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Diet and Activity Pattern of the White-Tailed Eagle (*Haliaeetus albicilla*) under the Midnight Sun

Einar Eriksen
Management of Natural Resources

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Abstract

I recorded prey deliveries at two nests of the white-tailed eagle (*Haliaeetus albicilla*) during the nestling period in May – July in Troms county in northern Norway. A total of 74 prey items were recorded delivered during 866 h monitoring time. Among the prey, 74.3 % were fish, 18.9 % birds, 5.4 % unidentifiable and one (1.4 %) was a tailfin from a harbour porpoise (*Phocoena phocoena*). Average mass of the prey items delivered was estimated to 425 g. Righteyed flounders (Pleuronectidae) constituted a larger share of the diet at the nest located near the shallow bay of Kobbvågen than at the nest at Brokskar, both located on the same peninsula with 12 km distance between. This suggests an element of functional response in the foraging strategy of the eagles. To measure the activity level, I used a logical factor of whether or not at least one prey was delivered within each hour-block. The eagles were most active when the tide was ebbing. Furthermore, they had an activity acrophase around 7 am and bathyphase around 7 pm not corresponding to studies on white-tailed eagles farther south, where white-tailed eagles have been regarded as strictly diurnal with an acrophase at midday. The eagles were also more active on low tidal levels when the tide was ebbing and somewhat opposite at flooding tide. Precipitation did not explain activity levels, but suggested there was a trend with higher activity levels at low precipitation. The estimated total prey mass delivered per day per nestling was 432 g. I recorded an event of siblicide, which are common in several other birds of prey but viewed as very rare in white-tailed eagles in Norway. One plausible explanation for this event can be found in the sibling rivalry hypothesis. Video monitoring is a precise way of exploring the diet of birds of prey in the breeding season. Feeding habitat and diet are relevant to the white-tailed eagles survival and reproduction, thus also for the conservation of the species. The noticeable local variation of the individual diets over short distance suggests that more studies are needed in other locations to better understand the feeding behaviour.

Sammendrag

Jeg videoovervåket reirene til to havørn (*Haliaeetus albicilla*) fra mai til juli på Malangshalvøya i Troms. Totalt ble det levert 74 byttedyrenheter til ungene i reiret i løpet av 866 t video. Av disse var 74,3 % fisk, 18,9 % fugl, 5,4 % uidentifiserbare og ett byttedyr (1,4 %) var en halefinne fra en nise (*Phocoena phocoena*). Gjennomsnittlig masse for byttedyrene ble estimert til 425 g. Flyndrefisk (Pleuronectidae) utgjorde en større del av dietten i reiret lokalisert ved langgrunne Kobbevågen sammenlignet med reiret på Brokskar 12 km lengre nordøst på den samme halvøya. Dette tyder på et element av funksjonell respons i ørnens furasjeringsstrategi. For å måle aktivitetsnivået brukte jeg en logisk faktor for om minst ett byttedyr ble levert innenfor en timesblokk eller ei. Ørnene viste seg å være mest aktive ved fellende tidevann. Videre hadde de høyest aktivitet omtrent kl. 7 på morgenkysten og var minst aktive rundt kl. 7 om kvelden. De var også mer aktive ved lavt tidevann ved fellende havnivå, og til en viss grad motsatt ved fløende havnivå. Nedbør forklarte ikke aktivitetsnivået, men viser likevel en trend hvor det er høyere aktivitet når det er lite nedbør og varmt i luften. Den estimerte totale byttedyrmassen per dag per unge var 432 g. Jeg fikk også opptak av et søskendrap, siblicid, som er vanlig hos mange andre rovfugler men ansett som veldig sjeldent blant havørn i Norge. En plausibel forklaring på hendelsen presenteres i søskenrivaliseringshypotesen. Videoovervåkning er en presis måte å undersøke dietten til rovfugler på i hekkesesongen. Furasjeringshabitat og diett er relevant for havørnens overlevelse og reproduksjon, og dermed også i bevaringsøyemed. Den bemerkelsesverdige variasjonen i diettene til indviduelt geografisk nærme hverandre taler for at flere studier bør gjennomføres andre steder for å bedre kartlegge havørnens furasjeringsadferd.

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Introduction

To conserve a raptor species, and also to understand its role in the ecosystem, knowledge about its diet is essential. The white-tailed eagle (*Haliaeetus albicilla*) is a large bird with 200 – 240 cm wing-span. It is generally littoral zone foraging, linked to the sea coast and other wetland areas offering aquatic prey mainly in northern Europe and northern Asia (Cramp and Simmons, 1980). In Norway, the population size has been estimated to 3312 – 4167 pairs, 600 – 800 in Troms county in northern Norway alone (Heggøy and Øien, 2014; Shimmings and Øien, 2015). The white-tailed eagle can be considered a symbol of conservation success, now being categorized as least concern (LC) both on the Norwegian Red List for Species (Kålås et al., 2010) as well as on the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species (IUCN, 2014). This despite the fact that the majority of local populations all over Europe became extinct in the 1960s due to e.g. hunting and DDT contamination, leaving only sub-populations (Kenntner et al., 2001; Krone et al., 2006; Helander et al., 2009). However, there are still threats against the species. Lead is for instance a major cause of death for white-tailed eagle (Kenntner et al., 2001; Krone et al., 2006; Helander et al., 2009), and also wind farms regularly kill white-tailed eagles, e.g. in the archipelago Smøla on the Norwegian western coast (Follestad et al., 2007).

The diet of the white-tailed eagle has been studied by examining remains and pellets (Sulkava et al., 1997; Nadjafzadeh et al., 2013, 2015; Sandor et al., 2015), by observations combined with examining remains and pellets, collecting reports and newspaper articles (Willgohs, 1961), and by taking still photos of the nest bed (Tornberg and Reif, 2007). Recently the diet of the white-tailed eagle was studied by analyzing stable isotope ratios (Nadjafzadeh et al., 2016). In the latter case it is largely not possible to identify species, but mainly different taxonomical parent groups. The indirect method of using pellets and remains for diet analysis generally overestimates large prey and avian prey while underestimating smaller prey and mammalian prey (Willgohs, 1961; Tornberg and Reif, 2007; Homme, 2008; Slagsvold et al., 2010a).

The activity level of the white-tailed eagle has been studied by direct observations (Willgohs, 1961) and with the aid of Global Positioning System (GPS) datalogger (Krone et al., 2009), both substantiating diurnality. However, to my best of knowledge, such activity studies has not been done where and when the sun is above the horizon day and night. Moreover, the activity level has only been associated to time of day.

In this study I investigated the prey composition and activity level of white-tailed eagles by camera monitoring two nests north of the polar circle in northern Norway during summer. I reasoned that the activity levels of the white-tailed eagle would prove different where the midnight sun makes it hard to tell the difference between day and night. More specifically I predictet activity closer to midnight, and generally a more vague diurnal behaviour compared to other studies. I predicted that whether the tide

was flooding or ebbing would be of importance for the activity level, because ebbing tidal levels might unveil dead fish, fish trapped in small ponds in shallow bays, or other dead prey items, and because the fish might be closer to the surface. I also predicted that the tidal level might be of importance because shorebirds start feeding at the shoreline at ebb (Evans, 1976) and because fish in the littoral zone should be easier to catch at full ebb because they come closer to the surface (cf. Rangeley and Kramer, 1998; Gibson, 2003). Moreover I expected the precipitation to have an effect on the activity pattern, because a wet plumage may restrict foraging activity. I also reasoned that ambient temperature might affect prey availability, and that higher ambient temperatures would lead to less energy use for the eagles and their nestlings in the relatively cold environment, so that more energy could be allocated to e.g. foraging. Finally, the camera monitoring also allowed for recording all prey items, estimating their mass and finding out how much prey biomass was delivered to the nests.

Methods

Study area, prey availability and study species

I collected data at two nests of the white-tailed eagle located in Tromsø municipality in Troms county in the northern part of Norway. Tromsø municipality had 73,296 inhabitants as of fourth quarter of 2015 (Statistisk Sentralbyrå (SSB), 2016), most of them situated in Tromsø city c. 20 km north/northeast of my study area (figure 1).

The nests were located near the village Kobbervågen (69°28'N, 18°28'E) and the hamlet Brokskar (latitude 69°31'N, longitude 18°34'E), both on the peninsula Malangen, which adjoins the fjords Malangen on the west and Balsfjord on the east side, as well as the strait Straumfjorden on the north side (figure 1).

The area has a humid subarctic continental climate with an average temperature of 6.0°C in May, 7.5°C in June and 11.5°C in July of 2015 (Norwegian Meteorological Institute and Norwegian Broadcasting Corporation, 2016) at the nearest meteorological observation station which is on the island of Tromsø, c. 16 and 19 km north from the sites at Kobbervågen and Brokskar, respectively. The area experiences midnight sun from 20 May to 22 July (Johnsen, 2013), including the whole monitoring time in my study.

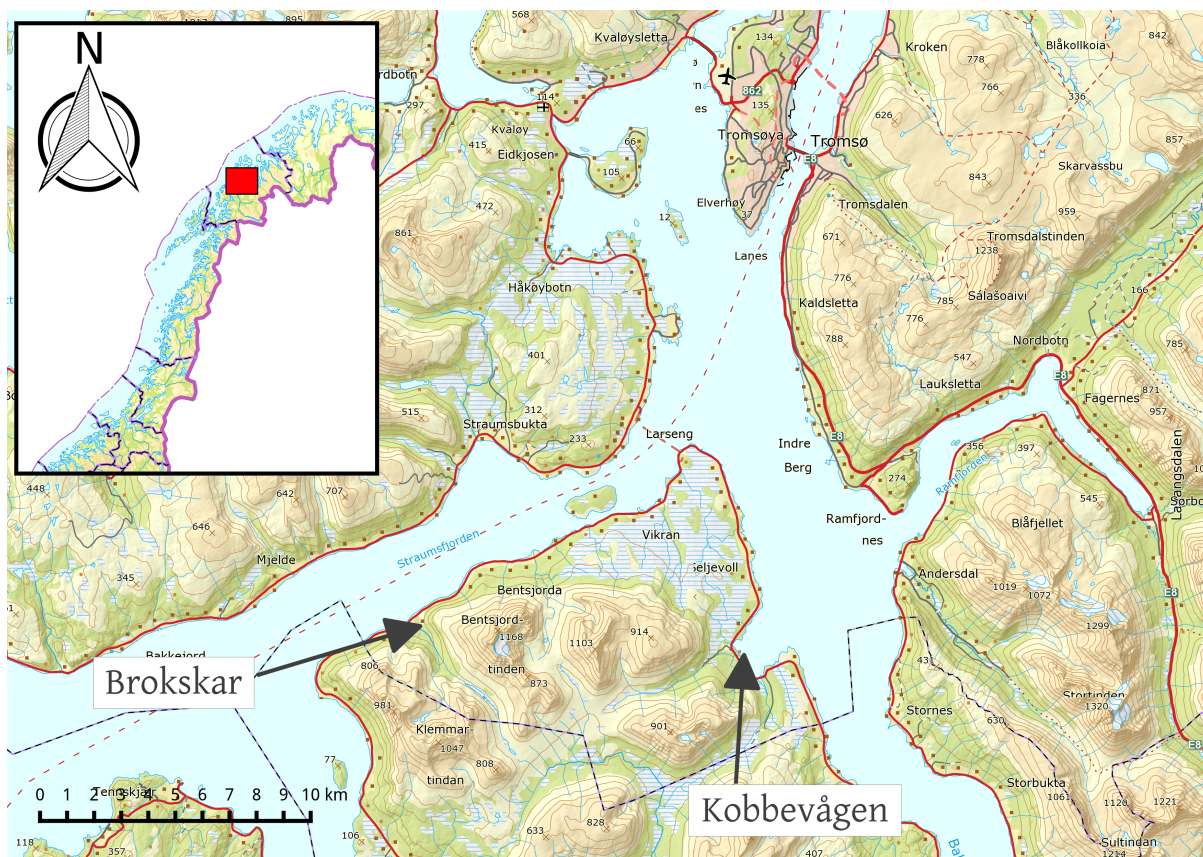


Figure 1: The approximate locations of the two white-tailed eagles nests I studied near Brokskar and Kobbervågen in northern Norway. Distance between the nests were c. 12 km. (Basemap from The Norwegian Mapping Authority.)

Kobbevågen area and its availability of avian prey The nest near Kobbevågen was located 100 m above sea level, and had been built c. 10 m above ground in a downy birch (*Betula pubescens*) with a view towards the bay of Kobbevågen.

Kobbevågen (literally translated “the bay of seals”), contains a wetland system protected by the Ramsar Convention as well as by its nature reserve status (Avd. for naturvern og kulturminner, 1995; Ramsar Convention, 2002; Klima- og miljødepartementet, 2009). This brackish water bay is located on the northeast side of the Peninsula of Malangen, hence it has its shoreline facing Balsfjord (figure 2). Within the protected area there are two large rivers, coastal forests of grey alder (*Alnus incana*) and downy birch, a grazed wet meadow, large mudflats of moraine and watercourse deposits and shallow waters (Miljødirektoratet, 1995; Ramsar Convention, 2002; Miljødirektoratet, 2012; Sommersel and Skottvoll, 2014). The mudflats stretching around the headland south of the bay of Kobbevågen to the promontory Balsnes approximately 9 km farther north is categorized as being of the highest national importance. The same goes for the brackish water delta inside the bay of Kobbevågen (Miljødirektoratet, 2009, 2012; Sommersel and Skottvoll, 2014). The area experiences low human impact (Ramsar Convention, 2002).

Kobbevågen is an important resting area for migrating shorebirds (Charadriiformes) and ducks (Anatidae). There have further been observed large numbers (> 200) of long-tailed ducks (*Clangula hyemalis*), velvet scoters (*Melanitta fusca*), common eiders (*Somateria mollissima*), Eurasian oystercatchers (*Haematopus ostralegus*), red knots (*Calidris canutus*), dunlins (*Calidris alpina*), purple sandpipers (*Calidris maritima*) and European golden plovers (*Pluvialis apricaria*). Relatively high numbers of Yellow-billed looms (*Gavia adamsii*), whooper swans (*Cygnus cygnus*), Northern pintails (*Anas acuta*) and Eurasian curlew (*Numenius arquata*) have also been observed (Miljødirektoratet, 1995).

Balsfjord is a 70 km long single-basin fjord with three discrete sills of 9 m, 10 m and 35 m depths, while much of the fjord is deeper than 100 m with a maximum depth of 190 m (Hopkins et al., 1989; Bax and Eliassen, 1990). From April to June, the fjord contains a metalimnion separating a cold hypolimnion and a warm epilimnion (Pedersen, 2014). Thus, the water is noticeable warmer near the surface down to almost 50 m depth than the 3.5 to 7°C water below, measured between 1976 to 1995 through all seasons (Aure et al., 1997).

Brokskar area and its availability of avian prey The nest near Brokskar was located in a steep area where numerous trees had fallen, signifying avalanches in winter. The nest itself was placed in an elevated area in the steep hills, at the foot of a downy birch angled from the hillside, laying just where the tree trunk was divided into two. The elevation at the nest location was c. 100 m above sea level.

Brokskar is located in the western part of the northern side of Peninsula of Malangen,

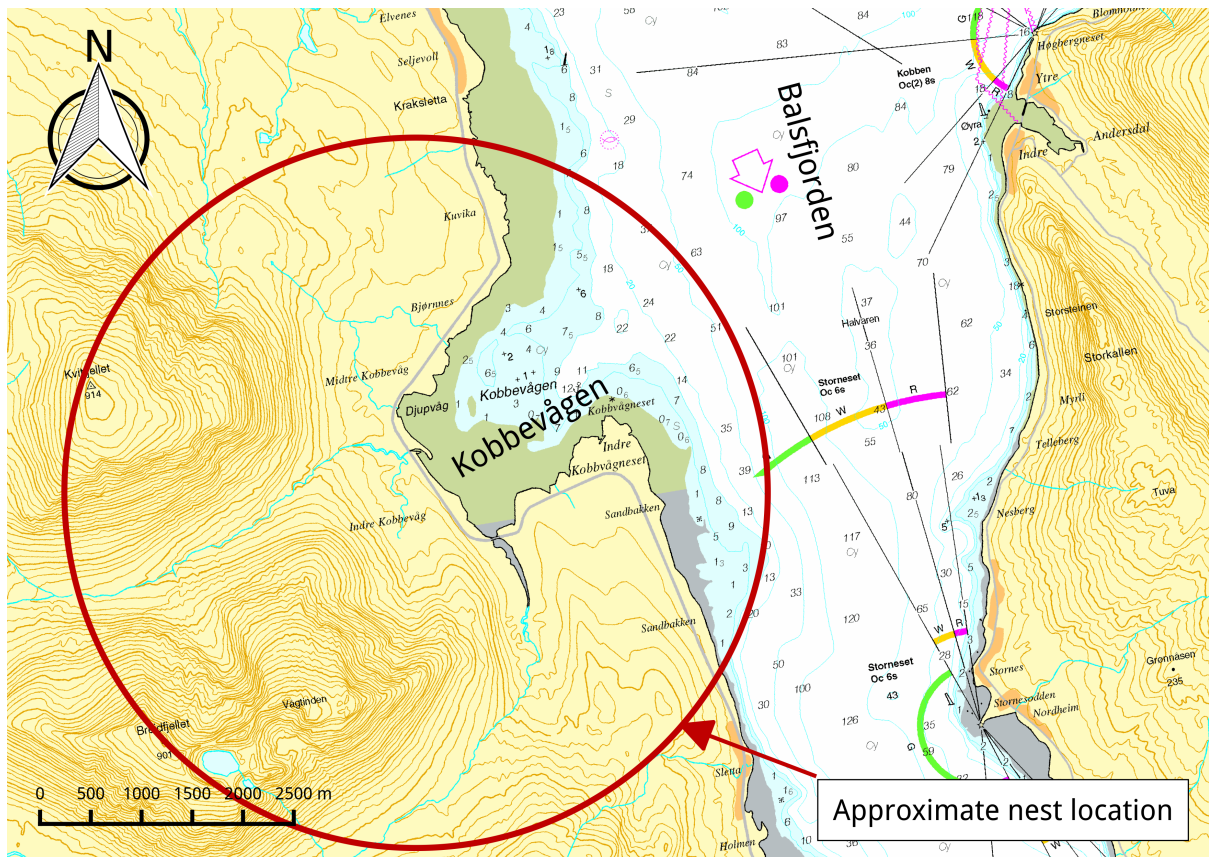


Figure 2: Kobbavågen, northern Norway, where one of the two monitored white-tailed eagle nests was located, showed on a nautical chart with contour lines for illustrating the shape of underwater relief. (Basemap from The Norwegian Mapping Authority.)

hence the shoreline below the nest belongs to the strait Straumsfjorden, while parts of the fjord Malangen is within foraging range (figure 3).

Forøya is an island protected as nature reserve approximately 7 km from the white-tailed eagle nest and 500 m from the nearest terrestrial area of the peninsula of Malangen. The island is a nesting area for the European herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common eider (*Somateria mollissima*) and graylag goose (*Anser anser*) and an overwintering area for loons (Gaviiformes), cormorants (Phalacrocoracidae), gulls (Laridae) and alcides (Alcidae) (Miljødirektoratet, 2004).

Malangen has a sill depth of 230 m and the maximum depth is 400 m. The temperature range in the deep fjord was from 7.5 to 8°C during a warm period around 1990 and to 4.5°C in a colder period before 1981 (Aure et al., 1997).

Prey fish availability The availability of fish might differ somewhat in the fjords Malangen and Balsfjord. Nevertheless, the fjords are geographically close to each other, merged by the strait Straumsfjorden.

There are about 20 species of fish in Balsfjord (Hopkins et al., 1989). During a two year period of prawn trawling in Balsfjorden by Klemetsen (1982), 97 % of the catch, also comprising the bulk of the biomass, consisted of cod (*Gadus morhua*), herring (*Clupea*

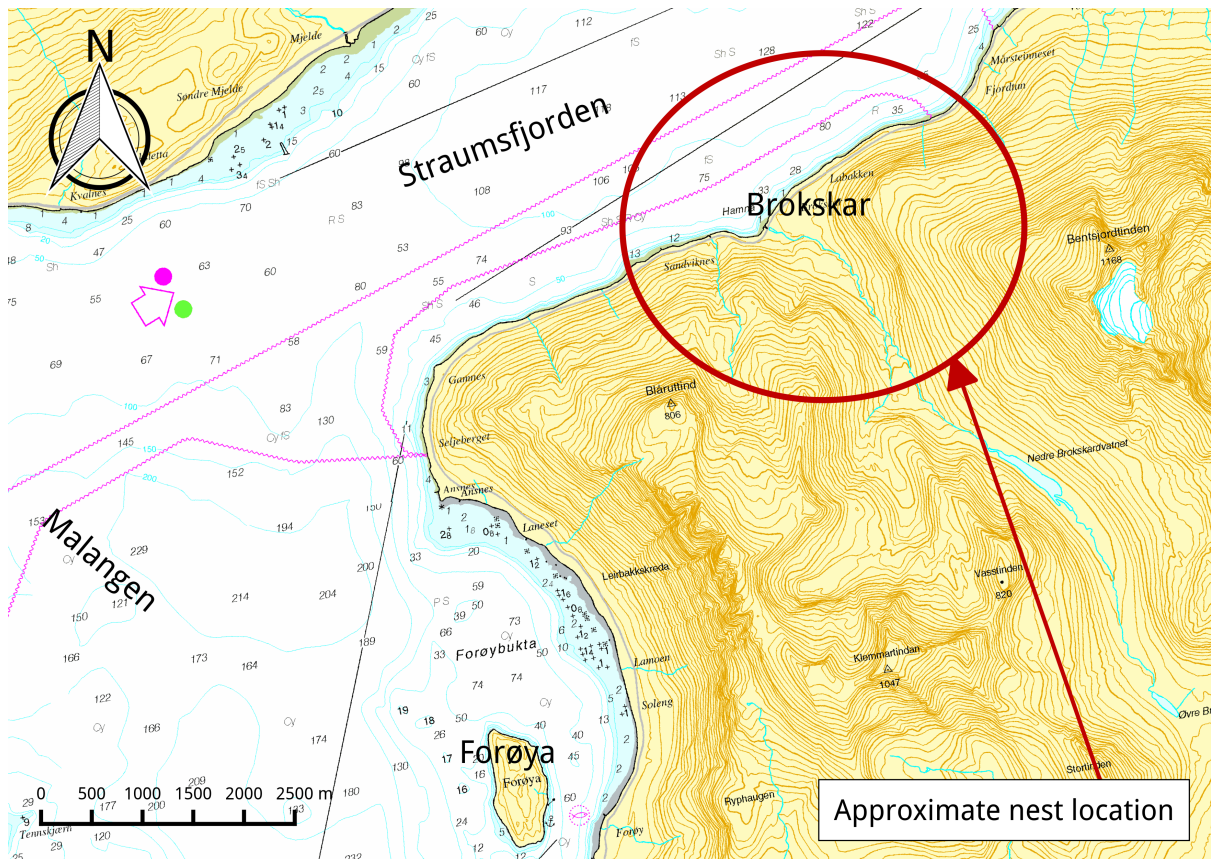


Figure 3: Brokskar, northern Norway, where one of the two monitored white-tailed eagle nests was located, showed on a nautical chart with contour lines for illustrating the shape of underwater relief. (Basemap from The Norwegian Mapping Authority.)

harengus) and capelin (*Mallotus villosus*). Other species were American plaice (*Hippoglossoides platessoides*), sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*), haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes* sp.), snake blenny (*Lumpenus lumpretaeformis*) and sand eel (*Ammodytes* sp.). Although cod is considered the apex predator (Hopkins et al., 1989), other Gadiformes species are also present, e.g. saithe (*Pollachius virens*). Brown trout (*Salmo trutta*) has been caught in nets in the littoral zone along with sand lance (Ammodytidae), sea stickleback (*Spinachia spinachia*), rock gunnel (*Pholis gunnellus*), shorthorn sculpin (*Myoxocephalus scorpius*). In the benthic zone, one can also find European plaice (*Pleuronectes platessa*), witch flounder (*Glyptocephalus cynoglossus*) and the right-eyed flounder family. In the littoral zone e.g. shorthorn sculpin (*Myoxocephalus scorpius*) (Pedersen, 2014).

Video monitoring

A camera was installed at each of two white-tailed eagles nests in March 2015, prior to the onset of breeding. These nests were fairly easy to access and considered highly likely to be used for nesting. This assessment was based on the recent level of activity near the nests, and whether the eagles had taken a break from nesting last year, as the latter

raises the probability for nesting the current season (K.B. Strann, pers. comm.).

The camera was a bullet formed type with a Charged Coupling Devices (CCD) image sensor, 12 V input and analog video output. This was connected to the Digital Video Recorder (DVR) Secumate H.264 Mini Portable DVR, with a build-in slot for Secure Digital (SD) memory cards in which I used a card with 64 GB capacity, as well as video and audio input and output. The resolution of the video material was 704×576 pixels, and the speed 25 frames per s (fps). The video input was used for transferring video from the camera to the DVR, whereas the video output was used only for connecting to a portable display to manage settings and to test the system in the field. The power source was a Valve-Regulated Lead-Acid (VRLA) battery with 80 mAh capacity. I replaced the battery and the memory card approximately every week at the two nests. To avoid disturbing the eagles I installed a 120 m and an 80 m long siamese coaxial cable between the camera in the nest and the DVR and battery at Brokskar and Kobbevågen, respectively. The monitoring ended 9 July (table 10).

The DVR was set to use its built-in Video Motion Detector (VMD) and record only when movement was detected. The VMD sensitivity was set to high, to record too much rather than too little. Due to broad-leaved trees in the video image, the actual recording time turned out to be very long. The monitoring started 23 May at Brokskar and 25 May at Kobbevågen, when the hatched nestling was approximately 5 days and 28 days (4 weeks) old, respectively, and ended at 3 July at Brokskar when the eaglet was at estimated age 45 days (c. 6.5 weeks) and at 9 July at Kobbevågen when the eaglet was at estimated age 73 days (c. 10.5 weeks) (table 10). The monitoring time was divided into 866 hour blocks.

I used VLC version 2.2.1 for GNU/Linux to fast-forward through all the video material to register incoming birds with prey, incoming birds without prey, and birds departing from the nests. With the aid of Screen Ruler 0.9.6 for GNU/Linux I measured the lengths of all delivered prey items and compared that to measurements of the adult eagles, i.e. the distance from the mouth corner to the bill, the distance from the hind claw to the forward claw and the distance from the left to the right claw. The ratio was multiplied by the equivalent measurements of a stuffed white-tailed eagle to estimate the actual length of the prey items. The measurements were useful to help determine some of the prey to species or a higher taxa, but were primarily used to calculate the body mass of the prey.

Identifying the prey and estimating its body mass

All prey items recorded on video were identified to species or to the lowest possible taxon. This was done by repeatedly playing the sequences of the video material where prey deliveries were made, mainly frame by frame, until a decision could be made.

The body mass of the fish recorded was calculated by a standard weight–length relationship (WLR) formula $W = aL^b$, where W is the mass and L is the length, proposed

by Keys (1928) and recommended by Froese (2006). The intercept a varies between species. As the current WLR formula is modification of the cube law by Spencer (1864), b is normally ≈ 3 , but in this more updated and precise method also varies between species. The values for a and b (table 1) are extracted from Fishbase.org, the largest compilation of weight-length studies of fish (Froese, 2006; Froese and Pauly, 2016). In the cases where I was unable to identify the prey to species (N=22), I used the values for the species within the higher taxon that appeared to be most delivered most frequently. For the Wolffish family (Anarhichadidae) (N=1), I used a and b values from Atlantic wolffish (*Anarhichas lupus*), because it is more coastal and attached to shallow waters than the other species in this family (Nedreaas, 2012). For the salmonids (N=5) I used a and b values from brown trout (*Salmo trutta*), because it occurs more frequently near the water surface and in coastal systems, and because both the fjords Malangen and Balsfjorden, within range of the eagles at Brokskar and Kobbevågen, respectively, have higher catch statistics for brown trout than for the alternative Atlantic salmon (*Salmo salar*) (T. van der Meeren, pers. comm).

Table 1: The a and b values for the fish species recorded, delivered at two white-tailed eagles nests in northern Norway. The values was gathered from Fishbase.org (Froese, 2006; Froese and Pauly, 2016)

Taxa	a	b
Cod (<i>Gadus morhua</i>)	0.00741	3.06
Saithe (<i>Pollachius virens</i>)	0.00759	3.05
Gadiformes (Gadiformes)*	0.00741	3.06
European flounder (<i>Platichthys flesus</i>)	0.00776	3.07
Righteye flounders (<i>Pleuronectidae</i>)**	0.00776	3.07
Lumpsucker (<i>Cyclopterus lumpus</i>)	0.02291	3.01
Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)	0.00977	3.09
Cusk (<i>Brosme brosme</i>)	0.00490	3.12
Wolffish (Anarhichadidae)***	0.00347	3.22
Angler (<i>Lophius piscatorius</i>)	0.01778	2.90
Salmonids (Salmonidae)****	0.00851	3.03

* using a and b values from Cod (*Gadus morhua*)

** using a and b values from European flounder (*Platichthys flesus*)

*** using a and b values from Atlantic wolffish (*Anarhichas lupus*)

**** using a and b values from The brown trout (*Salmo salar*)

Some of the prey items identified as cod or as Gadiformes of unknown species were fish heads within the respective taxa (table 9). Hence, the mass of the whole fish would be an imprecise estimation of the mass of the items. To find a more realistic estimate, I collected eight cod heads from a local fisherman, measured their length and the mass (table 2), and made a simple plot fitted with a linear polynomial to describe the data (figure 4a). The intercept was specified to zero, so that the regression line would run through origin (0, 0).

The mass of a fish head can be assumed to be a linear function of its volume, so the cube root of the fish heads mass $\sqrt[3]{W_{fishhead}}$ are therefore used in my model. This also gave a better fit to the data (figure 4a) ($R^2 = 0.998$) than a standard linear regression ($R^2 = 0.983$) or a second degree polynomial model ($R^2 = 0.989$). Hence, the mass of a

fish head could be calculated by the following equation

$$W_{fishhead} = (0.4686 \times L_{fishhead})^3,$$

where $L_{fishhead}$ is the measured length of the item as it appeared on the video (figure 4a).

Table 2: Length and mass of heads of cod (*Gadus morhua*) measured to estimate the body mass of delivered prey at white-tailed eagles nests in northern Norway.

Fish head ID	Length (cm)	Mass (g)
1	19	600
2	13	200
3	17	500
4	19	910
5	16	420
6	19	775
7	15	370
8	27	2000

The same problem occurred for the avian prey items, though I had no way to collect different sized birds to gather the data necessary for the same approach as I used for the fish heads. Nevertheless, three of the birds delivered was identified to species (table 3). A common scoter weighs c. 1000 g, a willow ptarmigan c. 500 g, and a common gull c. 400 g (Cramp and Simmons, 1977, 1980, 1983). As for the fish heads, the intercept was specified so that the regression line would run through origin (0, 0).

Because the mass of a bird is directly related to its volume, as also for fish heads, and because the R^2 proves slightly higher with $\sqrt[3]{W_{bird}}$ as the response variable ($R^2 = 0.9827$) compared to W_{bird} ($R^2 = 0.9685$), I used the cube root as response variable in my simple regression containing the three data points. This gives following equation for the bird mass calculation

$$W_{bird} = (0.3983 \times L_{bird})^3,$$

where L_{bird} is the measured length of the item as it appeared on the video.

Table 3: The body length on the video screen and the body mass from the literature (Cramp and Simmons, 1980, 1977, 1983), of three avian prey identified to species among prey delivered at the white-tailed eagles nests in northern Norway.

Bird species	Length (cm)	Mass (g)
Common scoter (<i>Melanitta nigra</i>)	27	1000
Willow ptarmigan (<i>Lagopus lagopus</i>)	20	500
Common gull (<i>Larus canus</i>)	15	400

Some of the avian prey had been decapitated prior to delivery, while others had most likely been decapitated, as the head should have been distinct on the video images but was not. Thus, I assume that all the birds were decapitated ahead of delivery. A birds head has a mass of 12.9 % of the whole body mass on average (T. Slagsvold and G.A. Sonerud, unpubl. data), and I subtracted this percentage from the total estimated body mass.

The unidentified prey items, as well as one tail fin from a whale, was assumed to have the average mass of all prey items where the mass has been determined.

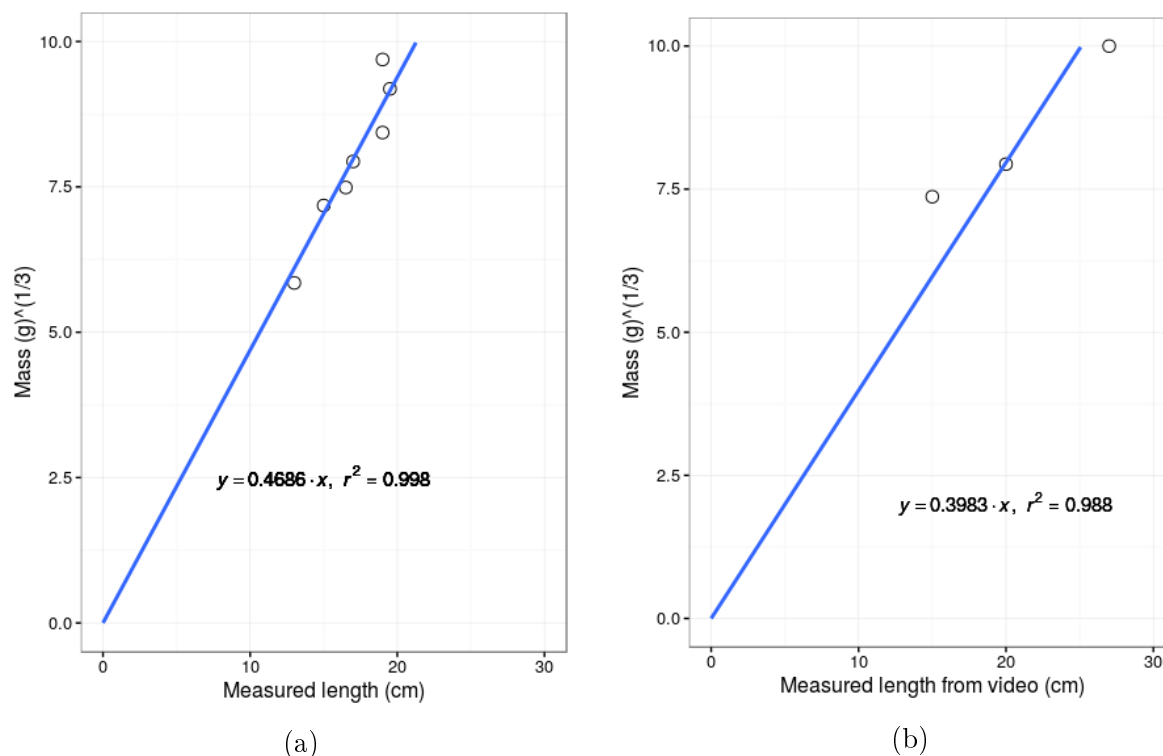


Figure 4: The background data for estimating the mass of the fish heads, and the body mass of birds not identified to species, delivered at the white-tailed eagle nests. (a) The mass of a fish head in relation to the length of the fish head, as measured on collected fish heads. (b) The mass of a bird in relation to the length of the bird as measured on the video screen.

Statistical analysis

The statistical analysis were done in R version 3.2.2 on the platform Linux 64 bits x86. I used the package lme4 (Bates et al., 2015) for fitting generalized linear mixed models, AICcmodavg (Mazerolle, 2016) to extract AICc from various model object classes, MuMIn (Bartoń, 2016) to sort models by AICc, xtable (Dahl, 2016) and texreg (Leifeld, 2013) to generate tables for LaTeX from models and data sets fitted to R and ggplot2 (Wickham, 2009) and SigmaPlot Version 11.0 to make graphs. The text was written in LaTeX. Some of my basic calculations, e.g. the prey mass, were done in the spreadsheet program LibreOffice Calc, producing .csv files for R to read.

To find the differences between the frequency of righteye flounders as prey items delivered in the two separate nests, I made a table differentiating the two nests as well as righteyed flounders from the other prey. This was asserted with logistic regression and the probability for the prey to be a righteyed flounder as the response variable. The explanatory variable was set to the logical variable for the nest ID.

Logistic regression was also applied to test which explanatory variables could best

explain the nestlings feeding without assistance from the adults, with prey item mass and age of the nestlings as explanatory variables. The age was determined by inquiring an ornitologist and expert on white-tailed eagles who estimated the age of the nestlings at Brokskar at 23 May to between 3 and 6 days and the age of the nestling at Kobbevågen at 25 May to approximately four weeks (A. O. Folkestad, pers. comm).

The average mass was estimated by fitting a linear regression with random effects

In the analysis of the daily pattern of prey deliveries, the dependent variable was the probability of prey deliveries within each hour block, which thus represented the activity level in terms of foraging success. The models contained ten single explanatory variables and five interaction terms, as well as a log-transformed tide level for some of the models when that was necessary due to large eigenvalues. Three of the variables represent a continuous cycle from 0 to 23 hours and were connected with the use of a cosinor analysis method described by Stolwijk et al. (1999). This method involves two separate explanatory variables in the form of a cosine and a sine function. These are handled like a group, hence one is never fitted to a model without the other. The cosinor variables for my analysis were

$$\sin(2 \times \pi \times \text{HOUR}/24) \text{ and } \cos(2 \times \pi \times \text{HOUR}/24),$$

respectively. I produced a Midline Estimating Statistic of Rhythm (MESoR), which was the intercept of a model with random effects for nest ID as the only explanatory variable. In the models where the daytime activity was an explanatory variable, I also fitted so-called harmonies, interpreted

$$\sin(2 \times 2 \times \pi \times \text{HOUR}/24) \text{ together with } \cos(2 \times 2 \times \pi \times \text{HOUR}/24)$$

and

$$\sin(3 \times 2 \times \pi \times \text{HOUR}/24) \text{ together with } \cos(3 \times 2 \times \pi \times \text{HOUR}/24)$$

in case the daytime rythm of the white-tailed eagles would be more intricate, but still vary as a response of the time of the day or the corresponding light conditions.

I used several other independent variables in attempting to identify if and when the white-tailed eagles had periods of higher foraging success. The explanatory variables in addition to the cosinor variables were precipitation (mm/h), ambient temperature (°C), tidal level (cm), and whether there was an ebbing or flooding tide. The five interaction terms were namely precipitation \times temperature, precipitation \times tide, precipitation \times ebbing, temperature \times ebbing and ebbing \times tide. The tidal level values were often high (up to 286 cm). To avoid unnecessary log-transformation, I used a relative convergence criterion which involves scaling the gradient by the Hessian matrix. This is a more progressive test than the test offered through the glmer package.

Additionally I included random terms to account for differences between the two nests

that would not be explained by the explanatory variables. These effects are not expected to be normally distributed with mean zero, and random effects are expected rather than fixed effects.

I used the Akaike information criterion corrected for finite sample size, AICc, to measure the relative quality of my statistical models (Anderson et al., 1998; Anderson and Burnham, 2002). Further, I required an AICc increase with > 2 per extra variable in the model to weigh a more complicated model as better than the simpler. The significance level α was set at $p = 0.05$.

The average mass was estimated by fitting a linear regression with random effects so that random effects of the nest ID was an explanatory variable for the fitted average mass. For this model I excluded the prey items with unknown mass ($N = 5$), and the fitted average was subsequently used also as body mass of these five prey items.

Results

Within the 865 h 33 s of video recording from the two white-tailed eagles nests, 74 prey items were recorded delivered. That gives a rate of 0.085 prey deliveries per hour, equivalent to 11 h 41 m between deliveries. Two prey items were delivered within the same hour at the same nest only once, hence there were 73 cases of activity measured within the video recording.

Dietary selection and mass of prey

Of the prey items delivered (table 4), 74.3 % were fish or just fish heads, 18.9 % were birds, 5.4 % were unidentified prey items that could affect e.g. the distribution between fish and birds slightly, and one prey item, 1.35 %, was a tail from a Harbour porpoise (*Phocoena phocoena*) (table 4).

The total prey mass delivered at the nest within the monitoring period was 34,412 g (table 4). One of the nests was inhabited by two nestlings from the start of the monitoring period, at 23 May, until 3 June, while the other nest has only one nestling in addition to one unhatched egg. Accounting for this, the body mass delivered to the two surviving nestlings in separate nests was 31,166 g in total, given that the nestling that died was able to consume the same amount per day as the sibling that survived until the time of death. The amount of food delivered to the nest per nestling per day can thereby be estimated to 432 g. The fitted average prey body mass was estimated to 425 g ($SD = 170.3$).

Differences in dietary preferences between the two nests

Most of the righteyed flounders in my video material, including the European flounder, were delivered to the nest at Kobbenvågen. More specifically eleven righteye flounders as

Table 4: Number of prey items delivered at two white-tailed eagle nests in northern Norway, and body mass for each prey category.

Prey category	N	%	Estimated body mass	% of total estimated body mass
Cod (<i>Gadus morhua</i>)	7	9.46	2888.00	8.39
Saithe (<i>Pollachius virens</i>)	2	2.70	400.00	1.16
Gadiformes	9	12.16	6102.00	17.73
European flounder (<i>Platichthys flesus</i>)	8	10.81	1051.00	3.05
Righteye flounders (<i>Pleuronectidae</i>)	8	10.81	1198.00	3.48
Lumpsucker (<i>Cyclopterus lumpus</i>)	8	10.81	3769.00	10.95
Angler (<i>Lophius piscatorius</i>)	2	2.70	1012.00	2.94
Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)	1	1.35	230.00	0.67
Cusk (<i>Brosme brosme</i>)	1	1.35	2798.00	8.13
Wolffish (<i>Anarhichadidae</i>)	1	1.35	296.00	0.86
Salmonids (<i>Salmonidae</i>)	5	6.76	3883.00	11.28
Fish (<i>Pisces</i>)	3	4.05	674.00	1.96
Total fish (<i>Pisces</i>)	55	74.31	24301.00	70.62
Common scoter (<i>Melanitta nigra</i>)	1	1.35	871.00	2.53
Willow ptarmigan (<i>Lagopus lagopus</i>)	1	1.35	440.00	1.28
Common gull (<i>Larus canus</i>)	1	1.35	348.00	1.01
Dabbling ducks (<i>Anatinae</i>)	5	6.76	2032.00	5.90
Bird (<i>Aves</i>)	6	8.11	4299.00	12.49
Total birds (<i>Aves</i>)	14	18.92	7990.00	23.22
Harbour porpoise (<i>Phocoena phocoena</i>)	1	1.35	425.00	1.24
Total mammals (<i>Mammalia</i>)	1	1.35	425.00	1.24
Unidentified	4	5.41	1698.40	4.94
Total	74	100.00	34412.00	100.00

Table 5: The probability of a prey item delivered in the white-tailed eagles nests in Kobbevågen and Brokskar, northern Norway, being a righteyed flounder explained with nest ID.

	Estimate	Std. Error	z value	p value
(Intercept)	-2.1972	0.4714	-4.66	0.0000
KobbevTRUE	2.0302	0.6245	3.25	0.0012

opposed to five at Brokskar. This was a significant difference ($p = 0.0012$) (table 5). There was also a tendency for a higher catch rate of Gadiformes at Brokskar compared with Kobbevågen, but that was not significant. Salmonids were delivered only at Brokskar (table 6).

Unassisted feeding

The monitoring covered the nestling at Brokskar from age 3 – 6 days to age 43 – 46 days and the nestling at Kobbevågen from age 28 days to age 73 days, with a gap between 53 and 70 days of age. The white-tailed eagle nestlings fed without assistance three times during the monitoring. Among the two explanatory variables prey item mass and nestling age, only the latter was significant in any of the models. Hence, the model for the probability of a nestling feeding unassisted can be interpreted for $time = t$

$$\text{Logit } P(\text{unassisted}) = \beta_0 + \beta_1 x_{1i} + \alpha_i + v_{it}, i = 1, 2, \dots, N,$$

Table 6: Number of prey items delivered at the white-tailed eagle nests at Kobbvågen and at Brokskar, northern Norway.

Prey category	N Kobbvågen	N Brokskar	% Kobbvågen	% Brokskar
Cod (<i>Gadus morhua</i>)	1	6	4.17	12.00
Saithe (<i>Pollachius virens</i>)	1	1	4.17	2.00
Gadiformes	1	8	4.17	16.00
European flounder (<i>Platichthys flesus</i>)	7	1	29.17	2.00
Righteye flounders (<i>Pleuronectidae</i>)	4	4	16.67	8.00
Lumpsucker (<i>Cyclopterus lumpus</i>)	4	4	16.67	8.00
Angler (<i>Lophius piscatorius</i>)	0	2	0.00	4.00
Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)	1	0	4.17	0.00
Cusk (<i>Brosme brosme</i>)	0	1	0.00	2.00
Wolfish (<i>Anarhichadidae</i>)	0	1	0.00	2.00
Salmonids (<i>Salmonidae</i>)	0	5	0.00	10.00
Fish (<i>Pisces</i>)	0	3	0.00	6.00
Total fish (<i>Pisces</i>)	19	36	79.17	72.00
Common scoter (<i>Melanitta nigra</i>)	1	0	4.17	0.00
Willow ptarmigan (<i>Lagopus lagopus</i>)	1	0	4.17	0.00
Common gull (<i>Larus canus</i>)	1	0	4.17	0.00
Dabbling ducks (<i>Anatinae</i>)	1	4	4.17	8.00
Bird (<i>Aves</i>)	1	5	4.17	10.00
Total birds (<i>Aves</i>)	5	9	20.83	18.00
Harbour porpoise (<i>Phocoena phocoena</i>)	0	1	0.00	2.00
Total mammals (<i>Mammalia</i>)	0	1	0.00	2.00
Unidentified	0	4	0.00	8.00
Total	24	50	100.00	100.00

where x_1 is nestlings age. v_{it} is the unobserved individual effect between the two nesting sites and α_i is the error term that cannot be observed econometrically. N = number of prey = 74

The age of the first unassisted feeding was approximately 41 days, the next two at 72 and 73 days of age which includes all prey delivered after age 70 days. According to the best model, the shift, where the nestlings feed unassisted on 50 % of the prey, can be reverse predicted to age 76.2 days. Nestling age had a significant effect on the probability that the nestlings ingested prey unassisted (table 7).

Intrabrood conflict: Siblicide

One of the nestlings at Brokskar died during the monitoring on the account of siblicide. Ahead of its death, the nestling was noticeably smaller than its sibling even if they had virtually the same size when the video recording started at Brokskar on 23 May. The smaller nestling was pecked on by its sibling occasionally from 24 May at the latest. This escalated to more frequent and violent pecking on 1 June, just after the smaller nestling, positioned nearest the adult female, had been fed noticeably more than its larger sibling. The pecking intensified on 4 June, and subsequently the smaller nestling died and was buried by the female adult, who witnessed the siblicide.

Table 7: Statistical models for the probability that the two nestlings of the white-tailed eagle in northern Norway fed without assistance rather than being fed, sorted by AICc. SD in parentheses.

	Model 1	Model 2	Model 3	Model 4
(Intercept)	-8.25** (2.50)	-7.92** (2.62)	-2.77 (41.19)	-2.63** (0.83)
Age	0.11** (0.04)	0.13* (0.05)	- -	- -
PreyMass	- -	-0.00 (0.00)	- -	-0.00 (0.00)
log10(Age)	- -	- -	3.00 (24.80)	- -
log10(PreyMass)	- -	- -	-14.30 (21.25)	- -
log10(Age):log10(PreyMass)	- -	- -	7.08 (12.28)	- -
Log Likelihood	-7.27	-6.80	-6.19	-12.13
AICc	20.89	22.19	23.28	30.61
Δ AICc	0.00	1.30	2.40	9.72
AICc-weight	0.55	0.28	0.16	0.00
Num. obs.	73	73	73	73
Num. variables (K)	1	2	3	1

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Activity level

There were periods when the white-tailed eagles were more successful in bringing food to the nests than other periods, and this variation was explained by various variables. Among all the models considered, five models had $\Delta AICc < 2.0$ (table 8). All of these included whether there was an ebbing or flooding tide as a significant variable.

The most parsimonious model was M18, showing the effect of time of day and precipitation as well as whether there was an ebbing or flooding tide. According to this model, the activity level acrophase was at 7 am and bathyphase at 7 pm, and the activity level was considerably higher on low precipitation (figure 5), even if the precipitation term was non-significant, and at ebbing tide (figure 5a). The model M24iii had just slightly lower AICc and the same number of variables. In this model, the cosinor terms were absent, replaced by tidal level and an interaction term between the ebbing factor and the tidal level. The model predicts highest activity levels at ebbing tide and at low tidal levels at ebbing tide (figure 6a). On flooding tide, the activity levels was predicted somewhat higher at high tidal levels (figure 6b). Also in this model, the precipitations effect is considerable despite not being significant.

M18 can be interpreted for $time = t$

$$\text{Logit } P(\text{prey})_{it} = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_4 x_{4i} + \beta_6 x_{6i} + \alpha_i + v_{it}, i = 1, 2, \dots, N,$$

and M24iii

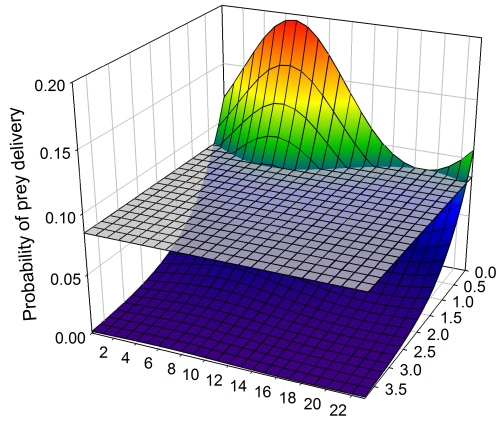
$$\text{Logit } P(\text{prey})_{it} = \beta_0 + \beta_3 x_{3i} + \beta_4 x_{4i} + \beta_5 x_{4i} x_{3i} + \beta_6 x_{6i} + \alpha_i + v_{it}, i = 1, 2, \dots, N,$$

Table 8: Models for explaining the probability for prey deliveries in the white-tailed eagles nests in northern Norway with $\Delta AICc < 2.0$, ranked by AICc. SD in parentheses.

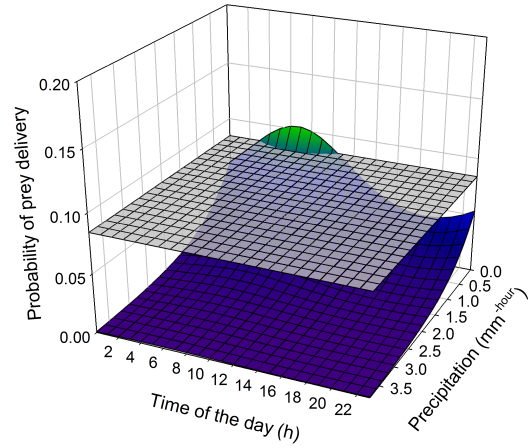
	M21i	M29	M18	M24iii	M32
(Intercept)	-0.99* (0.46)	-1.47*** (0.38)	-1.90*** (0.25)	-0.86 (0.46)	-2.21*** (0.49)
I(cos(2 * pi * Hour/24))	-0.13 (0.18)	-0.07 (0.18)	-0.09 (0.18)	-	-0.04 (0.19)
I(sin(2 * pi * Hour/24))	0.48** (0.18)	0.51** (0.18)	0.48** (0.18)	-	0.53** (0.19)
TideLevel	-0.01** (0.00)	-0.00 (0.00)	-	-0.01* (0.00)	-
Ebbing_factorUP	-2.10** (0.75)	-0.63* (0.31)	-0.75** (0.27)	-2.15** (0.75)	-0.76** (0.27)
Ebbing_factorUP:TideLevel	0.01* (0.00)	-	-	0.01* (0.00)	-
Precipitation	-	-1.20 (0.65)	-1.19 (0.65)	-1.07 (0.63)	-1.04 (0.66)
Temperature	-	-	-	-	0.04 (0.05)
Log Likelihood	-238.81	-238.93	-240.20	-240.43	-239.93
AICc	491.75	492.00	492.49	492.95	494.00
$\Delta AICc$	0.00	0.24	0.74	1.20	2.24
AICc-weight	0.29	0.26	0.20	0.16	0.09
Num. obs.	866	866	866	866	866
Num. variables (K)	5	5	4	4	5

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

where β_0 is y-intercept, β_1 is $\cos(2 \times 2 \times \pi \times \text{HOUR}/24)$, β_2 is the slope for $\sin(2 \times 2 \times \pi \times \text{HOUR}/24)$, β_3 for the tide level, β_4 for the ebbing factor, β_5 for the interaction term of ebbing factor and tide level and β_6 for the precipitation. v_{it} is the unobserved individual effect between the two nests and α_i is the error term that cannot be observed econometrically. N = number of hour blocks = 866

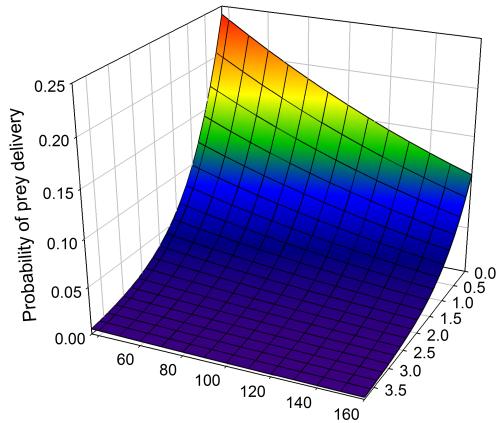


(a)

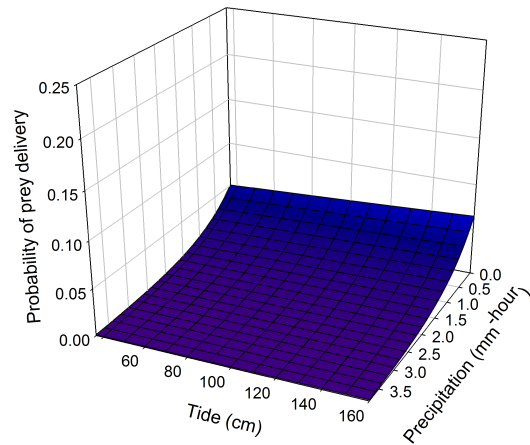


(b)

Figure 5: The probability of prey delivery within an hour at the white-tailed eagle nests in northern Norway as a function of time of day and precipitation, based on model M18. (a) ebbing tide (b) flowing tide



(a)



(b)

Figure 6: The probability of prey delivery within an hour at the white-tailed eagle nests in northern Norway as a function of tidal level and precipitation, based on model M24iii. (a) ebbing tide (b) flowing tide

Discussion

Dietary selection and mass of prey

During the monitoring period of 865 h 33 m, each nestling received 432 g of prey items per day with average mass of 425 g. Fish was the main prey group delivered by the white-tailed eagles, constituting 74 % of deliveries by number, while birds constituted 19 % of the deliveries. As 5 % of the delivered items remained unidentified, the real figures for the proportion of either fish or birds, or both, were probably somewhat higher. In Kobbevågen, where the nest was located near the shallow bay, more righteye flounders prey were delivered than at Brokskar, despite the relatively short distance between the two nests.

My study showed a higher percentage of fish among prey delivered at the nests than reported in a prior study of the diet of the white-tailed eagle in Norway by Willgoths (1961, 1963), who found that 50.4 % of indefinite or 33.5 % of definite items of vertebrate species were fish (Pisces), while 39.5 % and 53.5 % of the indefinite and definite prey items, respectively, were birds (Aves). The data presented by Willgoths (1961, 1963) were based on field observations and examination of prey remains and pellets, as well as information from locals gathered through inquiry forms, personal conversations and newspaper notes. In the Danube Delta, Romania, Sandor et al. (2015), by examining remains and pellets, found that 44.6 % of the prey were fish and 50.0 % were birds. Furthermore a study in Finland by Sulkava et al. (1997) found that fish constituted 42 % of the prey and birds 51 %.

Willgoths (1961), however, pointed out the problem that the remains from fish in pellets were fewer than direct observation would lead one to suggest, and admitted that the fish portion of the prey items may have been underestimated. The explanation was that the fragile fishbones might disappear to a larger extent than the more solid bones from terrestrial organisms, because fish are more completely digested or because the pellets for other reasons were less likely to include fish remains (cf. Tornberg and Reif, 2007; Homme, 2008; Slagsvold et al., 2010a).

With the aid of stable isotope analysis of liver and muscle tissues of white-tailed eagles found dead, Nadjafzadeh et al. (2016) concluded that 90.7 % of the diet of studied white-tailed eagles northeastern Germany was made up of aquatic prey, thus terrestrial prey accounted for 9.3 %. This also suggests that the amount of fish in the diet might be underestimated when examining remains and pellets.

The diet of the white-tailed eagle has, however, been proved to vary geographically and seasonally. Sulkava et al. (1997) found that fish constituted 67 % of the diet in the Finnish lapland, but only 32 % and 27 % in the Quark region and Åland islands, respectively. Nadjafzadeh et al. (2016) found that the isotope ratios varied between Germany, Greenland and Finland. By sampling pellets and remains in Norway, Willgoths

(1961) found a more bird-based diet in winter time than in the summer, and reasoned that this occurred due to many fish species having a tendency to use deeper water in winter. Nadjafzadeh et al. (2016) also found seasonal dietary variations in white-tailed eagles in northeastern Germany. Both a geographical and a seasonal variation support the documentations of functional response in the white-tailed eagle by e.g. Nadjafzadeh et al. (2013), and substantiate that the white-tailed eagle is a generalist exploiting the locally most available prey.

Video monitoring nests of birds of prey in the breeding season allows one to observe each prey delivered at the nest. Determining whether the prey item is a fish or a bird can mostly be done with high certainty. However, a functional response of white-tailed eagles, in my study suggested by the higher frequency of righteyed flounders in Kobbbevågen than at Brokskar, shows that any study of white-tailed eagles diet in a specific area and season can not be generalized to other areas and other seasons.

Furthermore, identifying prey items to species or family are not always possible. I was unable to identify four of the 74 prey items. Moreover, 18 of the prey items was inconclusively identified to species or family, but in such way that the decision was seen as plausible and the most probable based on the morphology and size. Furthermore, one of the registered items was only probably a prey, as the sun's position at the time disrupted the image, but was registered as prey due to the following feeding behaviour. In total 33 items were, conclusively or inconclusively, identified to species and 29 items to family.

The estimated daily biomass of 432 g delivered per nestling is an overestimate. Numerous bits were occasionally eaten off the prey by the adults, largely just before feeding the nestling. This happened primarily if the prey was delivered by the male, and the female had been at the nest for a longer period. Because the adults often had their back turned to the camera while feeding the young, and the video resolution was limited, I was unable to quantify the amount eaten by the adults. In comparison, according to Cramp and Simmons (1980) and Willgohs (1961) the daily food requirement of an adult white-tailed eagle is 500 – 600 g.

The most striking result in prey species selection compared to the results of Willgohs (1961) is the high amount of relatively small righteyed flounders. However, that was only the case for the nest near the shallow bay of Kobbbevågen, suggesting a functional response for more accessible prey in the white-tailed eagle on a small spatial scale. In my video material, the righteye flounders were easy to identify to family level. Hence, the higher frequency of prey in that family at the nest at Kobbbevågen than at Brokskar was based on high-quality observations.

The average prey mass of 425 g is not impressive for a raptor with a wing-span of 200 – 240 cm (Cramp and Simmons, 1980). According to optimal foraging theory, a large predator should select large prey (Krebs and Stephens, 1978). High availability of intermediate size prey could, however, make that the more profitable prey choice (Nad-

jafzadeh et al., 2015). Choosing smaller prey items may also relieve the adults from prey partitioning later in the nestling period when the eaglets feed increasingly unassisted, allowing especially the female adult to forage in a larger degree at an earlier stage (cf. Slagsvold and A Sonerud, 2007; Slagsvold et al., 2010b; Sonerud et al., 2013).

Unassisted feeding

Age was a significant explanatory variable for the probability for the nestlings to feed unassisted. The first unassisted feeding was registered at the Brokskar nest at 39 – 42 days of age on an approximately 16 cm long Gadiformes with a mass of c. 36 g. Unassisted feeding happened twice more at 72 and 73 days of age in Kobbbevågen on a European flounder (c. 22 cm, 103 g) and a cod (c. 18 cm, 600 g). There were several other occasions where the eaglets fed partly unassisted by handling large pieces, but the adults had in those cases quartered the specimens beforehand. The age for the fitted shift was 76.2 days given by my model.

According to Cramp and Simmons (1980), the young of white-tailed eagles feed themselves at 35 – 40 days. Willgohs (1961) observed that eaglets at five to six weeks (35 to 42 days) of age were able to pick up pieces from the nest, and from six to seven weeks (42 to 49 days) were able to tear off pieces from partly quartered prey, but still then failed to feed from intact prey of e.g. lumpsucker. At an age of seven to nine weeks (49 to 63 days), the eaglets dismembered prey largely by themselves (Willgohs, 1961).

The monitoring of the nest at Brokskar was terminated at a nestling age of 43 – 46 days, hence it is understandable that few incidents of unassisted feeding occurred. In Kobbbevågen, the monitoring lasted until the nestling was 73 days old. However, there was a gap in my video material between the nestling age 53 and 70 days. In the video material recorded after the nestling was 70 days old, there were only two deliveries of prey in total, and the eaglet fed unassisted both times. This can explain the late shift from my fitted model. It is likely that the shift in reality occurred earlier.

Additionally, because I primarily targeted only the video sequences where there was an adult landing or taking-off for a more thorough video review, I might have overlooked instances before the nestling was 53 days old where the eaglet fed itself with food remains in the nest subsequent to delivery. My video recordings nevertheless demonstrated that the adults invested substantially by feeding the eaglets at least until 53 days of age.

Intrabrood conflict: Siblicide

One of the nestlings in the nest at Brokskar was killed by its sibling. Subjected to pecking by its larger sibling, the smaller one became increasingly lackadaisical and passive until it was pecked to death 4 June. Such an event can be caused by asynchronous hatching, and are commonly viewed as adaptive reduction of brood size in response to food shortage

to make sure the maximum number of nestlings are raised to independence (Lack, 1947). There was a small difference in size between the nestlings when I started the monitoring approximately 3 – 6 days after hatching, increasing to a noticeable difference on the days before the death of the smallest nestling. However, delivered prey items throughout this conflict were left untouched in the nest for considerable amount of time before feeding, suggesting no acute food shortage.

Siblicide is highly unusual amongst white-tailed eagles and has been registered only a few times before in Norway (A. O. Folkestad, pers. comm.). Willgohs (1961) does not mention this type of behaviour, despite extensive observations of young in nests. A well known explanation for intrabrood conflicts was presented by Trivers (1974), who according to Hamilton's rule reasoned that each sibling is more genetically related to itself than its sibling, while the parents are similarly related to both. Hence, the siblings both demand more than their fair share from the parents point of view, and compete against each other for resources. This is commonly known as the sibling rivalry hypothesis. The parental approaching hypothesis predicts that the parents care more for the weakest nestling and in such way counter selfish behaviour (Trivers, 1974). However, I could not ascertain that the smaller nestling was prioritized, as the nestling receiving most of the food seemed to be the one positioned closest to the parent feeder, and the parent did not strive to feed the nestling positioned further away. Because the larger nestling usually was better positioned, the food was impartially distributed.

Hence, my video material substantiates the sibling rivalry hypothesis, and none of the adult seemed to behave according to the parental approaching hypothesis.

Activity level

During my video monitoring, which took place in northern Norway when the sun does not set, there were several prey deliveries around the time the sun is positioned lowest (c. 0:45), e.g. 11:18 pm, 0:05 am, twice 0:09 am, 0:13 am, 2:16 am and 2:42 am. I further registered incoming birds without prey or with nest material at 0:34 am and 1:42 am, and departing birds at 23:22 am, 0:34 am, 1:20 am, 1:39 am, 2:11 am and 2:16 am.

The time of day explained the probability of prey deliveries, but the bathyphase was around 7 pm, and not around midnight. Furthermore, the acrophase was around 7 am, and not around midday. Thus, the white-tailed eagles in northern Norway was not strictly diurnal.

In other studies, the white-tailed eagle has been regarded as diurnal (Krone et al., 2009). During March – April in Norway they become active on average 44 min before sunrise and start to rest on average 11 min before sunset, according to Willgohs (1961). In northern Germany Krone et al. (2009) registered nearly no activity of a white-tailed eagle with a GPS logger during night in autumn and winter, while the distribution of activity at daytime varied, with an acrophase around midday.

Time of day, precipitation, tide, and whether it was an ebbing or flowing tide all contributed as explanatory variables for the probability of prey delivery within an hour block, used as a measure for the activity level. Whether there was an ebbing or flooding tide had a noticeable influence for explaining the probability for prey. The activity level was highest at ebbing tide, and in one of my best models the tidal level was a significant explanatory variable suggesting higher activity levels at low tidal levels in ebbing tide, and somewhat higher activity levels at high tidal levels in flooding tide (figure 6b). Precipitation did not explain the activity level in any of the five models with $\Delta AICc < 2$, but nevertheless was included in four of them, improving a poorer model with a tendency to less activity at rainfall. Ambient temperature was part of the fifth best model, but was not significant despite the wide range from 1.4 to 15.7°C during the monitoring period.

To the best of my knowledge, no study has investigated the effect of tidal levels and tidal flows on the activity level of any bird of prey. Moreover, precipitation or ambient temperatures has never before been attempted as predictors for the activity level of the white-tailed eagle. There are, however, reasons to expect that these abiotic components would have effect on the activity level.

The individuals studied here had their nests close to the sea, which supplied the eagle with most of its food. The tide affects the whereabouts of several fish species. By selective tidal-stream transport (STST), fish uses the tidal streams to transport them in the required direction (Gibson, 2003). Moreover, upshore migrating fish also move into the intertidal zone at high tides to maximize food input and/or reproductive output as well as minimizing predation (Rangeley and Kramer, 1998; Gibson, 2003). At ebbing tide, fish might become stranded (Willgohs, 1961). Furthermore, fish situated in the littoral zone may be easier to catch on ebb tide because their habitat in the littoral zone outside the intertidal part would be located closer to the surface. Dead fish, e.g. from fishermens gutting, may also be revealed on the shore on ebbing tide (Willgohs, 1961). Many downstream migrating shorebirds feed more intensively on increasingly exposed prey in the ebbing tide (Evans, 1976), hence expose themselves for birds of prey.

A wet plumage from rainfall would be an obstacle for non-diving birds including the white-tailed eagle. The white-tailed eagle, however, use most of their diurnal time perch-hunting, i.e. sit and wait for prey (Nadjafzadeh et al., 2015), hence rainfall might be less of an obstacle than it would be for species that more often hunt through e.g. soaring flights. When it comes to the ambient temperature, higher temperature in the cold northern climate may save energy which can be allocated to foraging. However, quick changes in ambient temperatures are unlikely to affect aquatic organisms, constituting most of the white-tailed eagles prey in my study, and the temperature in the littoral zone locally might have been a better explanatory variable.

Implications and further prospects

This study is, to the best of my knowledge, the first where the diet of white-tailed eagle has been assessed by video monitoring at the nest. There was a noticeable difference between the diet that I found and that found in studies where pellets and remains have been examined. I claim that video monitoring is a more accurate and cost-effective method for studying the diet in the breeding season than is collecting remains and pellets. Even with simple video equipment it was generally obvious whether each prey was a fish or a bird, and further identification to family or species were often possible. The stable isotope analysis (Nadjafzadeh et al., 2016) is interesting for several reasons, but can largely not be used for identifying species at this point.

Lead poisoning is a major cause of death in white-tailed eagles (Kenntner et al., 2001; Krone et al., 2006; Helander et al., 2009), and lead ammunition is the main source (Helander et al., 2009). A widespread assumption is that scavenging on hunter-killed game animals and gut piles containing lead fragments is the main cause of lead poisoning in raptors (Pain et al., 1993; Hunt et al., 2006). During my monitoring no prey item could be classified as mammal remains, except one whale tail-fin. However, examining the diet of white-tailed eagles in the breeding season does not contribute much information on lead poisoning, given the variation in diet throughout the year, and given that the breeding season does not coincide with the hunting season.

The white-tailed eagle has an energy-maximizer foraging strategy, rather than time-minimizer, and strongly select prey species according to optimal foraging theory, but can also opportunistically consume game carrion during periods with low prey availability (Krebs and Stephens, 1978; Nadjafzadeh et al., 2015). Nadjafzadeh et al. (2016) found that the white-tailed eagle in Germany shifted to a diet containing substantially more terrestrial prey in winter, including carrion from game mammal carcasses. The breeding season, corresponding with a time of high prey availability, e.g. fish situated shallow areas near the shore and migrating birds feeding at the shorelines, seem to allow the white-tailed eagle to select its prey according to the optimal foraging theory. The eagles I studied might, however, have shifted to more opportunistic behaviour after my monitoring period was over.

Conclusion

Fish were by far the most common prey group in the diet of the white-tailed eagles studied, and the prey delivered at the nest in Kobbbevågen suggested a strong selection for righteysed flounders. Prey deliveries were most frequent when the tide level was ebbing to full ebb, and the time of the day acrophase was in the early morning between 7 am and the bathyphase around 7 pm. This suggests that the white-tailed eagles in northern Norway might not be diurnal to such a degree as described for more southerly conspecifics. Whether the tide was flowing or ebbing largely explained the variation in activity level.

My study also showed that the adults quartered prey and fed the nestlings at least until 53 days of age.

Many studies on the diet of the white-tailed eagle have been based on collecting pellets and remains. The camera technology empowers more accurate studies on the matter within the breeding season. Due to spatially varying diet in conspecifics, more studies by video monitoring are needed to understand the diet of the white-tailed eagle. With the documented threat of lead poisoning to avian scavengers (e.g. Redig et al., 1980; Custer et al., 1984; Redig, 1997; Kenntner et al., 2001; De Francisco et al., 2003; Fisher et al., 2006; Hunt et al., 2006; Krone et al., 2006; Helander et al., 2009; Nadjafzadeh et al., 2013), knowledge about the diet of raptors also in autumn and winter is important for conservation and animal welfare. In terms of the white-tailed eagle, few studies have asserted this.

My study demonstrate that our knowledge regarding the activity patterns in the white-tailed eagle is limited, at least in my study area at high latitude where the light conditions were stable and where tidal levels had a wide range. This could be asserted more accurately by combining video recording of the nest with a GPS logger or an equivalent positioning system on the white-tailed eagle, than my approach based on prey deliveries.

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Appendix

Table 9: Information about length and mass for all the prey items delivered to the two white-tailed eagles nests in northern Norway during 866 h of video monitoring.

NestID	Type of prey	Taxa	Length (cm)	Comment	Est. mass (g)	N nestlings	Est. m pr. nestl.
1	Aves	Lagopus lagopus	20	Decapitated	440	1	440
1	Aves	Larus canus	15	Decapitated	348	1	348
1	Aves	Melanitta nigra	27	Decapitated	871	1	871
1	Aves	Anatinae	20	Decapitated	440	1	440
2	Aves	Anatinae	20	Decapitated	440	2	220
2	Aves	Anatinae	20	Decapitated	440	1	440
2	Aves	Anatinae	17	Decapitated	270	1	270
2	Aves	Anatinae	20	Decapitated	440	1	440
1	Aves	Bird	16	Decapitated	225	1	225
2	Aves	Bird	12	Decapitated	95	1	95
2	Aves	Bird	32	Decapitated	1803	1	1803
2	Aves	Bird	31	Decapitated	1640	1	1640
2	Aves	Bird	20	Decapitated	440	1	440
2	Aves	Bird	12	Decapitated	95	1	95
2	Mammalia	Phocoena phocoena		Tailfin	425	1	425
2	Pisces	Brosme brosme	70	-	2798	1	2798
2	Pisces	Lophius piscatorius	26	-	226	2	113
2	Pisces	Lophius piscatorius	40	-	787	2	393
1	Pisces	Myoxocephalus scorpius	26	-	230	1	230
1	Pisces	Cyclopterus lumpus	10	-	23	1	23
1	Pisces	Cyclopterus lumpus	20	-	189	1	189
1	Pisces	Cyclopterus lumpus	25	-	370	1	370
1	Pisces	Cyclopterus lumpus	30	-	640	1	640
2	Pisces	Cyclopterus lumpus	27	-	2025	2	1013
2	Pisces	Cyclopterus lumpus	17	-	116	2	58
2	Pisces	Cyclopterus lumpus	24	-	327	2	163
2	Pisces	Cyclopterus lumpus	15	-	79	1	79
1	Pisces	Gadus morhua	18	Head	600	1	600
2	Pisces	Gadus morhua	21	Head	953	2	476
2	Pisces	Gadus morhua	10	Head	103	1	103
2	Pisces	Gadus morhua	29	-	221	1	221
2	Pisces	Gadus morhua	32	-	299	1	299
2	Pisces	Gadus morhua	30	-	245	1	245
2	Pisces	Gadus morhua	37	-	466	1	466
1	Pisces	Pollachius virens	26	-	157	1	157
2	Pisces	Pollachius virens	30	-	243	2	121
2	Pisces	Gadiformes	25	Head	1608	1	1608
2	Pisces	Gadiformes	26	Head	1809	1	1809
2	Pisces	Gadiformes	15	Head	347	1	347
1	Pisces	Gadiformes	30	-	245	1	245
2	Pisces	Gadiformes	16	-	36	2	18
2	Pisces	Gadiformes	55	-	1568	1	1568
2	Pisces	Gadiformes	35	-	393	1	393
2	Pisces	Gadiformes	19	-	61	1	61
2	Pisces	Gadiformes	16	-	36	1	36
1	Pisces	Platichthys flesus	15	-	32	1	32
1	Pisces	Platichthys flesus	20	-	77	1	77
1	Pisces	Platichthys flesus	18	-	55	1	55
1	Pisces	Platichthys flesus	21	-	89	1	89
1	Pisces	Platichthys flesus	35	-	427	1	427
1	Pisces	Platichthys flesus	25	-	152	1	152
1	Pisces	Platichthys flesus	22	-	103	1	103
2	Pisces	Platichthys flesus	23	-	118	2	59

1	Pisces	Pleuronectidae	16	-	39	1	39
1	Pisces	Pleuronectidae	15	-	32	1	32
1	Pisces	Pleuronectidae	18	-	55	1	55
1	Pisces	Pleuronectidae	18	-	55	1	55
2	Pisces	Pleuronectidae	33	-	356	2	178
2	Pisces	Pleuronectidae	38	-	549	1	549
2	Pisces	Pleuronectidae	10	-	9	1	9
2	Pisces	Pleuronectidae	22	-	103	1	103
2	Pisces	Anarhichadidae	34		296	2	148
2	Pisces	Salmonidae	45	-	869	1	869
2	Pisces	Salmonidae	54	-	1510	1	1510
2	Pisces	Salmonidae	14	-	25	1	25
2	Pisces	Salmonidae	45	-	869	1	869
2	Pisces	Salmonidae	40	-	608	1	608
2	Pisces	Fish	12	Head	178	2	89
2	Pisces	Fish	10	Head	103	1	103
2	Pisces	Fish	35	-	393	2	197
2	-	Unidentified	-	-	425	1	425
2	-	Unidentified	-	-	425	1	425
2	-	Unidentified	-	-	425	1	425
2	-	Unidentified	-	-	425	1	425

Table 10: The monitoring time for the video monitoring of two nests of the white-tailed eagle in northern Norway.

Surveil.No	ID	OnsetDate	OnsetTime	TermDate	TermTime
1	Brokskar	23/05/2015	16:10:00	24/05/2015	16:31:57
2	Brokskar	27/05/2015	18:30:13	08/06/2015	09:20:55
3	Brokskar	11/06/2015	10:00:11	12/06/2015	10:39:32
4	Brokskar	18/06/2015	14:03:15	30/06/2015	05:26:55
5	Brokskar	02/07/2015	21:57:07	03/07/2015	13:22:21
6	Kobbevaagen	25/05/2015	19:01:25	26/05/2015	13:24:51
7	Kobbevaagen	27/05/2015	17:05:35	29/05/2015	23:29:13
8	Kobbevaagen	01/06/2015	15:56:57	02/06/2015	07:21:44
9	Kobbevaagen	04/06/2015	21:15:40	07/06/2015	05:09:19
10	Kobbevaagen	11/06/2015	10:59:08	11/06/2015	15:48:15
11	Kobbevaagen	18/06/2015	15:05:32	19/06/2015	15:27:59
12	Kobbevaagen	06/07/2015	13:47:10	09/07/2015	04:54:46

Table 11: Models for the probability for prey delivery at a white-tailed eagles nest with explanatory variables time of the day, precipitation, temperature, tide level, flowing or ebbing tide and relevant interaction terms, ranked by AICc. $c = 2 \times \pi^{HOURL/24}$

	(Intercept)	$\cos(c)$	$\sin(c)$	$\cos(2c)$	$\sin(2c)$	$\cos(3c)$	$\sin(3c)$	Precipitation	Temp	Tide	Ebbing	Prec:Temp	Prec:Tide	Prec:Ebbing	$\log_{10}(\text{Tide})$	$\log_{10}(\text{Tide}):Temp$	Temp:Ebbing	Ebbing:Tide	df	logLik	AICc	delta	weight	
M21i	-0.99	-0.13	0.48							-0.01	+							+	7	-238.8	491.8	0.0	0.13	
M29	-1.47	-0.07	0.51					-1.20		-0.00	+									7	-238.9	492.0	0.2	0.12
M18	-1.90	-0.09	0.48					-1.19			+									6	-240.2	492.5	0.7	0.09
M24iii	-0.86							-1.07		-0.01	+							+	6	-240.4	493.0	1.2	0.07	
M32	-1.77	-0.02	0.56					-1.05	0.04	-0.00	+								8	-238.7	493.5	1.7	0.05	
M27	-2.21	-0.04	0.53					-1.04	0.04		+								7	-239.9	494.0	2.2	0.04	
M18H2	-1.90	-0.10	0.44	-0.25	-0.01			-1.19			+								8	-239.2	494.7	2.9	0.03	
M18H3	-1.93	-0.13	0.44	-0.22	-0.06	-0.25	-0.27	-1.18			+								10	-237.2	494.7	3.0	0.03	
M21	-1.61	-0.10	0.48							-0.00	+								6	-241.5	495.1	3.3	0.02	
M28	-2.13	-0.02	0.58						0.07	-0.00	+								7	-240.5	495.1	3.4	0.02	
M30	-2.13	-0.02	0.58						0.07	-0.00	+								7	-240.5	495.1	3.4	0.02	
M15i	-1.02									-0.01	+							+	5	-242.6	495.3	3.5	0.02	
M9	-2.04	-0.13	0.45								+								5	-242.7	495.5	3.8	0.02	
M20	-2.56	-0.04	0.55						0.07		+								6	-241.7	495.6	3.8	0.02	
M17	-1.61	-0.07	0.52					-1.20		-0.00									6	-241.8	495.8	4.0	0.02	
M21H3	-1.52	-0.15	0.42	-0.29	-0.02	-0.27	-0.26			-0.00	+								10	-237.8	495.9	4.2	0.02	
M12	-1.90							-1.07			+								4	-244.0	496.1	4.3	0.02	
M28H3	-2.02	-0.07	0.53	-0.27	-0.01	-0.27	-0.27		0.07	-0.00	+								11	-236.9	496.1	4.4	0.01	
M21H2	-1.50	-0.12	0.43	-0.31	0.03					-0.00	+								8	-240.0	496.1	4.4	0.01	
M24	-1.51							-1.07		-0.00	+								5	-243.0	496.1	4.4	0.01	
M28H2	-1.99	-0.04	0.53	-0.30	0.04				0.06	-0.00	+								9	-239.1	496.5	4.7	0.01	
M25iii	-1.20								0.02	-0.01	+							+	6	-242.5	497.0	5.3	0.01	
M26	-1.94	-0.02	0.58					-1.04	0.04	-0.00									7	-241.5	497.2	5.4	0.01	
M31H2	-1.94	-0.02	0.58					-1.04	0.04	-0.00									7	-241.5	497.2	5.4	0.01	
M31H3	-1.94	-0.02	0.58					-1.04	0.04	-0.00									7	-241.5	497.2	5.4	0.01	
M9H3	-2.06	-0.16	0.40	-0.22	-0.07	-0.26	-0.26				+								9	-239.6	497.4	5.7	0.01	
M20H3	-2.58	-0.08	0.50	-0.22	-0.06	-0.27	-0.27		0.07		+								10	-238.6	497.5	5.8	0.01	
M9H2	-2.03	-0.13	0.41	-0.25	-0.02						+								7	-241.7	497.6	5.8	0.01	
M20i	-2.54	-0.04	0.55						0.06		+						+		7	-241.7	497.6	5.9	0.01	
M17i	-1.59	-0.07	0.52					-1.51		-0.00			0.00						7	-241.8	497.8	6.0	0.01	
M20H2	-2.53	-0.05	0.51	-0.24	-0.01				0.06		+								8	-240.8	497.8	6.1	0.01	
M12i	-1.91							-0.91			+							+	5	-244.0	498.0	6.2	0.01	
M24ii	-1.52							-0.90		-0.00	+							+	6	-243.0	498.1	6.3	0.01	
M23	-1.86							-1.09	-0.01		+								5	-244.0	498.1	6.3	0.01	
M24i	-1.49							-1.35		-0.00	+		0.00						6	-243.0	498.1	6.4	0.01	
M31	-1.45							-1.10	-0.01	-0.00	+								6	-243.0	498.2	6.4	0.01	
M5	-2.02										+								3	-246.2	498.3	6.6	0.00	
M15	-1.63									-0.00	+								4	-245.2	498.5	6.7	0.00	
M26H2	-1.80	-0.04	0.52	-0.30	0.02			-1.05	0.03	-0.01									9	-240.2	498.6	6.8	0.00	
M27H2	-1.80	-0.04	0.52	-0.30	0.02			-1.05	0.03	-0.01									9	-240.2	498.6	6.8	0.00	
M29H2	-1.80	-0.04	0.52	-0.30	0.02			-1.05	0.03	-0.01									9	-240.2	498.6	6.8	0.00	
M30H2	-1.80	-0.04	0.52	-0.30	0.02			-1.05	0.03	-0.01									9	-240.2	498.6	6.8	0.00	
M19	-2.29	-0.02	0.59						0.07	-0.00									6	-243.3	498.7	6.9	0.00	
M26H3	-1.85	-0.07	0.52	-0.27	-0.03	-0.25	-0.26	-1.02	0.03	-0.01									11	-238.2	498.8	7.0	0.00	
M27H3	-1.85	-0.07	0.52	-0.27	-0.03	-0.25	-0.26	-1.02	0.03	-0.01									11	-238.2	498.8	7.0	0.00	
M29H3	-1.85	-0.07	0.52	-0.27	-0.03	-0.25	-0.26	-1.02	0.03	-0.01									11	-238.2	498.8	7.0	0.00	
M30H3	-1.85	-0.07	0.52	-0.27	-0.03	-0.25	-0.26	-1.02	0.03	-0.01									11	-238.2	498.8	7.0	0.00	
M8	-1.75	-0.11	0.49							-0.00									5	-244.4	498.8	7.1	0.00	
M6	-2.32	-0.10	0.48					-1.18											5	-244.4	498.9	7.2	0.00	
M19i	-1.05	0.00	0.60						0.24						-0.92	-0.08			7	-242.7	499.6	7.8	0.00	

M8H3	-1.67	-0.14	0.43	-0.30	-0.03	-0.26	-0.25			-0.01						9	-240.7	499.7	7.9	0.00
M8H2	-1.65	-0.11	0.44	-0.32	0.02					-0.01						7	-242.8	499.7	7.9	0.00
M19H3	-2.20	-0.06	0.54	-0.27	-0.03	-0.27	-0.26		0.07	-0.01						10	-239.8	499.8	8.1	0.00
M23i	-1.89								-0.50	-0.00		+		-0.11		6	-243.9	499.9	8.2	0.00
M23ii	-1.86								-0.94	-0.01		+			+	6	-243.9	500.0	8.2	0.00
M19H2	-2.16	-0.03	0.54	-0.30	0.02				0.06	-0.01						8	-241.9	500.0	8.2	0.00
M14	-2.20								0.02			+				4	-246.0	500.1	8.3	0.00
M23iii	-1.88								-1.09	-0.00		+				6	-244.0	500.1	8.3	0.00
M25	-1.81								0.02	-0.00		+				5	-245.1	500.2	8.5	0.00
M11	-1.65								-1.08	-0.00						4	-246.2	500.4	8.6	0.00
M16	-2.63	-0.06	0.53						-1.03	0.04						6	-244.2	500.4	8.7	0.00
M6H2	-2.33	-0.10	0.44	-0.23	-0.06				-1.17							7	-243.5	501.2	9.4	0.00
M6H3	-2.36	-0.13	0.44	-0.20	-0.10	-0.25	-0.26		-1.16							9	-241.5	501.3	9.5	0.00
M25i	-1.91								0.26			+				6	-244.6	501.3	9.5	0.00
M1	-2.42	-0.14	0.45													4	-246.8	501.7	10.0	0.00
M7	-2.96	-0.06	0.55						0.07							5	-245.8	501.8	10.0	0.00
M14i	-2.23								0.03			+				5	-246.0	502.1	10.3	0.00
M25ii	-1.83								0.03	-0.00		+				6	-245.1	502.3	10.5	0.00
M11i	-1.62								-1.47	-0.00				0.00		5	-246.1	502.3	10.6	0.00
M16i	-2.66	-0.06	0.53						-0.60	0.04				-0.08		7	-244.1	502.4	10.6	0.00
M22	-1.59								-1.11	-0.01	-0.00					5	-246.1	502.4	10.6	0.00
M2	-2.29								-1.06							3	-248.3	502.7	10.9	0.00
M4	-1.77									-0.00						3	-248.3	502.7	10.9	0.00
M16H2	-2.61	-0.06	0.49	-0.23	-0.05				-1.03	0.03						8	-243.3	502.8	11.0	0.00
M16H3	-2.65	-0.09	0.48	-0.20	-0.10	-0.25	-0.26		-1.01	0.03						10	-241.3	502.9	11.1	0.00
M22iii	-1.49								-1.11	0.29						6	-245.5	503.1	11.3	0.00
M1H3	-2.46	-0.17	0.40	-0.22	-0.12	-0.26	-0.25									8	-243.8	503.7	11.9	0.00
M1H2	-2.43	-0.14	0.41	-0.24	-0.06											6	-245.8	503.8	12.0	0.00
M7H3	-2.99	-0.09	0.50	-0.20	-0.10	-0.26	-0.26		0.07							9	-242.8	503.8	12.1	0.00
M7H2	-2.94	-0.06	0.50	-0.23	-0.05				0.06							7	-244.9	504.0	12.3	0.00
M22i	-1.62								-0.48	-0.00	-0.00			-0.12		6	-246.1	504.2	12.5	0.00
M22ii	-1.56								-1.50	-0.01	-0.00			0.00		6	-246.1	504.3	12.6	0.00
M13	-1.95								0.02	-0.00						4	-248.2	504.4	12.7	0.00
M10	-2.24								-1.09	-0.01						4	-248.3	504.7	12.9	0.00
M0	-2.39															2	-250.4	504.8	13.0	0.00
M13i	-1.92								0.32							5	-247.5	505.1	13.4	0.00
M3	-2.57								0.02							3	-250.2	506.5	14.7	0.00
M10i	-2.27								-0.58	-0.00				-0.10		5	-248.3	506.6	14.8	0.00



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

Postboks 5003
NO-1432 Ås
Norway