Isnes and Skjeberg, time of day had an impact on foraging behavior, as also found by Stinson (1978), Flemming and Smith (1990) and Bjørgeengen (2016). The activity pattern was quite alike for the two nests, with activity during the whole day, but with especially high peaks early in the morning and in the afternoon and early evening, as also found by Bjørgeengen (2016) in the same area in 2015, and by Dennis (2008) for an osprey population in Scotland. Because it is dark during night and the ospreys are dependent on seeing the fish through the water surface, the activity pattern complies with what is expected. After a night, the adult ospreys, and even more the nestlings, are in need for energy. As judged from the deliveries, the male starts hunting as soon as the light conditions allowed. Also in the evening, it is important to gain energy to avoid starvation, and to keep the metabolism on a sufficient level during the night. However, as Bjørgeengen (2016) stated, the dark period in the Norwegian summer nights is short, and the nestlings do not necessarily wait longer for feeding from the evening to the morning than during the day.

Because the osprey’s choice of prey depends on the abundance and availability of prey near the water surface, usually no deeper than 1 m (Cramp & Simmons, 1979; Edwards, 1988), diel activity may also depend on the activity pattern of the osprey´s prey, and on the prey of the prey fish, if predatory. Fish may be more easily preyed on while rising in the water, especially fish who prey on insects on the water surface, or fish that move to shallower parts in summer. The diel activity pattern of fish may vary from species to species, and from one life stage to another. Whereas some fish are nocturnal, and some diurnal, they may also switch from one state to another due to ecological and physiological factors, so – called phenotypic plasticity (Reebs, 2002). However, because the ospreys prey on a variety of fish species, it is more likely that the activity pattern of the ospreys is due to its internal state pattern and the nestlings needs.

Carps

Carps was delivered throughout the day with peaks that corresponded well with the overall activity pattern for the ospreys at Isnes, as it was the most common prey type. Freshwater bream is a schooling and bottom – dwelling fish, and it can therefore be locally abundant. Their depth in water is usually from 1 m, but they can also go to shallower parts of the lakes in summer where the water is warmer (Froese, 2016b), making them more vulnerable to capture. According to studies by Alabaster and Robertson (1961), Lyons and Lucas (2002) and Bjørgeengen (2016), freshwater bream is relative inactive during daytime, and more active at dusk and dawn, which corresponds well with my results.

Perches

Perches were also delivered throughout the day and was the second most delivered prey type at Isnes, with European perch as the most delivered prey species. According to Rask (1986) and Froese (2016c), European perch is diurnal and those longer than 11 cm had activity peaks in the morning and evening in May and June, but at midday in July and August due to seasonal variation in prey. This corresponds well with my results, except for the fact that there was no peak at midday in July and August, even though most of the perches delivered were larger than 11 cm. This lack of fit may be due to differences in ecological factors and prey distribution, as the study of Rask (1986) was conducted in Finland. Eriksson (1978) found from a laboratory study that perches stayed at the bottom in winter while at summer they spent as much time in the upper and lower parts of the tank, showing that they would be more accessible for the ospreys in summer, while Craig (1977) found that perches were more active when temperature and water clarity increased, except in June due to spawning.

Pikes

The deliveries of northern pike had only one peak in activity during the day, which corresponds with the second activity peak at midday for all deliveries at Isnes and to the results of Bjørgeengen (2016). Pikes prey on carps (Pethon, 2012), so it would be expected that pikes and carps have quite similar activity pattern. However, Jepsen et al. (2001) found that pikes in a natural mesotrophic lake in Denmark were most often observed in the interval 18:00 – 00:00, although not significantly often than from activity at 12:00 – 18:00, which corresponds better with my results. From a study in England, Beaumont et al. (2005) found that the activity peaked at dusk and dawn, and that different individuals had different strategies. Pikes is also known to spawn in very shallow water, usually less than 17.8 cm (Froese, 2016d), and they are more easily preyed on in that state (Green, 1976; Häkkinen, 1978). However, since pike spawn in spring after the ice thaws (Department of Environment and Climate Change, 2017), it is not likely that spawning is the reason why pikes are preyed on by ospreys during the nesting season in Norway. In my analysis, I found the same pattern as Bjørgeengen (2016), where the peak of pike deliveries was at solar midday, whereas the other species had peaks in delivery in the morning and evening, with a drop at midday. Reasons for this difference may be that pikes hunt at midday, and therefore make themselves more vulnerable to predation, or that other prey species are more available in the morning and evening so that pikes are a less frequent prey at these times of the day (Bjørgeengen, 2016).

Flounders

Flounders was the most delivered prey type at Skjeberg. Delivery of flounders peaked twice a day, corresponding to two of three peaks for all deliveries at Skjeberg, one in the morning and one in the evening. In the summer, both juvenile and adult flounders occur in the sea as well as in brackish shallow water (Froese, 2016e), making them more vulnerable to predation. They are nocturnal and burrow in the sand, but were delivered during the whole day at Skjeberg. According to Gibson (1973), Wirjoatmodjo and Pitcher (1984) and Marquiss et al. (2007), flounders move and feed in relation to light conditions and tidal cycles, and Dennis (2008) found that ospreys in Scotland often captured flounders when the tide was low. I found that tide was not a significant predictor for a flounder being delivered to the nest. Because most delivered flounder species was European flounder, which is capable of living in brackish water (Froese, 2016e), therefore it is possible that tide is not as evident in the lower parts of Glomma than along the coastline. Deliveries of flounders also followed the osprey´s general activity pattern, as they were the most common prey type at Skjeberg. Marquiss et al. (2007) found that flatfish (Pleuronectidae) were taken at different tidal stages, so that they were delivered to the nest throughout the day, which also was the case in my study. Wind speed was not a significant predictor. One can argue that wind speed will have a larger impact in the future due to global climate changes (Bjørgeengen, 2016), even though Grubb (1977) found that weather conditions did not influence the foraging success of ospreys as much as other foraging parameters.

Distribution of prey mass during the nesting season

Prey mass received per nestling per day tended to increase during nestling season at Isnes, but not for the nest at Skjeberg. An increase in prey mass during the season was expected as the nestlings grow and are in need for more energy. Some prey items fell out of the analysis due to pauses in the recordings, so the amount of prey is therefore underestimated. Also, the female fed from the prey, especially in the beginning when she was tied to the nest, and this was not corrected for, so the nestlings received less than estimated. Similarly, Bjørgeengen (2016) found no change in prey mass delivered per nestling during the season, and argued that the nestlings received prey outside the nests after fledging, so that the amount of prey registered after fledging was underestimated. During the 35 hours of direct observations during the field season, I did not notice any prey deliveries outside the nest after fledging. The delivering parent, according to my knowledge, always went to the nest after capturing a prey, although I could not ignore that deliveries outside the nest may have occurred.

The female at Isnes occasionally hunted herself, and delivered a markedly proportion of prey mass to the nestlings. This contrasts to what Bjørgeengen (2016) found. The female at Isnes also delivered larger prey than her mate, while Bjørgeengen (2016) found that the female delivered smaller prey than the male. Since raptors has asymmetrical parental roles, the providing parent is selected for small body size (Sonerud et al., 2014a). The female is 5 - 10% larger than the male (Cramp & Simmons, 1979), and is therefore able to deliver larger prey to the nestlings. Another possible explanation is that the male is selected to deliver smaller prey in relation to a family conflict. The nestlings starts earlier to feed by themselves if the prey is smaller, and smaller prey is more efficient to ingest when the male self – feeds (Sonerud et al., 2013). Also, if the distance from the nest site to fishing grounds are short, the male may include smaller prey in the diet, as suggested by central place foraging theory (Davies, 2012). The male at Isnes delivered markedly smaller prey than the female, which supports the theory.

Seasonal distribution of prey species

Ospreys shifts between prey species throughout the nesting season due to seasonal fluctuations in prey (Cramp & Simmons, 1979), or maybe also as a response of nestling age due to the nestling's ability to digest different types of prey at different stages (Steen et al., 2012). In my study, only deliveries of pikes and flounders had a change in distribution during nesting season, and both had a decrease in the daily number of deliveries. Bjørgeengen (2016) also found a decrease in pike deliveries during the season, but not for flounders. The decline in both pikes and flounders in my study can be due to changes in their behaviour during nesting season. Summers (1979) stated, for instance, that flounders enters estuaries in late June and early July, and that they leave for deeper sea again during July, making them difficult, or impossible, to reach for the ospreys. Also, pikes and flounders may also have been favourable prey types earlier in the nestling season than later, when the nestlings were unable to ingest prey unassisted. Flounders might have been easier to ingest as they have a slim cross section (Bjørgeengen, 2016), although they often were alive at delivery to the nest (pers. obs.). The decline in delivery of pikes can be due to freshwater bream and perches being more abundant, and therefore more easily to prey upon, although there was no change in delivery of carps and perches during the season. Seasonal change in deliveries of pike is nevertheless unlikely as they are highly territorial (Froese, 2016d).

Possible biases

The results in my study must be interpreted with some caution. The nests were in a restricted area and ospreys feeds on a wide range of prey around the world, due to different habitat and climate. There may also be human errors in identification of prey or estimates of body size due to poor visibility, or even when the visibility was sufficient. While estimating length, the prey had a wide range in length based on where in the nest the length was estimated from, and whether the prey laid far back or in front, or far to the left or to the right in the nest. The direction of the prey in the nest also affected the perception of length. If the head was directed against or away from the camera, it was assumed shorter than if the head was directed to the left or right. Some prey could not have their length estimated, and the mean body mass for pike and trout is somewhat underestimated due to difficulties in estimating length of the largest individuals. It was also hard to see if more than the head was missing for decapitated prey. In the estimates for prey mass, all flounders were assumed to be European flounder, although this was uncertain. Due to frequent pauses in the recordings due to technical problems, important data loss was also assumed to have occurred.

Conclusion

The ospreys were active all day during daylight, with most deliveries in the morning and evening. Carps were most frequently delivered to the two nests all over, although flounders were the most commonly delivered prey type at the nest at Skjeberg. The male delivered most of the prey, while the female did most of the brooding and feeding, as expected. The mean prey body mass overall delivered was found to be 318.5 g, and the female at Isnes apparently delivered larger prey than the male. Although, estimated prey mass as stated is exposed to biases, video monitoring is assumed to be more accurate than by using prey remains and carcasses at the nests. In future studies, it is important to collect data in different areas and habitats to get a more comprehensive understanding of prey choices during nestling season (Bjørgeengen, 2016). Prey mass can also be estimated more accurate if each prey item is measured several times by different observers, so the estimated length is an average from several estimates. More observations at different times during nesting season is also necessary to see if prey is handed over to the female and to the nestlings outside the nests.

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Appendix 1

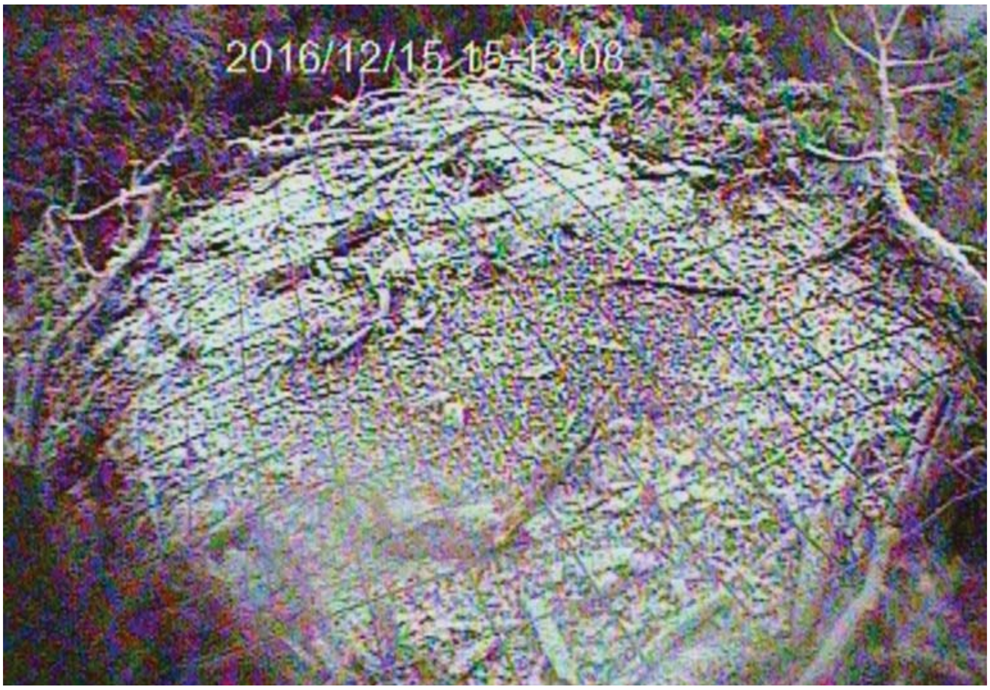

Figure I. Metal grid used for size reference at Isnes.

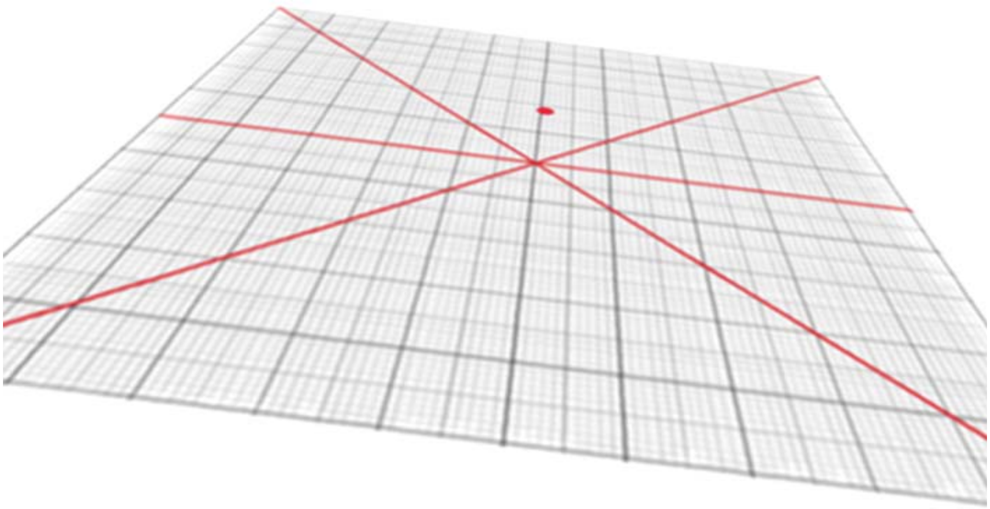

Figure II. Simulated grid used for size reference at Skjeberg.

Appendix 2

Table I. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item being delivered to the nest at Isnes within an hour block. See table 5 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
3	7	881.10	0.00	0.44
10	8	882.06	0.96	0.27
6	8	883.02	1.92	0.17
14	9	883.75	2.65	0.12
2	5	892.29	11.19	0.00
9	6	893.33	12.23	0.00
5	6	894.27	13.17	0.00
13	7	895.14	14.05	0.00
1	3	924.69	43.60	0.00
8	4	925.87	44.78	0.00
4	4	926.58	45.48	0.00
12	5	927.87	46.77	0.00
0	1	990.56	109.47	0.00
7	2	1549.71	668.62	0.00
15	3	1551.44	670.35	0.00
11	2	1562.15	681.06	0.00

Table II. Effects in model 3 on the predicted probability that at least one prey item was delivered to the osprey nest at Isnes within an hour block (random effect = nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-1.67448	0.12967	-12.913	0.0001
I(cos(2 x pi x Hour/24))	-1.60353	0.22091	-7.259	0.0001
I(sin(2 x pi x Hour/24))	-0.02874	0.11540	-0.249	0.80
I(cos(2 x 2 x pi x Hour/24))	-1.05243	0.17916	-5.874	0.0001
I(sin(2 x 2 x pi x Hour/24))	-0.05353	0.13406	-0.399	0.69
I(cos(3 x 2 x pi x Hour/24))	-0.53120	0.14529	-3.656	0.00026
I(sin(3 x 2 x pi x Hour/24))	-0.10372	0.13316	-0.779	0.44

Table III. Effects in model 10 on the predicted probability that at least one prey item was delivered to the osprey nest at Isnes within an hour block (random effect = nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-1.295017	0.388178	-3.336	0.00085
I(cos(2 x pi x Hour/24))	-1.613188	0.221337	-7.288	0.0001
I(sin(2 x pi x Hour/24))	-0.027780	0.115464	-0.241	0.81
I(cos(2 x 2 x pi x Hour/24))	-1.055586	0.179354	-5.885	0.0001
I(sin(2 x 2 x pi x Hour/24))	-0.048627	0.134194	-0.362	0.72
I(cos(3 x 2 x pi x Hour/24))	-0.533342	0.145445	-3.667	0.00025
I(sin(3 x 2 x pi x Hour/24))	-0.102928	0.133233	-0.773	0.44
Tide	-0.006643	0.006445	-1.031	0.30

Table IV. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item being delivered to the nest at Skjeberg within an hour block. See table 5 in methods for model specifications.

Model	K	AICc	ΔAICc	AICc - weight
3	7	531.32	0.00	0.52
6	8	533.26	1.94	0.20
10	8	533.34	2.02	0.19
14	9	535.28	3.96	0.07
2	5	538.29	6.98	0.02
5	6	540.29	8.98	0.01
9	6	540.31	9.00	0.01
13	7	542.31	11.00	0.00
1	3	554.62	23.30	0.00
4	4	555.53	24.21	0.00
8	4	556.59	25.27	0.00
12	5	557.47	26.15	0.00
0	1	561.83	30.51	0.00
7	2	1549.71	1018.40	0.00
15	3	1551.44	1020.13	0.00
11	2	1562.15	1030.84	0.00

Table V. Effects in model 3 on the predicted probability that at least one prey item was delivered to the osprey nest at Skjeberg within an hour block (random effect = nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-2.0176	0.1591	-12.684	0.0001
I(cos(2 x pi x Hour/24))	-0.9644	0.2608	-3.698	0.00022
I(sin(2 x pi x Hour/24))	-0.3407	0.1575	-2.163	0.03
I(cos(2 x 2 x pi x Hour/24))	-0.9229	0.2122	-4.349	0.0001
I(sin(2 x 2 x pi x Hour/24))	-0.3859	0.1824	-2.116	0.03
I(cos(3 x 2 x pi x Hour/24))	-0.4874	0.1827	-2.667	0.0076
I(sin(3 x 2 x pi x Hour/24))	-0.3460	0.1798	-1.924	0.05

Table VI. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey of carps being delivered to the osprey nest at Isnes within an hour block. See table 5 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
mod 10	8	670.82	0.00	0.33
mod 3	7	671.42	0.60	0.25
mod 14	9	671.96	1.14	0.19
mod 6	8	673.14	2.32	0.10
mod 9	6	674.72	3.90	0.05
mod 2	5	675.21	4.39	0.04
mod 13	7	676.00	5.18	0.03
mod 5	6	677.01	6.19	0.02
mod 8	4	696.23	25.41	0.00
mod 1	3	696.50	25.68	0.00
mod 12	5	698.16	27.34	0.00
mod 4	4	698.51	27.69	0.00
mod 0	1	723.84	53.01	0.00
mod 7	2	1549.71	878.89	0.00
mod 15	3	1551.44	880.62	0.00
mod 11	2	1562.15	891.33	0.00

Table VII. Effects in model 3 on the predicted probability that at least one prey item of carps was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P-value
(Intercept)	-2.3098	0.1601	-14.424	0.0001
I(cos(2 x pi x Hour/24))	-1.4089	0.2725	-5.170	0.0001
I(sin(2 x pi x Hour/24))	-0.1370	0.1413	-0.970	0.33
I(cos(2 x 2 x pi x Hour/24))	-1.0295	0.2163	-4.760	0.0001
I(sin(2 x 2 x pi x Hour/24))	-0.1298	0.1657	-0.783	0.43
I(cos(3 x 2 x pi x Hour/24))	-0.4590	0.1752	-2.619	0.0088
I(sin(3 x 2 x pi x Hour/24))	-0.1133	0.1629	-0.695	0.49

Table VIII. Effects in model 10 on the predicted probability that at least one prey item of carps was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-1.585229	0.473255	-3.350	0.00081
I(cos(2 x pi x Hour/24))	-1.427831	0.273299	-5.224	0.0001
I(sin(2 x pi x Hour/24))	-0.136167	0.141456	-0.963	0.34
I(cos(2 x 2 x pi x Hour/24))	-1.037425	0.216832	-4.784	0.0001
I(sin(2 x 2 x pi x Hour/24))	-0.121191	0.165954	-0.730	0.47
I(cos(3 x 2 x pi x Hour/24))	-0.463760	0.175642	-2.640	0.0083
I(sin(3 x 2 x pi x Hour/24))	-0.111552	0.163154	-0.684	0.49
Tide	-0.012800	0.007989	-1.602	0.11

Table IX. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey of perches being delivered to the osprey nest at Isnes within an hour block. See table 5 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc - weight
mod 2	5	381.50	0.00	0.36
mod 9	6	382.74	1.24	0.19
mod 5	6	383.53	2.02	0.13
mod 3	7	383.75	2.25	0.12
mod 13	7	384.68	3.17	0.07
mod 10	8	385.01	3.51	0.06
mod 6	8	385.79	4.29	0.04
mod 14	9	386.98	5.48	0.02
mod 1	3	394.49	12.99	0.00
mod 8	4	395.70	14.20	0.00
mod 4	4	396.35	14.85	0.00
mod 12	5	397.32	15.82	0.00
mod 0	1	404.12	22.61	0.00
mod 7	2	1549.71	1168.21	0.00
mod 15	3	1551.44	1169.94	0.00
mod 11	2	1562.15	1180.65	0.00

Table X. Effects in model 2 on the predicted probability that at least one prey item of perches was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-3.22490	0.21538	-14.973	0.0001
I(cos(2 x pi x Hour/24))	-1.24066	0.33661	-3.686	0.00023
I(sin(2 x pi x Hour/24))	-0.02586	0.19140	-0.135	0.89
I(cos(2 x 2 x pi x Hour/24))	-0.97865	0.26230	-3.731	0.00019
I(sin(2 x 2 x pi x Hour/24))	0.03680	0.22708	0.162	0.87

Table XI. Effects in model 9 on the predicted probability that at least one prey item of perches was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-3.785338	0.669354	-5.655	0.0001
I(cos(2 x pi x Hour/24))	-1.231427	0.336966	-3.654	0.00026
I(sin(2 x pi x Hour/24))	-0.028134	0.191521	-0.147	0.88
I(cos(2 x 2 x pi x Hour/24))	-0.978986	0.262450	-3.730	0.00019
I(sin(2 x 2 x pi x Hour/24))	0.029271	0.227399	0.129	0.90
Tide	0.009608	0.010721	0.896	0.37

Table XII. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey of pikes being delivered to the osprey nest at Isnes within an hour block. See table 5 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc - weight
mod 1	3	270.40	0.00	0.41
mod 8	4	272.35	1.94	0.16
mod 4	4	272.38	1.98	0.15
mod 2	5	274.07	3.67	0.07
mod 12	5	274.35	3.95	0.06
mod 3	7	274.47	4.07	0.05
mod 9	6	276.03	5.63	0.02
mod 5	6	276.07	5.67	0.02
mod 10	8	276.45	6.05	0.02
mod 6	8	276.48	6.08	0.02
mod 13	7	278.05	7.65	0.01
mod 14	9	278.48	8.07	0.01
mod 0	1	294.49	24.09	0.00
mod 7	2	1549.71	1279.31	0.00
mod 15	3	1551.44	1281.04	0.00
mod 11	2	1562.15	1291.75	0.00

Table XIII. Effects in model 1 on the predicted probability that at least one prey item of pikes was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-3.6851	0.2509	-14.690	0.0001
I(cos(2 x pi x Hour/24))	-1.5030	0.3329	-4.515	0.0001
I(sin(2 x pi x Hour/24))	0.2213	0.2702	0.819	0.41

Table XIV. Effects in model 8 on the predicted probability that at least one prey item of pikes was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-3.887350	0.792220	-4.907	0.0001
I(cos(2 x pi x Hour/24))	-1.499852	0.333162	-4.502	0.0001
I(sin(2 x pi x Hour/24))	0.222164	0.270248	0.822	0.41
Tide	0.003493	0.012916	0.270	0.79

Table XV. Effects in model 4 on the predicted probability that at least one prey item of pikes was delivered at the osprey nest at Isnes within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-3.75407	0.43148	-8.700	0.0001
I(cos(2 x pi x Hour/24))	-1.47463	0.36249	-4.068	0.0001
I(sin(2 x pi x Hour/24))	0.23430	0.27816	0.842	0.40
FF	0.01882	0.09521	0.198	0.84

Table XVI. Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey of flounders being delivered to the osprey nest at Skjeberg within an hour block. See table 5 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
mod 2	5	369.99	0.00	0.24
mod 3	7	370.20	0.21	0.21
mod 5	6	370.84	0.85	0.15
mod 6	8	371.23	1.24	0.13
mod 9	6	371.96	1.98	0.09
mod 10	8	372.18	2.19	0.08
mod 13	7	372.86	2.87	0.06
mod 14	9	373.26	3.27	0.05
mod 0	1	387.40	17.41	0.00
mod 1	3	390.75	20.77	0.00
mod 8	4	392.64	22.65	0.00
mod 4	4	392.77	22.78	0.00
mod 12	5	394.66	24.68	0.00
mod 7	2	1549.71	1179.72	0.00
mod 15	3	1551.44	1181.46	0.00
mod 11	2	1562.15	1192.17	0.00

Table XVII. Effects in model 2 on the predicted probability that at least one prey item of flounders was delivered at the osprey nest at Skjeberg within an hour block (random effect = Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-2.5749	0.1719	-14.977	0.0001
I(cos(2 x pi x Hour/24))	-0.1314	0.2552	-0.515	0.61
I(sin(2 x pi x Hour/24))	-0.1335	0.1815	-0.736	0.46
I(cos(2 x 2 x pi x Hour/24))	-0.8451	0.2251	-3.754	0.00017
I(sin(2 x 2 x pi x Hour/24))	-0.6519	0.2180	-2.991	0.0028

Table XVIII. Effects in model 5 on the predicted probability that at least one prey item of flounders was delivered at the osprey nest at Skjeberg within an hour block (random effect= Nest ID).

Variable	Estimate	SE	z value	P
(Intercept)	-2.967945	0.405669	-7.316	0.0001
I(cos(2 x pi x Hour/24))	0.006009	0.285882	0.021	0.98
I(sin(2 x pi x Hour/24))	-0.077221	0.188818	-0.409	0.68
I(cos(2 x 2 x pi x Hour/24))	-0.882426	0.227951	-3.871	0.00011
I(sin(2 x 2 x pi x Hour/24))	-0.676797	0.219782	-3.079	0.00207
FF	0.103248	0.094178	1.096	0.27

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