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Video Monitoring of Ospreys (*Pandion haliaetus*) at the Nest: Prey Deliveries, Feeding Time and Potential Family Conflicts

Tuva Flor Lien
General Ecology

Acknowledgements

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Abstract

Prey deliveries and feeding time was recorded and analyzed at two osprey *(Pandion haliaetus)* nests located in Østfold county, Norway during the breeding season of 2016. Feeding time analysis was only done when the nestlings were assisted by a parent. 201 prey deliveries were used for feeding time analysis. I found that carp species were the most important prey at the osprey nest in Isnes, while flounders were most important at the osprey nest in Skjeberg, and that this discrepancy was likely due to the difference in proximity to freshwater and saltwater fishing localities. 60% of prey items were delivered decapitated, and the frequency of decapitation was higher for carps and flounders, and low for perches and pikes. At Isnes, the probability of decapitation was affected by prey weight, while none of the explanatory variables affected probability of decapitation at the Skjeberg nest. Nestlings were just as likely to feed assisted as unassisted when they reached 50 days of age. The feeding parent spent an average of 1,678 s feeding a prey item to the nestlings, and there was a strong positive relationship between prey mass and feeding time. Decapitation reduced feeding time in all prey except for large carps at the Isnes nest, while the male at Skjeberg spent less time feeding a prey item to the nestlings than the female. The female at Isnes assisted the nestlings in 98% of feeding sessions, while the male delivered most of the prey. This supports the general conception that ospreys exhibit strongly divided parental care tasks. However, when the female at the Skjeberg nest disappeared prior to the nestlings being able to feed unassisted, the male continued to feed the nestlings, showing that these divided roles have some degree of plasticity. The female at Isnes continued feeding the nestlings although they appeared to be able to feed unassisted, suggesting a strategy of maximizing the control over allocation of resources delivered by the male between her and the nestlings. This suggests that a sexual conflict may be present in ospreys during the nesting period.

Sammendrag

Byttedyrleveringer og spisetid på to fiskeørnreir (*Pandion haliaetus*) i Østfold fylke, Norge, ble videoovervåket gjennom hekkesesongen i 2016. Analyse av spisetid ble kun gjort for byttedyr der ungene ble matet av en forelder. Totalt ble 379 byttedyr registrert, og spisetid ble analysert for 201 av disse. Karpefisk ble oftest levert på reiret i Isnes, mens flyndrefisk oftest ble levert på reiret i Skjeberg, og denne forskjellen i byttedyrvalg synes å ha sammenheng med reirets avstand til ferskvanns- og saltvannsfiskelokaliteter. Av byttedyrene som ble levert var 60% dekapiterte, og karpefisk og flyndrer var oftere dekapitert enn abbor og gjeddefisk. På Isnes økte sannsynligheten for dekapitering med fiskevekt, mens ingen av forklaringsvariablene påvirket sannsynlighet for dekapitering på Skjeberg. Det var like stor sannsynlighet for at ungene spiste selv som at de ble matet da de var 50 dager gamle. Forelderen som matet brukte i gjennomsnitt 1678 s på å mate ungene med ett byttedyr, og spisetiden økte med vekten på byttedyret. Dekapitering reduserte spisetiden for alle byttedyr med unntak av store karpefisk på reiret i Isnes, mens hannen på Skjeberg-reiret brukte kortere tid på å mate ungene med et bytte enn hunnen. Hunnen på Isnes-reiret matet ungene i 98% av måltidene, i mens hannen leverte mesteparten av byttedyrene. Dette støtter oppfatningen om at fiskeørn har klart adskilte foreldreoppgaver. På Skjeberg derimot, forsvant hunnen før ungene var i stand til å spise selv, noe som førte til at hannen begynte å mate ungene. Dette viser at de delte foreldrerollene hos fiskeørn til dels er plastiske. Hunnen på Isnes fortsatte å mate ungene selv om de var i stand til å spise selv, noe som antyder en strategi der hunnen maksimerer sin kontroll over fordelingen av mat levert av hannen mellom henne og ungene. Dette kan tyde på en seksuell konflikt mellom foreldrene hos fiskeørn i hekkeperioden.

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1. Introduction

Parental care is an important and highly divided task in most raptor species (i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes)). Providing and feeding nestlings are activities that demand a high energetic expenditure for the parents, thus potentially reducing their future reproductive success (Houston et al., 2005). Trivers (1972) coined the term parental investment, defining it as ‘any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring. Thus, parental care will involve trade-offs between investment in the current brood and future broods (Davies et al., 2012). These trade-offs are often governed by constraints such as food availability (Clutton-Brock, 1991) and can result in sexual conflict between the male and female over parental care (Barta et al., 2001).

Contrary to what is the case in other provisioning birds, in raptors the male is the main deliverer of prey to the nest, while the female assists with feeding the nestlings while brooding and only contribute to capturing prey towards the end of the nesting period (Sonerud et al. 2014). Raptors are single-prey loaders, and are predicted to maximize the net rate of prey delivery to the nest (Sodhi, 1992, Sonerud, 1992). This involves decision making for the provisioning parent, taking factors such as distance from the nest and prey abundance into account when selecting prey (Krebs, 1978, Sonerud, 1992).

Preparation of a prey item is commonly observed in raptors (Steen et al., 2010), and several hypotheses have been proposed as to why (see Kaspari, 1990). Removal of less profitable parts from the prey at the capture site, may reduce transport cost (Sodhi, 1992). Foraging is both time and energy consuming, and by consuming parts of the prey the providing parent can also save time needed for self-foraging (Rands et al., 2000). Small nestlings are often fed with prepared prey items due to the limitation imposed by factors such as gape size (Steen et al., 2010). As the nestlings grow older, the gape size increases and its limitation decreases. One would therefore expect a relationship between the probability of preparation and nestling age, as well as between probability of preparation and prey size. This relationship has previously been documented in Eurasian kestrels (*Falco tinnunculus*) (Steen, 2010).

Raptors capture prey with their feet, and use their bill to tear off pieces of the prey item before ingesting it. This makes feeding a time-consuming task (Slagsvold & Sonerud, 2007). Additionally, time spent feeding nestlings during the nesting period is often substantial in raptors. This confines the feeding parent, usually the female, to the nest for a prolonged period while the male is free to forage (Sonerud et al., 2014a). These asymmetric roles may have evolved as a solution to the conflict between foraging and feeding, whereas if both parents performed both tasks, a parent delivering prey to the nest might have to wait for the other parent to finish feeding the nestlings (Sonerud et al., 2014a). However, there is a potential for conflict between the male and female over how much to invest in parental care. Both parents will profit if the other provides more care, but the exploitation of the other parent must be balanced with sufficient provisioning of the nestlings (Hinde & Kilner, 2007; Parker et al., 2002). When the nestlings depend on assistance for feeding, the female has the power to allocate resources between herself and the offspring.

The osprey (*Pandion haliaetus*) is a medium-sized raptor (body mass 1400-2000 g, wingspan 140-170 cm) highly specialized in catching fish (Cramp, 1979). The female wingspan is 4-5% longer than that of the male, and females are up to 18% heavier than males (Schaadt & Bird, 1993). Prey is located by scouting from the air, followed by a swift dive down to a maximum of 1 m below water surface where fish is caught with the help of large talons. Choice of habitat is restricted by access to clear water with medium sized fish available near the water surface (Cramp, 1979). The osprey is found breeding on all continents except Antarctica and South America, and has shown the ability to adapt to human presence, utilizing constructions such as power lines and wind mills for nest building (Christie & Ferguson-Lees, 2001). However, nests are preferably build in trees in northern parts of the Palearctic range. In the 19th century, the osprey population in Norway plummeted as a result of extensive hunting and the issuing of a bounty for shooting birds of prey (Hagen, 1952). The population is now on the rise, and today consists of around 800-1200 reproductive individuals, mostly in the south-eastern region of Norway (Heggøy & Øien, 2014). The osprey is a migratory bird, usually present in Norway from April to September and wintering on the African continent south of Sahara (Cramp, 1979).

The diet of ospreys nesting in Scandinavia had up until recently only been investigated by prey remain analysis (Bjørgeengen, 2016). In recent years however, video monitoring of prey deliveries at raptor nests has proven to be a more precise method of investigating diet (e.g Steen 2004; Løw, 2006; Bech 2016; Eriksen 2016). The diet of nesting ospreys in south eastern Norway was investigated in 1972-1973 by Nordbakke (1974, 1980). In this study, prey remain analysis suggested a diet consisting mainly of ide (*Leuciscus idus*), pike (*Esox lucius*) and perch (*Perca fluviatilis*). Bjørgeengen (2016) did the first analysis of prey deliveries on four osprey nests by video monitoring in the same part of Norway as Nordbakke in the summer of 2015, and found freshwater bream (*Abramis brama*) to be the most common species delivered followed by European flounder (*Platichtys flesus*). Average gross prey body mass was 380 g per prey item, and average net prey body mass was 293 g.

In this study, I video monitored two osprey nests in Østfold county, Norway for two months during one nesting season. I recorded prey deliveries and analyzed feeding time when the nestlings were assisted by a parent. To the best of my knowledge, no study has previously analyzed feeding time in ospreys. By analyzing prey deliveries and recording assisted feeding of the nestlings, the objectives were to explore 1) the selection of prey species brought to the nests and whether prey selection varied between localities, 2) what factors explained the probability of decapitation of prey items, 3) the amount of time osprey parents spend feeding the nestlings and factors influencing feeding time and 4) what potential family and sexual conflicts arise in a raptor with highly divided parental care tasks.

2. Methods

2.1 Study area

This study was conducted on two osprey nests located in Østfold county, Norway (N 59°15'52.117" E 11°6'45.615"). The field work consisted of video monitoring two nests, one located at Isnes, and the other at Skjeberg, both in the municipality of Sarpsborg (Figure 1). The field work was conducted in the summer of 2016 and was done by me and a fellow masters student, Silje Klo Hansen. The nest located at Isnes was also video monitored in the summer of 2015 (see Bjørgeengen (2016)), while the Skjeberg nest had not previously been monitored and was located with the help of the local ornithology association in Østfold. The study period lasted from early June to mid-August. Both nests were situated on top of Scots pine trees. The surrounding areas consisted of mixed coniferous and deciduous forest. The nests' approximation to freshwater and saltwater differed. The Skjeberg nest was located approximately 250 m from saltwater and circa 9 km from the nearest freshwater lake Isesjøen, while the Isnes nest was located right next to the freshwater lake Vestvannet, and 14 km away from nearest saltwater fishing locality.

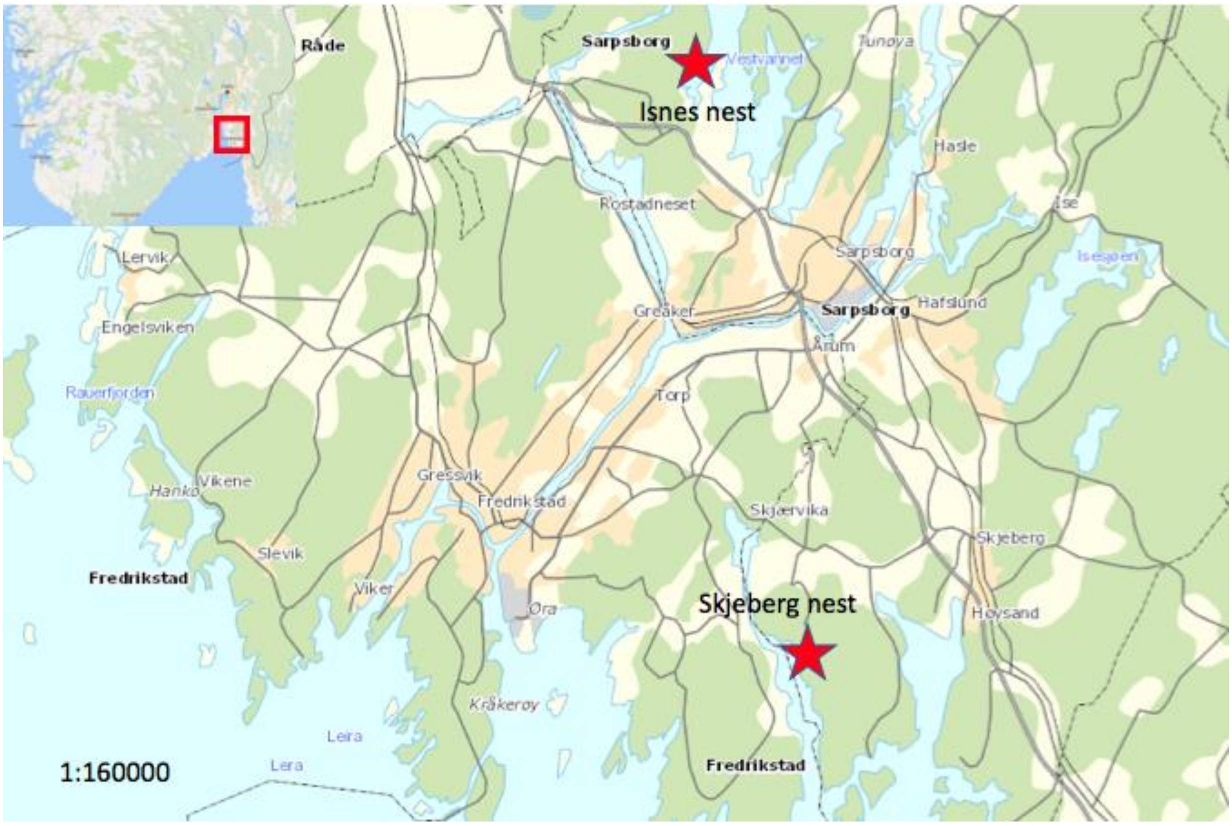

Figure 1. Map showing approximate locations of nests at Isnes and Skjeberg. Source: Turkart Østfold and Google Maps, edited with Microsoft PowerPoint.

Bjørgeengen (2016) recorded 22 different fish species present in the rivers and lakes surrounding the area (Table 1). The presence of some typical saltwater species in the rivers and lakes is due to brackish water in lower parts of some of the rivers and the lakes they run through.

Table 1. Recorded fish species in the freshwater rivers and lakes surrounding the two osprey nests in Østfold.

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

Both nests successfully reared three nestlings until fledging age. The male usually delivered the prey, while the female assisted nestlings in feeding. However, the female at Skjeberg disappeared somewhere between 30 June and 6 July, and was not seen again. Due to a piece of tape covering the lens of the camera during this period, we do not know exactly when the female disappeared. She might have deserted or died. The male at this nest then proceeded to bring prey and assist nestlings in feeding, but he rarely assisted with the whole prey. The females' disappearance happened before the nestlings were completely able to feed unassisted, resulting in a buildup of prey remains in the nest.

2.2 Video monitoring

The camera at the Isnes nest was already set up before the video recording the previous year (2015), while the camera and cables had to be installed at the Skjeberg nest after the nestlings were hatched. Video recording started when nestlings were 14 days old at Isnes and 27 days old at Skjeberg. The exact age of the nestlings at Isnes was known as they were observed when they hatched. The age of the nestling hatching first was chosen as the age of the whole brood. The age of the nestlings at the Skjeberg nest was estimated by comparing footage of them with the nestlings at the Isnes nest. Footage from dates where the nestlings at both nests looked approximately the same size was compared, and age estimated from the known age of the Isnes nestlings.

The camera used was a wide-angle miniature camera attached to a pole that was secured to the edge of the nest, providing a bird's eye view of the nesting platform. The camera was connected to a Secumate H.264 Mini portable DVR (digital video recorder) with a cable measuring approximately 100 m, so that the DVR could be placed on the ground away from the nest and memory cards and battery could be changed with minimal disturbance of the birds. The battery used to power both the camera and the DVR was a 12V lead battery that had to be changed once a week in both localities. Recordings were triggered by movement, and the motion sensitivity of the camera was set to 3 or 4. When a movement triggered the camera, a recording of maximum 17 minutes was saved as avi.-files on a 32 GB SD card. In addition, 5 s recordings prior to the triggering movement was also saved. This setup allowed for all prey deliveries to be recorded and most of the feeding sessions to be completely recorded. Due to the relatively high sensitivity, the SD cards had to be changed approximately once a day during the whole field work period. This is a very similar set up as was used in the study by Bjørgeengen (2016), and is a modified version of the set up described by Steen (2009).

There were some disruptions at both nests preventing continuous recording during the monitoring period. Part of the masking tape fastening the camera to the pole at the Skjeberg nest came off and covered the lens, making it impossible to see prey deliveries between June 30 and July 5. When the nestlings started to fledge at the Skjeberg nest, they also started to use the camera pole as a perch resulting in dislocation of the camera. At the Isnes nest, distortion of the lens happened twice, from water vapor and nestlings eliminating on the lens. The camera pole was also dislocated here for a short period. Sometimes we were not able to change SD cards before they were full and stopped recording. This happened randomly and at both locations. We also experienced problems with some SD cards not saving properly.

2.3 Video analysis

Prey deliveries were sorted out from all video recordings of both nests. Date, time of day, sex of delivering parent and prey identification to the lowest taxonomic level possible was then determined and stored in an Excel sheet (See Appendix 1 for all species recorded during the entire monitoring period). A separate Excel sheet was made for the analysis of feeding time. This included locality, date, time, prey species, prey body mass, delivering parent, feeding parent, whether the feeding parent also fed itself, and whether the nestlings at any time in the feeding session fed unassisted. In all recordings used for feeding time analysis it was possible to determine the feeding parent based on morphological features. The osprey is relatively easy to sex with certainty (Strandberg, 2013), and size of female versus male when both were present at the nest and width of the breast-band was used to identify the sex of the parents. If the feeding parent also ate some of the prey, it was estimated roughly how many percent of the prey the parent consumed; 0-10%, 10-50% or 50-100%.

Prey body mass was estimated using the same methods as described by Bjørgeengen (2016). Gross body mass was used as a measure of an intact prey, while net body mass was used as a measure for decapitated fish. For further details on how prey body mass was estimated, see Hansen (2017).

Gross feeding time for one feeding bout was determined from the moment the feeding parent bent down to tear of the first piece until the prey was completely eaten or abandoned. Pauses lasting more than 5 s were recorded both in number and duration. If a pause lasted for more than 5 minutes (300 s) the following feeding was recorded as a new session. The total duration of a feeding bout minus the total duration of pauses was defined as net feeding time. If the prey item was abandoned before it was completely consumed, the percentage of prey eaten was roughly estimated. The ingestion rate as a measure of feeding efficiency was defined as net prey body mass (g) divided by net feeding time (s).

Some feeding sessions lacked complete recording, because the camera sensitivity was set too low and therefore stopped recording before the prey was completely eaten, or missed parts of feeding time during the sessions. These sessions were recorded as incomplete. On a few occasions, the camera sensitivity was too high, resulting in recordings without prey delivery or handling filling up the SD cards.

For the entire period, 272 prey deliveries were recorded at Isnes, and 107 deliveries were recorded at Skjeberg. Of all the prey deliveries, 142 deliveries at Isnes were used for feeding time analysis, while 59 deliveries at Skjeberg were used for feeding time analysis. Feeding time was estimated only when the nestlings were assisted by a parent. In addition, some recordings could not be analyzed for feeding time because the camera was out of position or excrements from the nestlings on the camera lens made it impossible to see the feeding behavior.

2.4 Statistical analyses

Statistical analyses were carried out in JMP Pro version 13.0 (SAS Institute, 2017). The standard criterion of statistical significance was set to $\alpha = 0.05$. All residuals were checked for normality. Estimates of mass and duration are presented as mean ± SE (standard error).

Difference in prey selection between the two nests

To test the difference in prey selection between the two nests, a contingency analysis and a likelihood ratio test were made for prey at family level, in order to include prey that could be determined to family level but not to species level. A contingency analysis and likelihood ratio test was also made to test for difference in habitat of prey delivered to the two nests, i.e. whether the prey item was a typical freshwater species or saltwater species.

Decapitation of prey

Because of small sample size for several prey families, only the five most common prey families were used in order to achieve statistically reliable data in all analyses including prey family as a variable. For the Isnes nest, the three most common prey families were used (Cyprinidae, Percidae and Esocidae) and for the Skjeberg nest only the two most common families (Pleuronectidae and Percidae) could be used. This also made it possible to include the 21 unidentified items from the flounder family (Pleuronectidae).

Contingency analysis and likelihood ratio tests were used to test the difference in probability of a prey being decapitated prior to delivery. To test the difference in the probability of a prey item being decapitated between the nests, deliveries by the female were excluded. Only the male delivered prey items at Skjeberg. To test the difference in probability of delivering decapitated prey between the sexes, only deliveries by the female and male at the Isnes nest were used.

To explore which other variables affected the likelihood of a prey being delivered decapitated, a Generalized Linear Model with decapitation as the response variable, and prey family, delivering parent, gross prey body mass, age of nestlings, locality, and their interactions was run. Backward elimination was used to remove insignificant variables with a p-value of over 0.05, starting with the least significant variable or interaction.

Feeding time

Feeding time analysis was only done for prey items where the nestlings were assisted by a parent. In all recordings of prey deliveries, prey handler was either categorized as parent or nestling, and the 50/50 switch, the point where likelihood of a nestling feeding unassisted or assisted is equal, was calculated by inverse prediction in a logistic regression model.
For feeding time analysis, General Linear Models were run separately for four different response variables, each with five explanatory variables and their interactions (Table 2). Stepwise backward elimination of insignificant variables was then performed resulting in a final model with parameter estimates of only significant explanatory variables. For feeding

time analysis, only complete recordings of completely eaten (100%) prey were used, thereby reducing sample size.

Table 2. Response variables and explanatory variables used in the models for feeding time analysis. All explanatory variables and their interactions were tested for each response variable.

Response variables	Explanatory variables
Gross feeding time	Prey family
Net feeding time	Net prey body mass
Total duration of pauses	Age of nestlings
Number of pauses	Sex of feeder
	Decapitation
	Interactions between all variables

Gross and net feeding time, total duration of pauses, gross and net prey body mass and ingestion rate were all $\log_{10}$-transformed in order to achieve normal distribution of the residuals.

3. Results

3.1 Prey selection

A total of 379 prey items were recorded during the entire period of video monitoring. Of these prey deliveries 201 were used for feeding time analysis (Table 3). Of these 201 prey items 167 were identified to species level, while 21 (10.4%) were identified to flounder (Pleuronectidae) family level, 8 (4.0%) to order level, and 5 (2.5%) could only be identified as fish. At the Isnes nest, freshwater bream was the most common prey species delivered, with 76 out of the 139 items used for feeding time analysis, and 139 items during the whole recording period. At the Skjeberg nest, flounders (Pleuronectidae) were by far the most common prey item delivered with 37 items out of the 60 items in total delivered used for feeding time analysis. Northern pike was the second most delivered species at Isnes, while perch was the second most delivered at Skjeberg. Perch was the only species delivered in larger numbers at both nests.

Table 3. Prey items used in feeding time analysis at the two osprey nests monitored.

	Number of prey items		Net prey body mass at delivery (g)		
Prey species	N	% of total	Average ± SE	Total mass	% of total
Freshwater bream (*Abramis brama*)	76	37.8	208.11 ± 29.7	15816.4	44.1
Northern pike (*Esox lucius*)	32	15.9	113.21 ± 33.2	3622.7	10.1
Perch (*Perca fluviatilis*)	28	13.9	173.89 ± 40.2	4868.9	13.6
European flounder (*Platichthys flesus*)	16	8.0	156.05 ± 51.5	2496.8	7.0
Roach (*Rutilus rutilus*)	4	2.0	57.77 ± 28.7	231.1	0.6
Trout (*Salmo trutta*)	4	2.0	136.86 ± 58.8	547.4	1.5
Common dace (*Leuciscus leuciscus)*	2	1.0	153.43	306.9	0.9
Atlantic mackerel (*Scomber scombrus*)	2	1.0	128.14 ± 61.7	256.3	0.7
Atlantic cod (*Gadus morhua*)	1	0.5	84.96	85.0	0.2
European seabass (*Dicentrarchus labrax*)	1	0.5	334.87	334.9	0.9
Zander (*Sander lucioperca*)	1	0.5	195.98	196.0	0.6
Unidentified flounder (*Pleuronectidae*)	21	10.5	338.67 ± 101.8	7112.07	19.8
Unidentified Gadiformes	4	2.0	-	-	-
Unidentified carp (Cypriniformes)	4	2.0	-	-	-
Unidentified fish	5	2.5	-	-	-
Total	201	100.0		35874.3	100.0

*body mass estimated with flounder coefficients

3.2 Difference in prey selection between the two nests

There was a significant difference in the taxonomic distribution of families between the two nests (Figure 2; Likelihood ratio test, N=193, df = 7, $\chi 2$ = 192.9, p = <0.0001). Flounders (Pleuronectidae) were most commonly delivered at the Skjeberg nest, while none were delivered at the Isnes nest during the period used for feeding time analysis (Figure 2). There was however one prey item likely to be a flounder recorded at the Isnes nest when the nestlings had fledged and prey was still delivered at the nest platform (See Appendix 2). Bream was by far the most common species delivered at Isnes, but was never recorded at Skjeberg. Of nine prey families, six were recorded at one nest and not at the other.

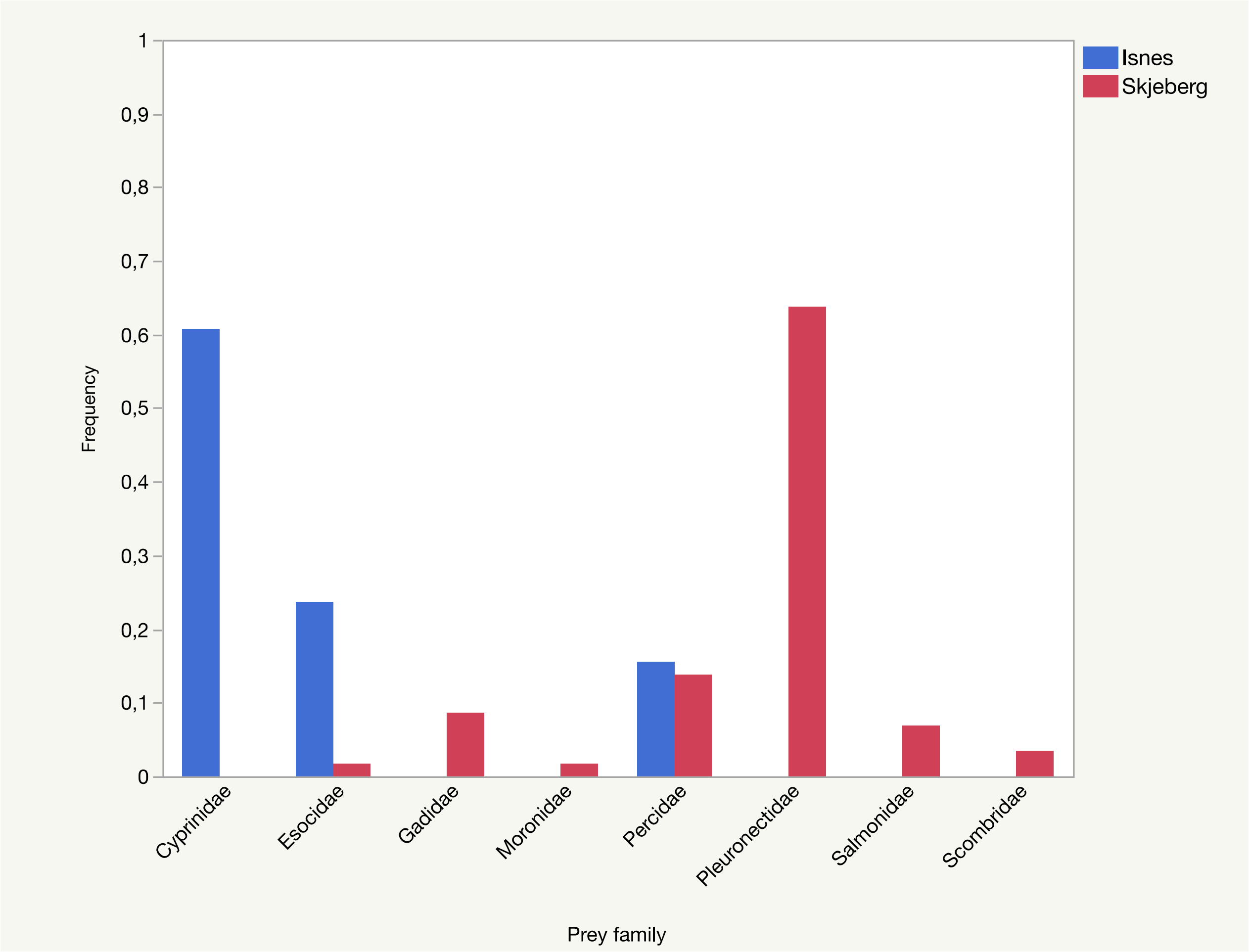

Figure 2. Frequency of prey types at family level delivered at the two osprey nests monitored. For Isnes N= 135, for Skjeberg N= 58. Prey items unidentified at family level are excluded.

There was a significant difference in habitats (saltwater or freshwater) of prey items delivered to the two osprey nests (Likelihood ratio test, N=194, $\chi2$=165.5, $p<0.0001$). Of prey items identified to the taxonomic level order at Skjeberg and used in feeding time analysis, 84% were typical saltwater species, while all prey items at Isnes were typical freshwater species.

Between the two nests, there was a significant difference in the probability of which parent delivered prey items (Likelihood Ratio Test, N = 201, $\chi2$ = 24.7, p = 0.0001). As judged from the video recordings used for feeding time analysis, the male delivered all the prey items at the Skjeberg nest, while the female delivered 23% of prey items and the male delivered 77% of prey items at the Isnes nest.

3.3 Decapitation of prey

Of all prey items used in the feeding time analysis 60% were decapitated prior to delivery. For both nests pooled, 45.0% of the prey items delivered by a male were decapitated. Among the females, only the one at Isnes delivered prey items, and among these only 12.5% were decapitated prior to delivery. There was a significant difference in the probability of a prey being decapitated between the males at the two nests (Figure 3; Likelihood ratio test, N = 169, df = 1, $\chi2$ = 4.40, p = 0.036), with the male at Skjeberg having a higher probability of delivering a decapitated prey. At Isnes the probability of delivering a decapitated prey was significantly higher for the male than the female (Figure 4; Likelihood ratio test, N = 142, df = 1, $\chi2$ = 8.90, p = 0.0027).

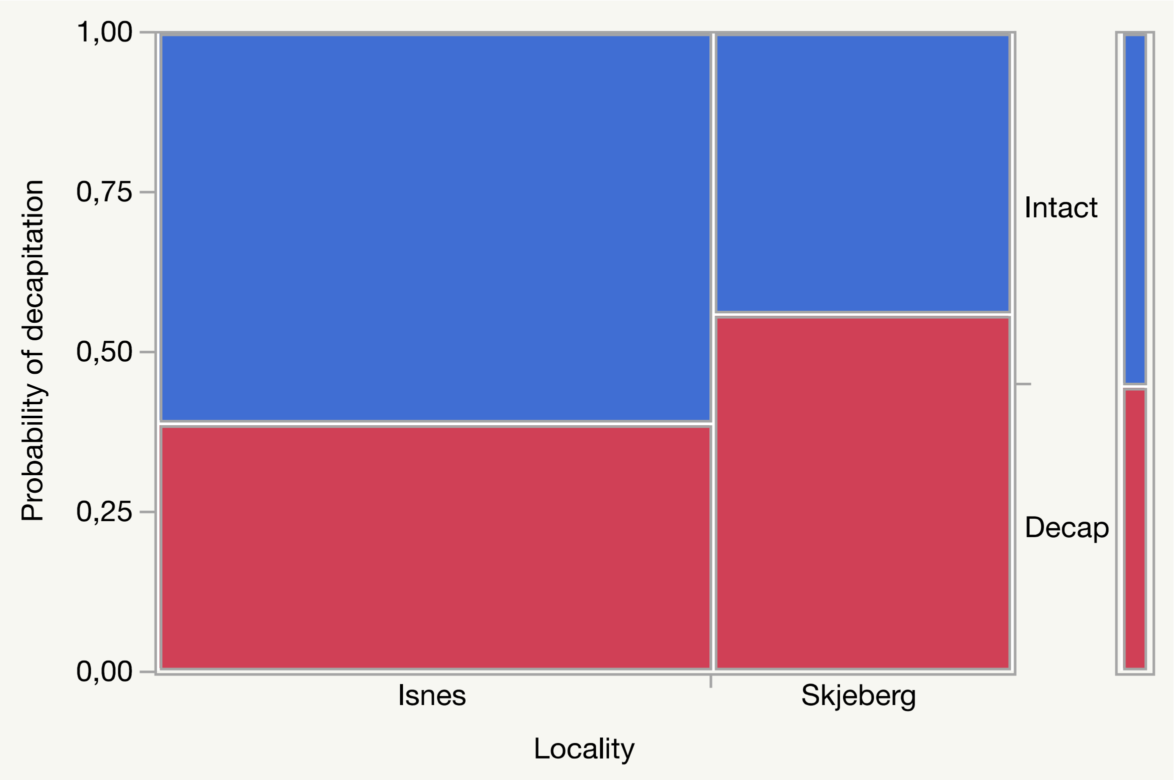

Figure 3. The probability that a prey captured by the male at the two osprey nests (Isnes and Skjeberg) was decapitated prior to delivery (N=169).

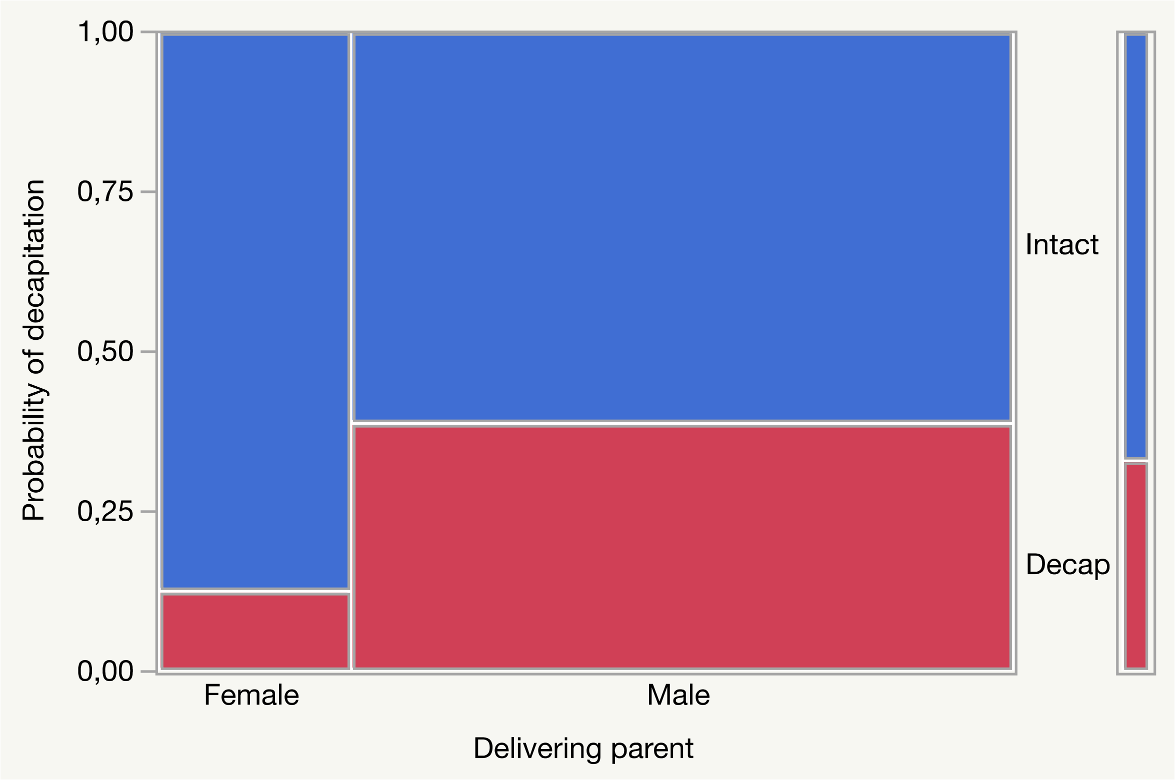

Figure 4. Probability of a prey being decapitated prior to delivery when delivered by the male and the female at the Isnes osprey nest (N=142).

There was a significant difference in the probability of decapitation prior to delivery between the prey families (Figure 5; Likelihood ratio test, N=181, df=3, $\chi2=24.89$, p=0.0001). 51.4% of flounders (Pleuronectidae) were delivered decapitated, 47.0% of carps (Cyprinidae) were delivered decapitated, while no more than 17.2% of perches (Percidae) and 9.4% of pikes (Esocidae) were delivered decapitated.

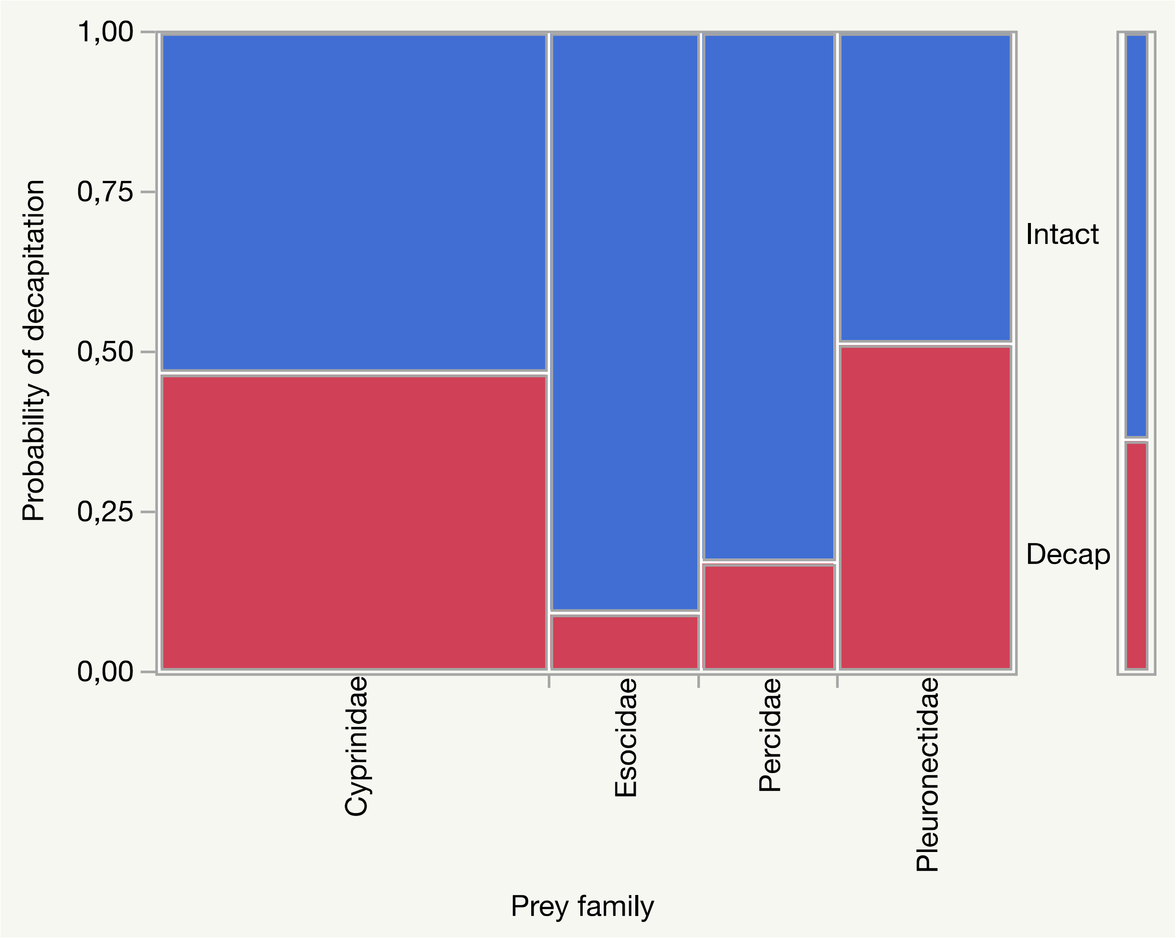

Figure 5. Probability of a prey being decapitated prior to delivery for the four most common fish families delivered at both osprey nests. N=181.

A Generalized Linear Model with decapitation as the response variable, and prey family, delivering parent, gross prey body mass, age of nestlings, locality, and their interactions, as explanatory variables, was run for both nests pooled (Table 4). The final model contained prey family and delivering parent as significant variables explaining the probability of decapitation. The female had a lower probability of delivering decapitated prey, while the lower probability of decapitated prey being delivered to the Isnes nest was marginally non-significant.

Table 4. Parameter estimates for the Generalized Linear Model of the probability of a prey item being decapitated prior to delivery for both osprey nests pooled. Pleuronectidae was selected as reference level for prey family. N=121.

Term	Estimate	SE	$\chi2$	p
Intercept	-4.428	1.90	5.44	0.0197
Prey family (Cyprinidae vs. Pleuronectidae)	1.764	0.59	9.09	0.0026
Prey family (Esocidae vs. Pleuronectidae)	-0.572	0.70	0.68	0.4111
Prey family (Percidae vs. Pleuronectidae)	-0.423	0.52	0.65	0.4198
Delivering parent (Female vs. male)	-1.411	0.46	9.24	0.0024
Locality (Isnes)	-0.922	0.51	3.21	0.0730
Gross prey body mass	1.004	0.71	2.00	0.1573
Locality*Gross prey body mass	1.370	0.70	3.79	0.0515

The interaction between locality and gross prey body mass was marginally non-significant. The interaction effect shows that prey items delivered at the Isnes nest had a significantly higher probability of being decapitated with increasing gross body mass (Figure 6a; N = 93, Estimate = 2.01, SE = 0.61, $\chi2$ = 10.72, p = 0.0011), while there was no significant effect of gross prey body mass on the probability of decapitation at the Skjeberg nest (Figure 6b; N = 35, Estimate = -0.2, SE = 0.98, $\chi2$ = 0.04, p = 0.83).

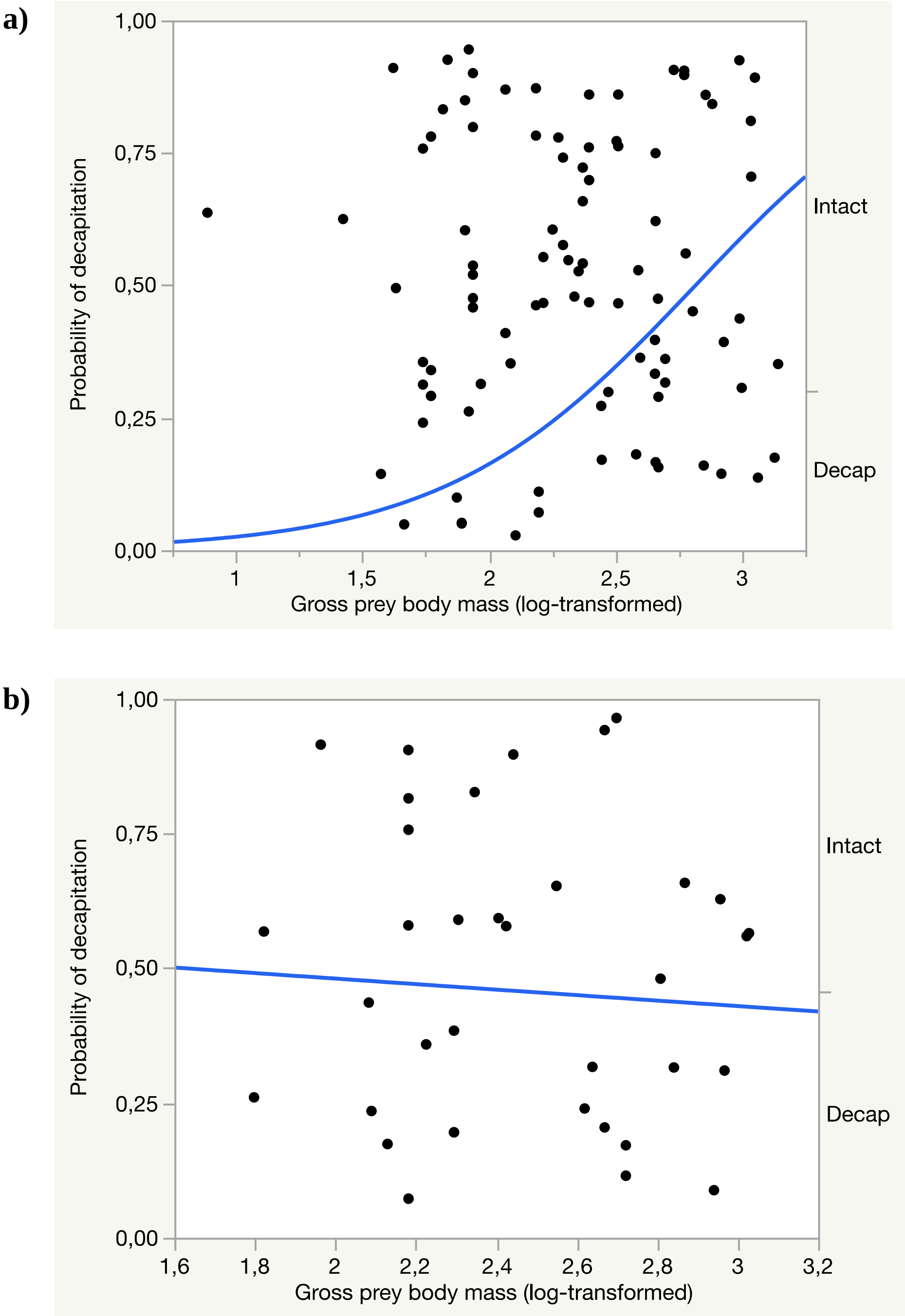

Figure 6. The probability of a prey item being decapitated prior to delivery as a function of gross prey body mass at **a)** the osprey nest in Isnes (N=93) and **b)** the osprey nest in Skjeberg (N=35).

In addition, the same model was also run for each nest separately. At the Isnes nest, carps had a significantly higher probability of being decapitated prior to delivery than perches (Table 5). Probability of decapitation also increased with increased prey body mass, and was higher when the male delivered the prey item than when the female did (Table 5).

Table 5. Parameter estimates for the Generalized Linear Model containing factors significantly affecting whether a prey item was delivered decapitated at the osprey nest in Isnes. N=93.

Term	Estimate	SE	$\chi 2$	p
Intercept	-8.268	2.161	14.64	0.0001
Prey family (Cyprinidae vs. Percidae)	1.538	0.493	9.73	0.0018
Prey family (Esocidae vs. Percidae)	-1.285	0.753	2.91	0.0881
Gross prey body mass ($\log_{10}$-transformed)	2.339	0.806	8.42	0.0037
Delivering parent (Female vs. male)	-1.402	0.463	9.17	0.0025

At the Skjeberg nest, delivering parent was not included in the full model as only the male provided prey to the nest. None of the variables had a significant effect on the probability of a prey item being delivered decapitated at the Skjeberg nest (N=28).

In addition, a model with decapitation as the response variable and nestling age as the explanatory variable was run to test whether the male at the Skjeberg nest changed the frequency of delivery of decapitated prey after the female disappeared. There was no significant difference in probability of decapitation with increasing nestling age (Generalized Linear Model, estimate = -0.01, SE = 0.04, $\chi 2$ = 0.09, p = 0.78).

3.4 Feeding time

Feeding time analysis was only done for prey items where the nestlings were assisted by a parent. The probability of a nestling feeding unassisted increased with age (Figure 7; N = 335, df = 1, $\chi 2 = 67.6$, $p < 0.0001$). The 50/50 switch, the point where the likelihood of a nestling feeding unassisted or assisted is equal, was estimated to occur when the nestlings were 50 days old (CI = 48.5, 51.8).

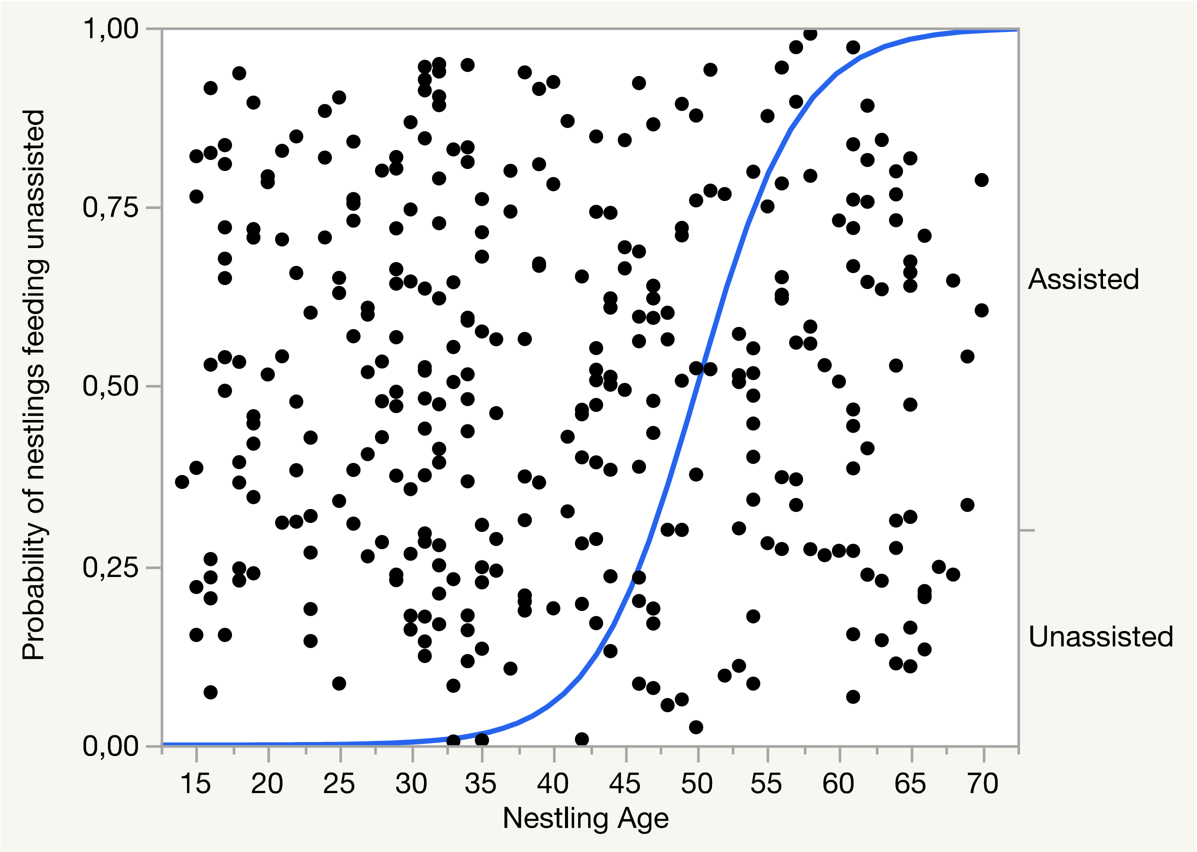

Figure 7. The probability of rather than being fed by a parent, a nestling handling a prey item unassisted as a function of nestling age for both osprey nests pooled (N=335).

The total estimated gross body mass of all prey items that could be measured and used for feeding time analysis was 45,274 g (see Appendix 2 for all delivered prey during the whole recording period), while the total estimated net body mass of these prey items, i.e. the weight of the prey item when delivered at the nest, was 35,874 g. The mean gross body mass of a prey item used in feeding time analysis was 353.7 ± 28.4 g (range 7.7 g – 1388.1 g). The mean net body mass of a prey item used in feeding time analysis was 281.0 ± 23.0 g (range 7.7 g – 1124.0 g). The mean net feeding time was 1611.0 ± 103.7 s, i.e. c. 27 minutes. The overall mean total duration of pauses in feeding per prey item was 67.7 ± 7.3 s. The mean number of pauses during a feeding bout was 3.7 ± 0.3. Mean duration per pause was 18.3 s. Mean gross feeding time per prey item was thus 1678.7 ± 108.0 s, i.e. c. 28 minutes.

The feeding parent always fed itself during a feeding bout, most of the time consuming an estimated <10% of the prey. Only once did a parent eat more than 50% of the prey itself. There was a significant difference between the nests in the sex of the parent assisting the nestlings (Likelihood ratio test, N= 201, $\chi2= 30.31$, $p <0.0001$). At Isnes the female assisted the nestling in 98 % of the feeding sessions, while the male assisted in 2% of the feeding sessions. At Skjeberg, the female assisted nestlings in 71% of the feeding sessions, while the male assisted in 29% of the feeding sessions.

3.4.1 Feeding time at the Skjeberg nest

Due to the disappearance of the female at the Skjeberg nest, the male started to feed the nestlings from 6 July, when the nestlings were approximately 42 days old. A model containing prey family, feeding parent, decapitation, net body mass, age of nestlings and their interactions, as variables explaining net feeding time was run. Only feeding parent and prey mass were significant variables explaining net feeding time (Table 6). The male used shorter time to feed the nestlings than the female for a prey item the same estimated net body mass (Table 6; figure 8). A model with the same variables were run with gross feeding time as response variable, yielding similar results with a slight increase in p-value for sex of feeder (Table 7; figure 9).

Table 6. Parameter estimates for the Generalized Linear Model of factors significantly affecting net feeding time (s, $\log_{10}$-transformed) at the osprey nest in Skjeberg (N=24).

Term	Estimate	SE	t	p
Intercept	2.683	0.279	9.61	<0.0001
Net prey body mass($\log_{10}$-transformed)	0.273	0.119	2.31	0.031
Sex of feeder	0.141	0.062	2.27	0.034

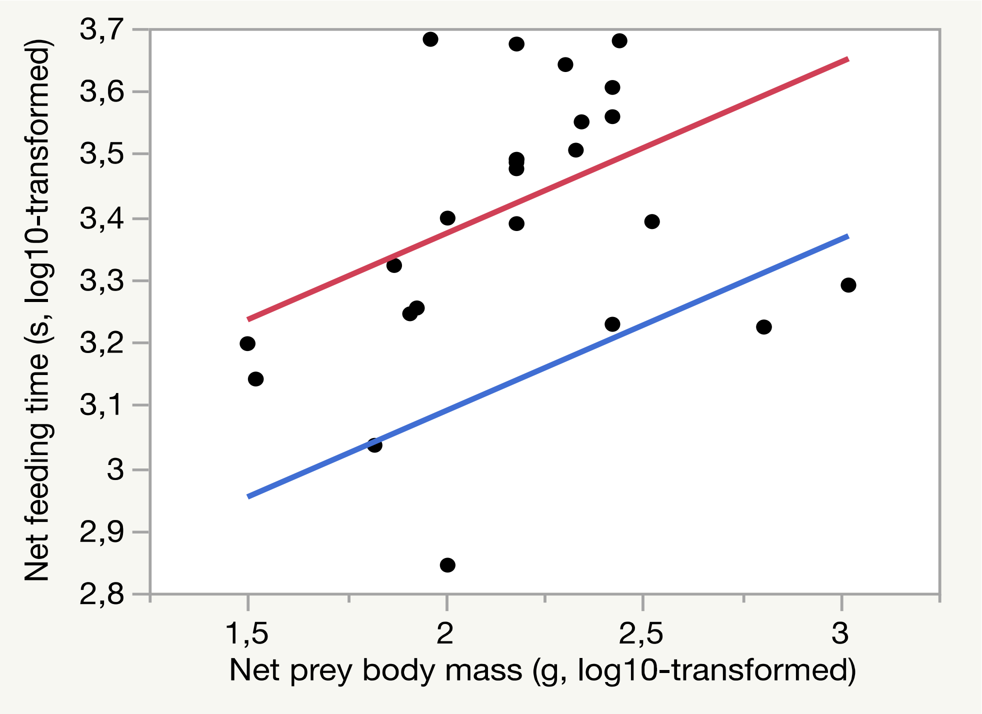

Figure 8. Net feeding time as a function of net prey body mass when nestlings were fed by the female (red line) and by the male (blue line) at the osprey nest in Skjeberg (N=24).

Table 7. Parameter estimates for the Generalized Linear Model of factors significantly affecting gross feeding time (s, $\log_{10}$-transformed) at the osprey nest in Skjeberg (N=24).

Term	Estimate	SE	t	p
Intercept	2.717	0.276	9.83	<0.0001
Net prey body mass ($\log_{10}$-transformed)	0.269	0.117	2.29	0.032
Sex of feeder	0.129	0.062	2.10	0.048

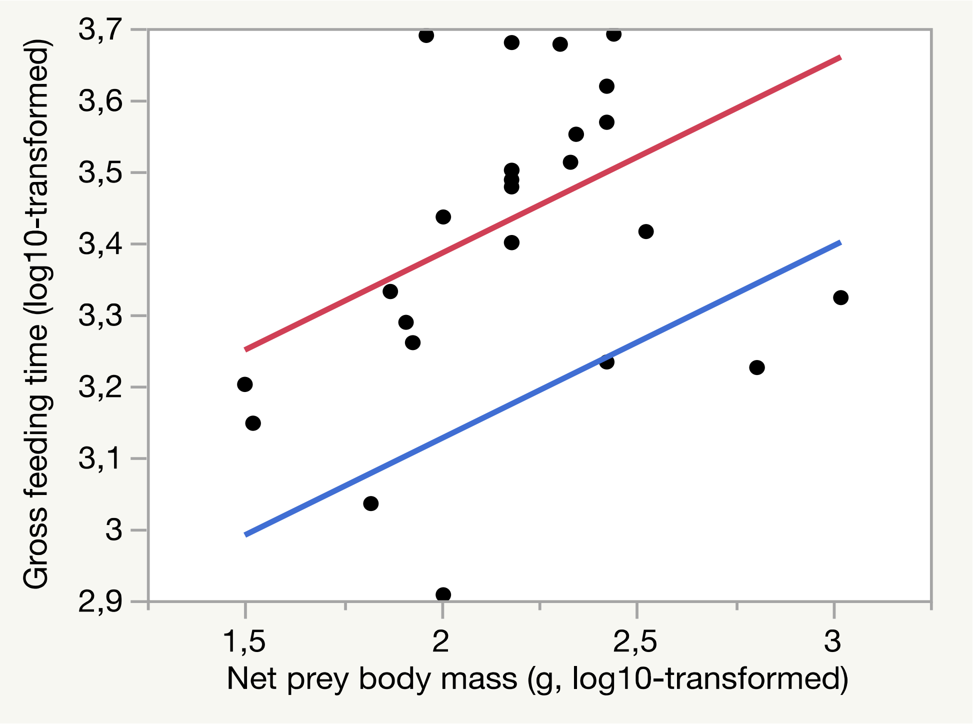

Figure 9. Gross feeding time as a function of net prey body mass when nestlings were fed by the female (red line) and by the male (blue line) at the osprey nest in Skjeberg (N=24).

3.4.2 Feeding time at the Isnes nest

For the Isnes nest, a model containing prey family, age of nestlings, decapitation and their interactions as explanatory variables was run for net feeding time. Net feeding time increased significantly with increasing prey mass and was lower for decapitated prey than intact prey. Feeding time marginally non-significantly decreased for carps (Cyprinidae) compared to perches (Percidae). The interaction between decapitation and carps (Cyprinidae) had a significant effect on net feeding time. The same model was run for gross feeding time, and the same variables were also significant here (Table 9).

In this model, one pike was excluded because its body mass was likely very underestimated. The pike excluded was estimated to have a net prey body mass of 7 g, while the female used 270 s to feed it, making it an outlier.

Table 8. Parameter estimates for the Generalized Linear Model of factors significantly affecting the net feeding time (s, $\log_{10}$-transformed) at the osprey nest in Isnes (N=78).

Term	Estimate	SE	t	p
Intercept	1.534	0.163	9.42	<0.0001
Prey family (Cyprinidae vs. Percidae)	-0.103	0.053	-1.94	0.056
Prey family (Esocidae vs. Percidae)	0.026	0.082	0.32	0.749
Decapitation	-0.164	0.049	3.37	0.001
Net prey body mass ($\log_{10}$-transformed)	0.700	0.070	9.96	<0.0001
Prey family(Cyprinidae)*Decapitation	-0.184	0.053	-3.48	0.0009
Prey family(Esocidae)*Decapitation	0.033	0.089	0.40	0.688

Table 9. Parameter estimates for the Generalized Linear Model of factors significantly affecting the gross feeding time (s, $\log_{10}$-transformed) at the osprey nest in Isnes (N=78).

Term	Estimate	SE	t	p
Intercept	1.504	0.164	9.20	<0.0001
Family (Cyprinidae vs. Percidae)	-0.103	0.053	-1.94	0.057
Family (Esocidae vs. Percidae)	0.018	0.082	0.22	0.824
Decapitation	-0.168	0.049	-3.45	0.001
Net prey body mass ($\log_{10}$-transformed)	0.704	0.071	9.98	<0.0001
Family(Cyprinidae)*Decapitation	-0.186	0.053	3.50	0.0008
Family(Esocidae)*Decapitation	-0.029	0.082	-0.35	0.724

The interaction between prey family and probability of decapitation significantly affected feeding time only for carps (Cyprinidae). Net feeding time was shorter for decapitated prey than for intact prey, while the opposite was the case for large carps (mainly bream) (table 10; figure 10). Large decapitated carps took longer to feed than intact carps, while small decapitated carps took shorter to feed than intact carps. The same was true for gross feeding time (table 11; figure 11).

Table 10. Parameter estimates for the Generalized Linear Model of factors significantly affecting net feeding time in carps (Cyprinidae) at the osprey nest in Isnes. N=42.

Term	Estimate	SE	t	p
Intercept	1.251	0.170	7.35	<0.0001
Net prey body mass ($\log_{10}$-transformed)	0.762	0.072	10.52	<0.0001
Decapitation	-0.015	0.029	-0.52	0.61
Net prey body mass*Decapitation	-0.236	0.072	-3.27	0.002

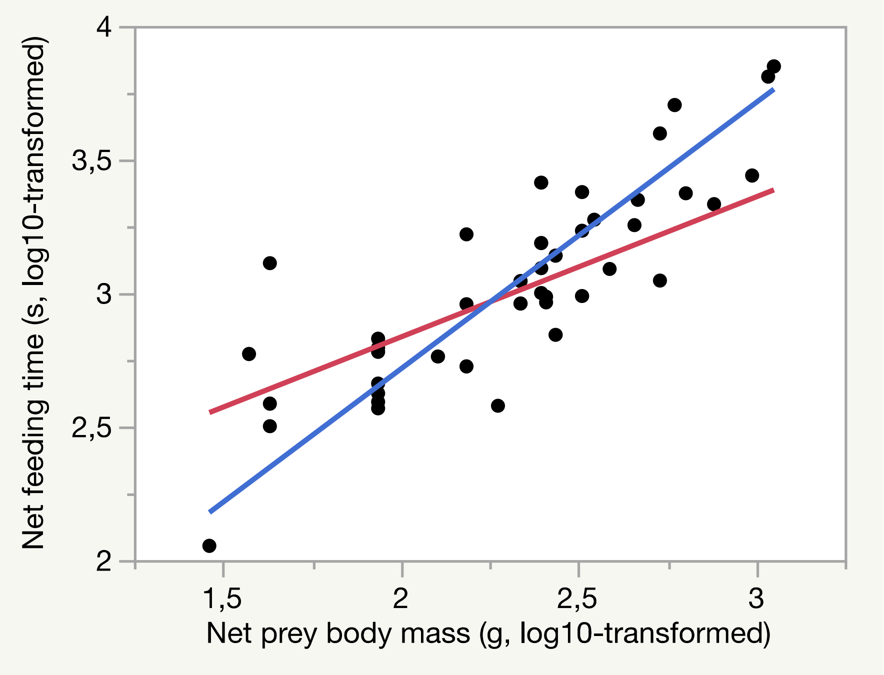

Figure 10. Relationship between net feeding time and net prey body mass for decapitated carps (blue line) and intact carps (red line) at the osprey nest in Isnes.

Table 11. Parameter estimates for the Generalized Linear Model of factors significantly affecting gross feeding time (s, $\log_{10}$-transformed) in carps (Cyprinidae) at the osprey nest in Isnes. N=42.

Term	Estimate	SE	t	p
Intercept	1.294	0.173	7.50	<0.0001
Net prey body mass ($\log_{10}$-transformed)	0.752	0.073	10.25	<0.0001
Decapitation	-0.017	0.029	-0.57	0.57
Net prey body mass*Decapitation	-0.227	0.073	-3.09	0.004

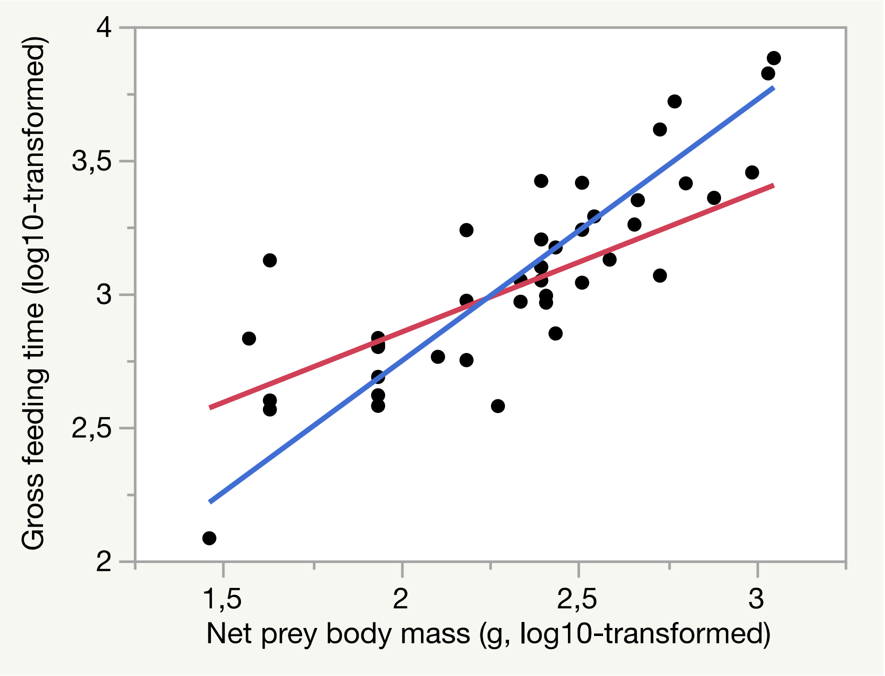

Figure 11. Relationship between gross feeding time and net prey body mass for decapitated carps (blue line) and intact carps (red line) at the osprey nest in Isnes.

3.5 Ingestion rate

The ingestion rate, i. e. the efficiency of the parent feeding the nestlings measured in g/s, increased with increasing net body mass of the prey item for both nests pooled and all prey families (Figure 12). Mean ingestion rate was 0.18 ± 0.01 g/s (N=102).

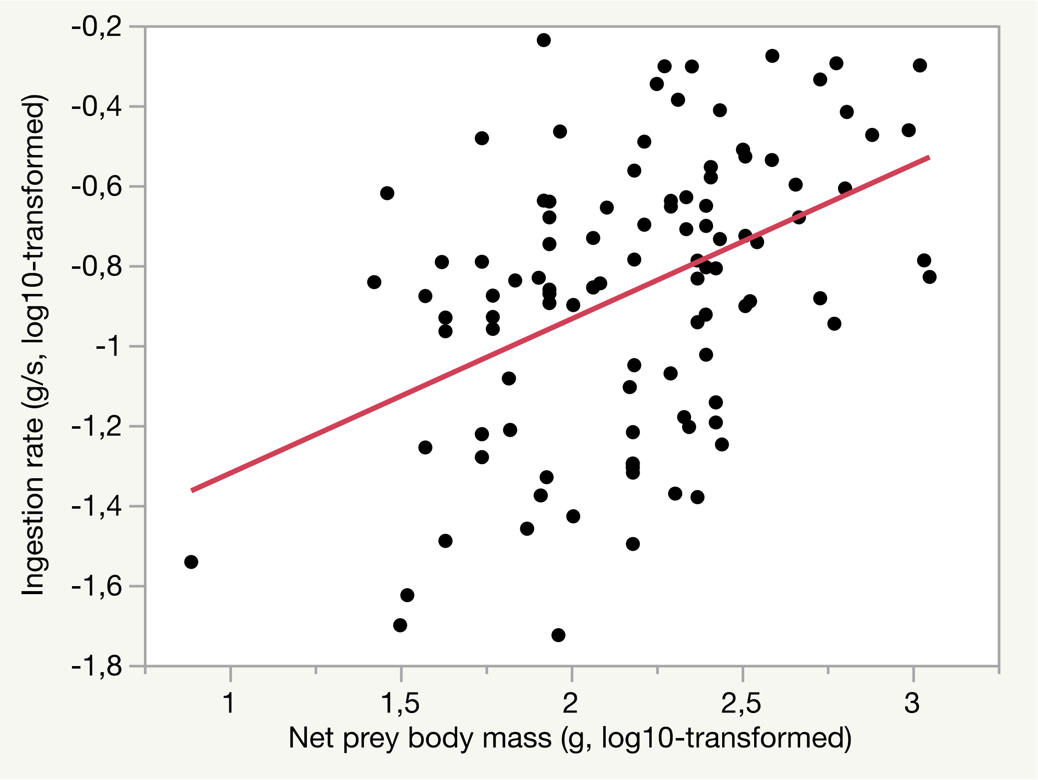

Figure 12. Ingestion rate (g/s) in relation to net prey body mass for both osprey nests pooled. N=84.

3.6 Number and duration of pauses

Two Generalized Linear Models containing sex of feeder, net prey body mass, whether the prey item was decapitated prior to delivery or not, prey family, and their interactions, as explanatory variables were run for both nests with number of pauses and duration of pauses as response variables. Net prey body mass was the only variable significantly affecting number of pauses (N=102, SE= 0.758, p=0.0001; table 12; figure 13). Number of pauses increased with increasing net prey body mass.

Table 12. Parameter estimates for a Generalized Linear Model of the effect of net prey body mass (g, $\log_{10}$-transformed) on number of pauses during a feeding bout at both osprey nests pooled. N=102.

Term	Estimate	SE	t	p
Intercept	-4.599	1.679	-2.74	0.007

Net prey body mass (log$_{10}$--transformed)	3.765	0.758	4.96	<0.0001

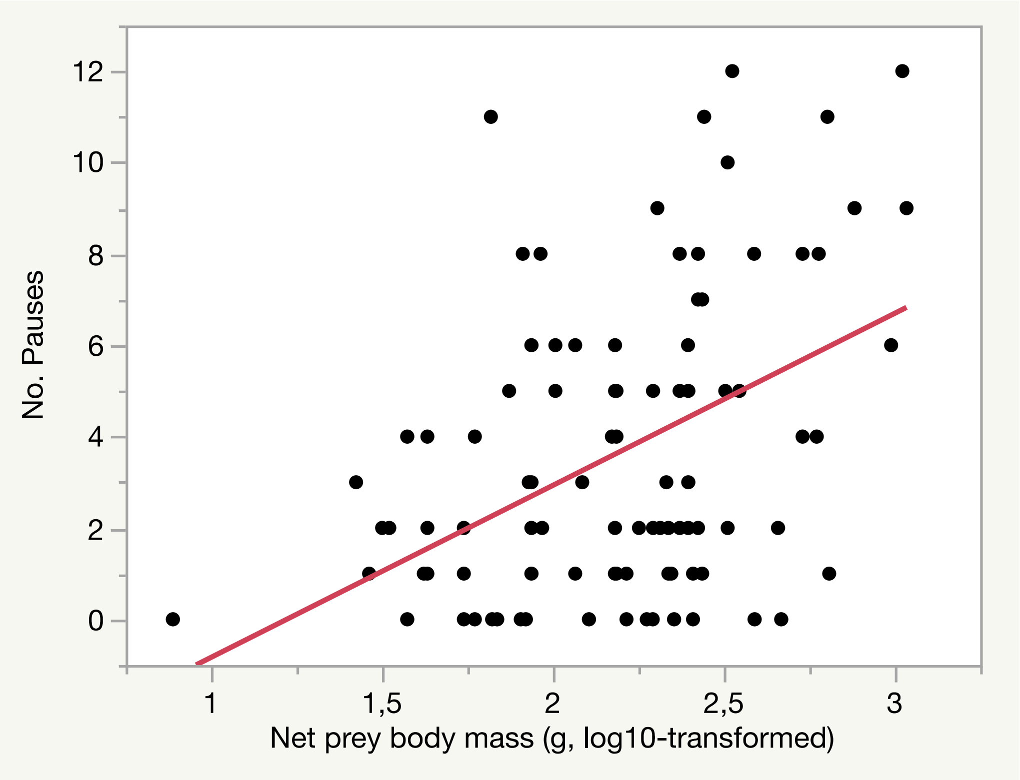

Figure 13. Number of pauses during one feeding bout as a function of net prey body mass at both osprey nests pooled.

Net prey body mass was the only variable significantly affecting the total duration of pauses. The total duration of pauses increased with increasing net prey body mass (Table 13; figure 14).

Table 13. Parameter estimates for a Generalized Linear Model of the effect of net prey body mass (s, log$_{10}$-transformed) on total duration of pauses during a feeding bout at both osprey nests pooled. N=84.

Term	Estimate	SE	t	p
Intercept	0.541	0.292	1.86	0.07
Net prey body mass (log$_{10}$-transformed)	0.493	0.129	3.83	0.0002

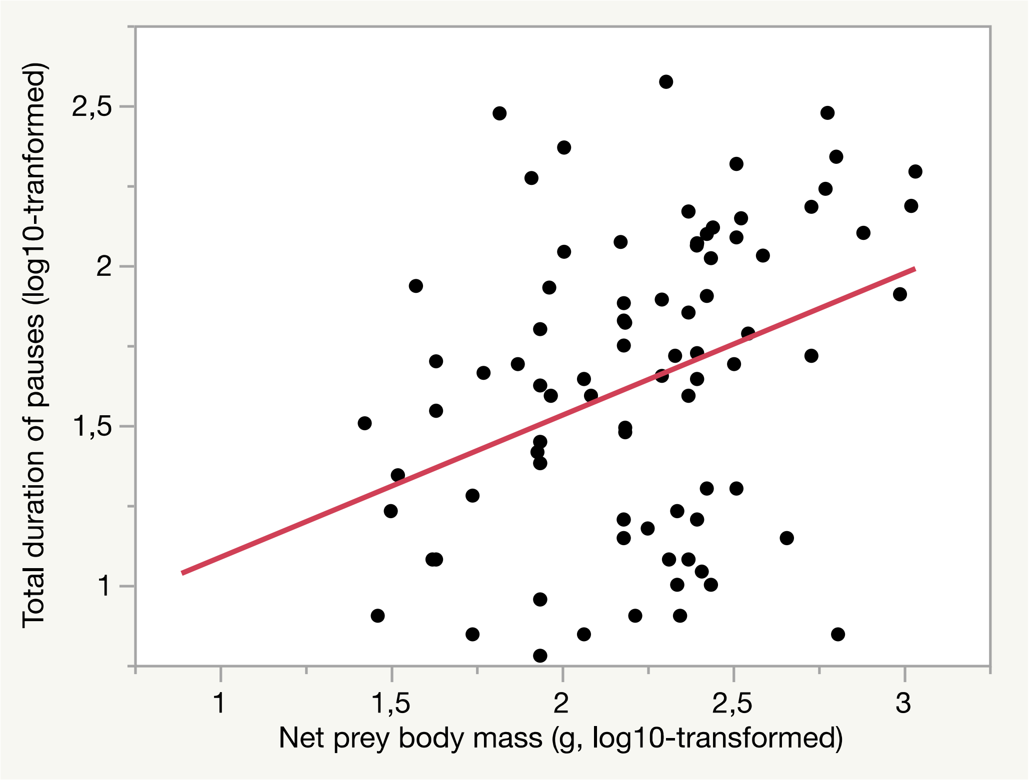

Figure 14. Total duration of pauses during one feeding bout as a function of net prey body mass at both osprey nests pooled.

4. Discussion

4.1. Prey selection

There was a distinct difference in prey selection between the two osprey nests. Bream was the most frequently delivered prey species at the Isnes nest, while flounders were the most important prey family delivered at the Skjeberg nest. It is likely that most of the flounders only identified to the taxonomic level family also were of the species European flounder, but determining species of these prey items with certainty was not possible. Thus, the majority of the flounders was only determined to the taxonomic level family. Among prey delivered, only two prey families were represented at both nests, namely pikes and perches. Most pikes were delivered at the Isnes nest, and only perches were delivered in larger numbers at both nests. Six prey families were recorded at one nest and not the other. In addition, all prey items delivered in the recordings used for the feeding time analysis at the Isnes nest were typical freshwater species, while 84% of prey items delivered at the Skjeberg nest were typical saltwater species.

This difference in prey selection was likely due to the proximity to saltwater and freshwater fishing localities. The Skjeberg nest was located c. 250 m from salt water and c. 9 km from nearest freshwater lake Isesjøen, while the Isnes nest was located right next to the freshwater lake Vestvannet, and 14 km away from nearest saltwater fishing locality. The hunting range for male ospreys is assumed to expand up to 10-20 km away from the nest (Cramp, 1979), and the male at Skjeberg had freshwater localities more closely available than the male at Isnes had saltwater localities. This also corresponds well with the findings by Bjørgeengen (2016), where saltwater species were the main prey items delivered at nests close to saltwater fishing localities, and freshwater species were most frequently delivered at nests closest to freshwater fishing localities. This suggests a functional response, supported by the fact that ospreys are opportunistic predators and previous studies showing that ospreys select the most abundant prey type (Cramp, 1979; Francour & Thibault, 1996).

The Isnes nest was also monitored by Bjørgeengen (2016) in the year prior to my study, showing a very similar prey species selection with bream being the most commonly delivered prey species. In study by Bjørgeengen (2016), flounder made up more than 60% of the total amount of delivered prey at the nest located closest to the sea (1.5 km). This is similar to the Skjeberg nest, where flounders made up 64 % of the prey items that were delivered. Previous studies conducted by analysis of prey remains have also shown similar results, with bream making up most of the diet of inland ospreys (Hagen, 1952; Häkkinen, 1978), although these studies provided a more uncertain estimate of prey selection as certain types of prey will leave more remains than others, which may lead to overestimating their proportion in the diet. Large prey will also leave more prey remains than small prey, thus increasing the risk of overestimating prey mass (Tornberg & Reif, 2007).

The mean net prey body mass of a prey item delivered at the nests was 281 g. This is very similar to the reported average of 293 g by Bjørgeengen (2016). Häkkinen (1978) estimated average gross prey body mass to be between 150 g and 300 g, while Nordbakke (1974,1980) reported an average gross prey body mass of 200-300 g. The estimates done by prey remain analysis does not take potential decapitation into account, but are still somewhat lower than the estimated net prey body mass in my study. This discrepancy might be due to a of difference in prey selection, as the most frequent prey types delivered at the nests in my study, breams and flounders, have generally large body mass. Additionally, as previously mentioned, estimating body mass from prey remains is more prone to inaccuracies (Slagsvold, Sonerud, Grønlien, & Stige, 2010). To the best of my knowledge, estimating prey body mass by video recording analysis has not been done in many predominantly fish-eating raptors. Eriksen (2016) reported an average net prey body mass of 425 g per prey item delivered to nests of White-Tailed eagles (*Haliaeetus albicilla*), with fish constituting 74 % of the diet.

It is important to note that the data on prey selection in this study is derived only from recordings used for feeding time analysis, and not all prey items delivered for the whole season. This may produce a skewed distribution of prey species and mass and should be interpreted with caution. However, the similarity in mean estimated prey body mass and prey species selection between my study and Bjørgeengen (2016) suggests that the prey items used for feeding time analysis represents the whole dataset quite well.

4.2. Decapitation

There was a dissimilarity in factors explaining decapitation prior to delivery between the two osprey nests. At Isnes, the probability of decapitation was higher for carps, increased with increasing prey body mass, and was higher for items delivered by the male than by the female. At the Skjeberg nest, there was no relationship between the probability of decapitation and any of the explanatory variables.

That the male at Isnes had higher probability of delivering a decapitated prey than the female is likely due to the role of the male, which mainly is to provide prey to the female and nestlings, a time-consuming task. Preparation of the prey item, e.g. decapitation, can be favorable in several ways (Rands et al., 2000). Removal of less profitable parts of the prey reduces the mass of the prey item, thereby reducing energy costs of transportation. When provisioning for the female and nestlings, it may also be favorable for the male to consume parts of the prey prior to delivery in order to reduce the time needed to forage for himself (Steen et al., 2010). The female at Isnes delivered only 12.5% of prey decapitated. If the reason for decapitation is to eat a portion of the prey to reduce foraging time, then this could explain why the female rarely delivered decapitated prey, as most of the prey items were delivered to her by the male. Because the male was the main provider of prey items, the female rarely hunted and was thus not as time-restricted when foraging as the male. Additionally, as noted by Bjørgeengen (2016), the nest at Isnes was situated in a Scots pine partially leaning over the edge of the lake Vestvannet. This may have enabled the female to observe prey from the nest platform itself and dive directly down to capture it. Since decapitation is likely to happen at the capture site (Newton, 1979), this might be the reason why prey captured close by the nest by the female would be delivered intact.

The possible desertion or death of the female at Skjeberg provided a basis for a natural experiment, because the role of the male changed from provider of prey to both provider and feeder of prey to the nestlings. Considering his role as both provider and feeder, one may assume that he would fly directly to the nest with the prey and not fly to another perching spot and eat the head of the prey item first, since he would have to feed the nestlings anyway. However, the male at Skjeberg delivered more decapitated prey than the male at Isnes. In addition, there was no negative change in probability of decapitation after the female disappeared. This suggests that no adjusting mechanism for decapitation has evolved in the male osprey as a response to female disappearance.

At the Isnes nest, there was a relationship between the probability of decapitation and prey body mass, with a higher probability of a prey item being delivered decapitated with increasing gross prey body mass. However, there was no such relationship between the probability of decapitation and gross prey body mass at the Skjeberg nest. An increase in the probability of a prey item being delivered decapitated with increasing prey body mass has previously been documented in raptors such as the peregrine falcon (*Falco peregrinus*) and Eurasian kestrel (Steen et al., 2010; Bech, 2016), in addition to the ospreys studied by Bjørgeengen (2016). This is in concurrence with the feeding constraint hypothesis, as larger prey items are more difficult to swallow, and therefore should be decapitated. However, since ospreys tear off small morsels and feed the nestlings, the gape size constraint is probably not applicable to this species when the nestlings are assisted by a parent.

Flounders were most commonly delivered decapitated at the Skjeberg nest, which was the only nest where flounders were delivered. Flounders are generally large prey items, and as the relationship between the probability of decapitation and prey body mass has been documented previously (Steen et al., 2010), one would expect that flounders were delivered decapitated more frequently because of their large size. However, there was no relationship between prey body mass and probability of decapitation for prey delivered to the Skjeberg nest, neither for flounders specifically. Another possible explanation is that only the male delivered prey at the Skjeberg nest, and since he delivered decapitated prey more frequently than the male at Isnes, the frequency of decapitation would also be higher in flounders. The lack of relationship between prey body mass and probability of decapitation at the Skjeberg nest does not support the feeding constraint hypothesis. However, the sample size for prey deliveries at Skjeberg is relatively small due to several periods of camera malfunction. This may be the reason for the failure to find variables explaining the probability for decapitation at the Skjeberg nest.

Carps, mainly bream, were most frequently delivered decapitated at the Isnes nest. This is likely because carps were generally larger than pikes and perches (Nielsen, 2011), and because the probability of decapitation increased with increasing prey body mass at the Isnes nest.

4.3. Feeding time

The switch, i.e. the age when the nestlings were predicted to handle 50% of the delivered prey themselves, occurred when they were 50 days old for all nestlings at both nests. This is similar to what Bjørgeengen (2016) found for ospreys in the same area the year prior to my study, where the switch was estimated to occur when nestlings were 51 days old. In comparison to other raptors (Sonerud et al., 2014a), the switch is relatively late, but similar to the 53 day switch previously found in white-tailed eagles (Eriksen, 2016).

I noted that the female at Isnes continued to feed the nestlings when they seemed able to handle prey items themselves. This is similar to what Bjørgeengen (2016) found, and may suggest a family conflict between the parent and nestlings. Throughout the period when the nestlings were dependent on a parent for feeding assistance, the female distributed the delivered prey items between herself and the nestlings, usually consuming about 0-10% of the prey item. The female's behavior with continued feeding after the nestlings were able to feed unassisted may suggest a female strategy of exploiting the food delivered by the male, as well as controlling the allocation of food between herself and the nestlings (Sonerud et al., 2013).

At the Skjeberg nest, the female fed the nestlings in 71% of the assisted feeding sessions. Since she disappeared before the nestlings were able to feed unassisted (see below), I do not deem it likely that this is typical for ospreys, which previously have been documented to have strongly divided parental care tasks where the male rarely assists nestlings with feeding (Cramp, 1979; Bjørgeengen, 2016). At Isnes however, the female assisted the nestlings in 98% of the assisted feeding bouts. During the period when nestlings needed assistance with feeding, a mean of 4 prey items were delivered to the nest per day. With an average gross feeding time of 1,678 s per prey item, the female was confined to the nest for nestling feeding approximately 8,390 s, or 2 hours and 19 minutes per day. For the first part of this period the female was also confined to the nest for protection and thermoregulation of the nestlings, but even when the nestlings no longer depended on the female, she was nearly always present in the nest or perching close by (pers. obs). This is time that could have been used for hunting and foraging, but instead it may indicate that the female utilizes the prey delivered by the male, thereby decreasing her own energy expenditure. This may suggest a sexual conflict between the male and female. In species with prolonged parental investment from both the male and the female, each sex has the possibility to exploit the resources of the other (Davies et al., 2012). Sonerud et al. (2013) suggested that the male in Eurasian kestrels could resolve this conflict by selectively allocating smaller prey to nestlings that were able to feed unassisted, leaving the female with less control over food allocation. Since my study only focused on prey delivery and feeding time during the period when the nestlings had to be assisted in feeding, I cannot compare my data with that of Sonerud et al. (2013). However, a study to investigate if similar strategies occur in ospreys would be interesting for the future.

Overall, there was a strong positive correlation between feeding time and prey body mass. Similar results have been shown in previous raptor feeding time studies when nestlings were fed assisted (Løw, 2006; Skouen, 2012; Fosså, 2013; Bech, 2016). Larger prey items would take longer to dismember and eat. Additionally, larger prey items have larger bones and more rigid ligaments, requiring more effort to prepare and dismember to appropriately sized pieces to feed nestlings (Slagsvold & Sonerud, 2007).

At Isnes, decapitation of prey items also reduced feeding time for perches, pikes and small carps. This has also been documented previously in Eurasian kestrels (Løw, 2006), and is in ospreys likely due to the removal of the bony fish head. If fish were delivered intact, dismembering the head would take up a substantial amount of the feeding time (pers. obs.). The female at Isnes used shorter time to feed the nestlings a carp than a perch with the same prey mass. This might be explained by the perches' spikes and rough skin (Nielsen, 2011), making it harder to dismember than a carp.

At Isnes, the relationship between feeding time and prey body mass was dependent on decapitation, but only for carps. The female spent more time to feed small intact carps than small decapitated carps of the same size. However, large intact carps were consumed faster than decapitated carps. It is difficult to suggest an explanation as to why this relationship shifts at a certain body mass, as removal of the bony structured head should make the meat more easily accessible and therefore reduce feeding time. One possible explanation is that the removal of the head has a larger effect on feeding time for small prey items, and large prey items already take a substantial amount of time to consume, thereby reducing the effect of decapitation. In addition, the prey body mass could have been incorrectly estimated, and this error may have increased with increasing weight of the decapitated prey.

At Skjeberg, the relationship between feeding time and prey body mass differed between the male and the female. The male spent less time feeding a prey item of a given mass than the female. Since ospreys have evolved very sex specific parental tasks, one could assume that the female, usually the sole feeder of the nestlings, would assist more efficiently than the male for a prey with a given mass. However, of the seventeen prey items that the male fed the nestlings only five were completely consumed, while the rest were abandoned half eaten. One possibility is that the male, not being selected for feeding nestlings, simply gave up on most attempts of feeding the nestlings. The five completely consumed prey items might have been easier to handle and prepare, and thus the male continued to feed these items to the nestlings until they were completely ingested.

Interestingly, the age of nestlings did not have an effect on feeding time in any of the models. This suggests that the parents did not adjust the bite size or feeding efficiency to the growing nestlings. Previous studies of feeding time in raptors have yielded similar results, with no effect of age of nestlings on feeding time (Løw, 2006; Bech, 2016), although one study on golden eagles (*Aquila chrysaetos*) showed a significant decrease in feeding time with increasing nestlings age (Skouen, 2012). When observing the parent osprey dismembering a prey item and feeding it to the nestlings, I noted that the pieces were almost always roughly of the same size. The explanation for this could be that due to the relatively high proportion of small bones in fish, it is difficult to tear of large pieces of flesh in one go. Thus, the feeding parent may not have adjusted bite size when the nestlings grew because it would have been too difficult to do so. However, to further investigate this, studies of feeding time in ospreys should also include number and size of morsels fed to the nestlings.

4.4 Possible desertion or death of the female at the Skjeberg nest

The female at Skjeberg did not appear at the nest in recordings after 30 June. She might have died or deserted. The nestlings were approximately 42 days old when she disappeared, and not yet able to completely consume prey without assistance. This prompted the male to start feeding the nestlings in addition to providing prey. However, ospreys exhibit strongly divided parental roles and at the Isnes nest where the female was present during the whole recording period, the male only fed the nestlings in 2% of the feeding sessions. Most of the prey items the male assisted with were not completely consumed, leading to a buildup of prey remains in the nest.

Female desertion in raptors with biparental care has previously been documented (Beissinger & Snyder, 1987; Eldegard & Sonerud, 2009). Desertion by the female has been found to be positively correlated with food abundance in Tengmalm’s owl (*Aegolius funereus*) (Eldegard & Sonerud, 2009). However, raptors preying on mammals and certain bird species are subject to large fluctuations in prey populations and thus food abundance, while ospreys almost exclusively prey on fish species near the water surface which seems to be a more stable food source. I have not succeeded in finding a documented case of female desertion in ospreys in previous research or literature, and for the 6 nestings recorded in Østfold in 2015 and 2016 (Isnes was recorded in both years) only the female at Skjeberg left the nest before the nestlings fledged. This suggests that female desertion in ospreys is not common. Mating a second time during the same season is often mentioned as a reason for desertion (Houston et al., 2005). Because of the extended period of incubation and caring for the nestlings and the short summers in Norway, I do not see this as a likely reason for desertion in osprey females in this region. Additionally, in other species where female desertion is documented, such as the Tengmalm’s owl (Eldegard & Sonerud, 2009), the nest has not been deserted until the nestlings are able to feed unassisted (Sonerud et al., 2014). The buildup of prey remains in the nest and the male’s continued feeding at Skjeberg shows that the nestlings were yet to be able to feed without assistance. This suggests that the female at the Skjeberg nest did not desert, but rather died. Interestingly, although the female disappeared before the nestlings were able to feed unassisted, and given that the male rarely fed the nestlings a whole prey item, all three nestlings survived and fledged successfully. In other documented cases of male-only care in raptors usually exhibiting bi-parental care nestlings often starved to death although the male delivered ample food to the nest, because of the males’ inability to assist in feeding (Schmutz et al., 2014). This suggests that the male osprey may exhibit a higher degree of plasticity in parental behavior.

4.5 Ingestion rate

Ingestion rate, i.e. the feeding efficiency of the parent increased with increasing prey mass. This has also been shown for the Eurasian kestrel by Løw (2006) and Steen (2010), when nestlings were assisted by a parent. However, this is contrary to patterns found for self-feeding raptors, where ingestion rate decreases with increased prey weight (Slagsvold & Sonerud, 2007). The decrease in efficiency is thought to be related to larger prey having larger skulls and more ligaments in birds and mammals (Slagsvold & Sonerud, 2007). It is difficult to suggest an explanation for this discrepancy. One possibility is that larger prey items have larger portions of meat that can be torn off in one bite, thereby increasing ingestion rate. However, as previously mentioned, I noted that the pieces torn off the prey items were generally equal and quite small. Estimates of bite size should therefore be included in future studies to further explore this potential explanation.

4.6 Number and duration of pauses

There was a positive relationship between number of pauses and prey body mass. Feeding bouts involving a large prey item had a higher number of pauses than a small item. One possible explanation for this is that the feeding parent paused regularly during long feeding bouts to check the surroundings for potential predators or invaders. Osprey nests may be subject to predation from other raptors, or disturbance from other ospreys (Cramp, 1979), and because tearing pieces of prey and feeding the nestlings demands focus, regular pauses are needed for the nestlings to be sufficiently guarded.

There was also a positive relationship between duration of pauses and prey body mass. When analyzing recordings, I noted that large prey items often were ample food for both nestlings and the parent, and the nestlings often appeared to be full before the fish was completely consumed. Especially the female at Isnes continued to try to feed the unwilling nestlings, resulting in long pauses before waiting to offer a new morsel. If the nestlings continued to be unwilling to accept food, the female would continue to consume the prey item herself (pers. obs). This behavior could explain why the duration of pauses increased with prey mass.

In addition, although I did not categorize this, I noted that the feeding sessions containing the most and longest pauses often showed some sort of disturbance of the nest. Because the camera lens was directed at the nest platform only, it was not possible to observe what kind of disturbance the ospreys reacted to. However, during my periods of observing the nests in the field, I observed other ospreys or birds such as crows (*Corvus cornix*) approaching the nest, prompting alarm calls and chasing by the nesting ospreys. The same behavior with alarm calls and flapping of wings during pauses in the feeding bouts recorded on camera suggests similar disturbance.

4.7 Possible biases

Some results of this study should be interpreted with caution. The prey selection recorded in this study cannot be generalized for all ospreys, as they are widely distributed opportunistic predators with a wide range of prey species (Cramp, 1979) and this study only recorded two osprey nests in one region of Norway.

Although video recording of nests arguably produces a more precise account of prey deliveries than analysis of prey remains, the estimation of prey mass is prone to inaccuracies, and prey mass may have been overestimated or underestimated. Human error may also occur when identifying species, although we were cautious about this and therefore estimated uncertain species only to family or order level. Because of incomplete recordings and dislocation of the camera at Skjeberg, the number of recorded deliveries here was low, and this may have limited this study in finding patterns regarding feeding time and prey delivery, or in fact may have created patterns that rather are coincidental. Only continued recording of prey delivery and feeding time can strengthen this type of study by revealing consistent patterns of behavior.

5. Conclusion

In conclusion, I found that carp species were most frequently delivered at the Isnes nest, while flounders were most commonly delivered at Skjeberg, and that prey choice is likely affected by the distance to freshwater and saltwater fishing localities. To further investigate prey selection and foraging behavior in ospreys, recording of prey deliveries at the nest should be combined with GPS tracking of the birds. 60% of prey items were delivered decapitated, and the male at Isnes delivered more decapitated prey than the female. It is likely that the male decapitates prey to get a portion of the prey and reduce the need to hunt additionally to feed himself. However, it is also possible that prey items are decapitated to reduce weight and thereby transport cost, and this is supported by the increased probability of decapitation with increasing prey mass at the Isnes nest. GPS trackers on the birds could also allow for further exploration of this hypothesis by analyzing the distance between fishing localities and the nest together with the frequency of decapitation. I found a strong positive relationship between feeding time and prey body mass in my study. However, the feeding efficiency of the parent assisting the nestlings increased with increased prey body mass. This is opposite to what has been found previously in adult raptors self-feeding, and future studies should include number and size of morsels fed to the nestlings to uncover the mechanisms behind this discrepancy. The parental tasks during nesting in ospreys are highly divided, and this was supported in my study, with the female at Isnes assisting the nestlings in 98% of the feeding sessions, and the female at Skjeberg never delivering prey to the nest. However, the disappearance of the female at Skjeberg prompted the male to start feeding the nestlings, showing that the distinct parental roles have some degree of plasticity in ospreys. The female at Isnes continued feeding the nestlings although they appeared to be able to feed unassisted, suggesting a strategy of maximizing the control over allocation of resources delivered by the male between her and the nestlings. This suggests that a sexual conflict may be present in ospreys during the nesting period, but further studies are needed to elucidate this issue.

6. References

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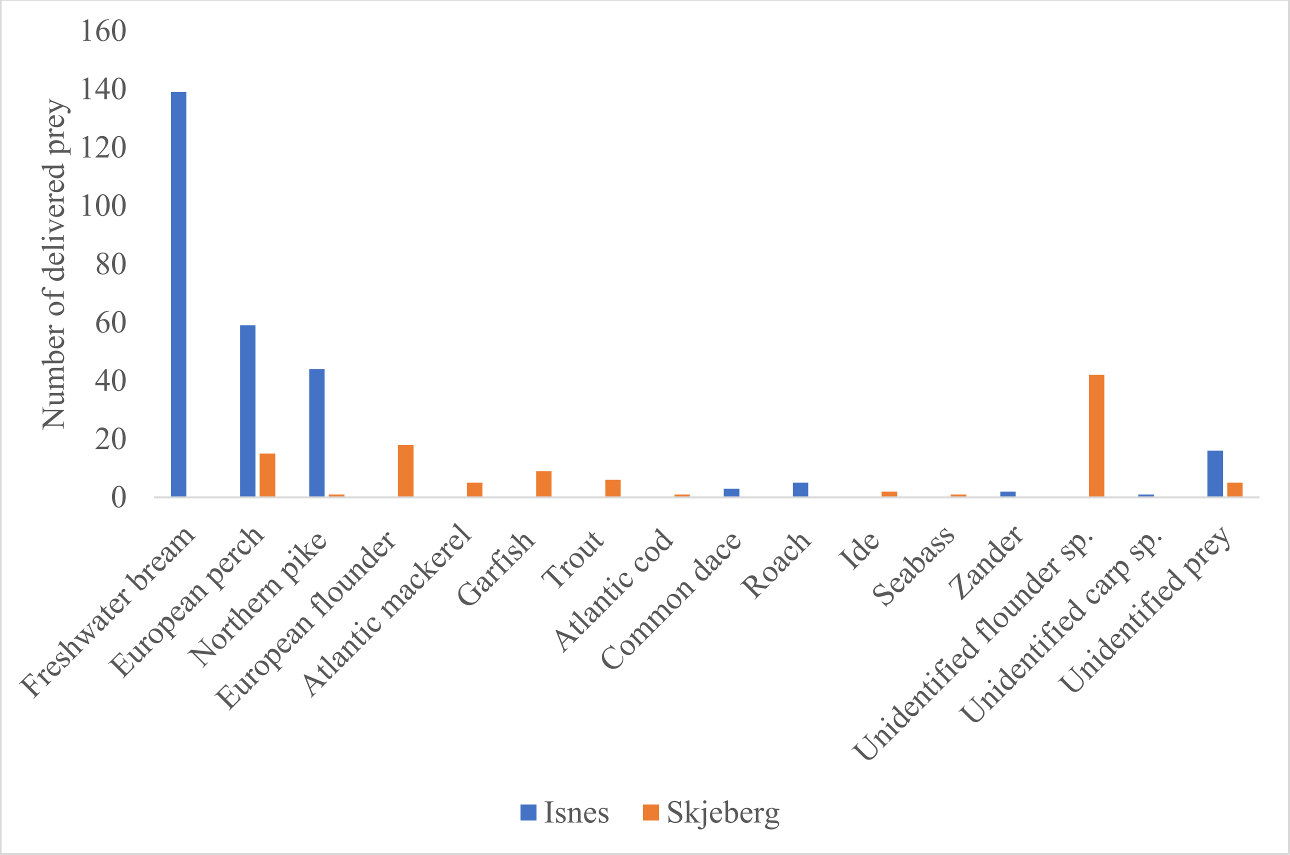
Appendices



Appendix 1. Distribution of all delivered prey species at both osprey nests in Østfold county, including prey only identified to family order, and unidentified prey.

Appendix 2. Gross prey body mass (g) of prey recorded delivered at the two osprey nests Isnes and Skjeberg.

Prey species	Mean 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		353	172259	100.0

Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway