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Monitoring Daily Activity and Parental Food Provisioning in the Atlantic Puffin (*Fratercula arctica*) by the Use of Camera Traps

Overvåkning av aktivitetsmønster og byttedyrleveringer hos lunde (*Fratercula arctica*) ved bruk av viltkamera

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Abstract

Seabirds are top predators in the marine environment, and because seabird diet may reflect fish availability, diet may function as an indicator of fish stocks and ecosystem status. Seabird diet is traditionally studied in colonies during the breeding season, often carried out by observing adult birds returning with food loads for the chick(s), or by catching fish-carrying adults using mist-nets or noose-poles and collecting the prey. In this study, remote photography was introduced as a less invasive method of monitoring chick diet in the Atlantic puffin (*Fratercula arctica*) at Bjørnøya, Svalbard. Camera traps were deployed at puffin burrow entrances to record activity in the 2015 and 2016 breeding seasons. Six of the eleven breeding attempts were successful, and 160 prey load deliveries were recorded. In addition, food samples collected by the Norwegian Polar Institute (NP) at Bjørnøya were analyzed and compared with data retrieved from camera trap images. Capelin (*Mallotus villosus*), daubed shanny (*Leptoclinus maculatus*), sandeel (*Ammodytes spp.*) and gadids (*Gadinae*) were identified in the prey load deliveries recorded by camera traps. Gadids were not found in the collected samples, but Atlantic herring (*Clupea harengus*) was identified. Mean length of prey fish recorded by camera traps was 58.3 mm, and mean number of fish per load was 3.2. Number of fish per load decreased with increasing fish length. Fish length and number of fish per load were used to calculate prey mass and load mass. Mean load mass was 5.6 g, while mean load mass for collected samples was 6.6 g. Mean number of daily deliveries was 1.4. Compared to reported rates of delivery ranging from 5.5 to 10.3 deliveries per day at Hornøya, Finnmark, camera traps in my study recorded one out of four prey load deliveries at best. Inter-annual variance in prey load composition suggests that feeding conditions were better in 2016 than in 2015. For puffins breeding at Bjørnøya, hatching date ranged from 27 June to 10 July. No daily activity pattern in parental food provisioning was found. Prior to this study, little was known about puffin diet at Svalbard. Results should be interpreted cautiously since they are based on relatively few prey load deliveries, but the method presented demonstrates the potential of using camera traps to monitor parental food provisioning in a colonial seabird species.

Sammendrag

Sjøfugler er toppredatorer i marine økosystemer. Dietten til sjøfugl gjenspeiler tilbudet av byttedyrfisk, slik at sjøfugldiett kan fungere som en indikator på fiskebestander og tilstanden til økosystemet. Vanligvis blir sjøfuglenes diett studert i hekketida, blant annet ved å observere voksne fugler som returnerer med mat til ungen(e) eller ved å fange voksne fugler i nett eller med en såkalt fleygustong (en stang med et utspilt nett i enden) og samle inn fisken de har med seg. I dette studiet introduseres viltkamera som en ny metode for overvåking av dietten til lunde (*Fratercula arctica*). Viltkameraer ble montert i inngangen til lundereir på Bjørnøya, Svalbard i hekkesesongene 2015 og 2016. Seks av elleve hekkinger var vellykkede, og totalt 160 matleveringer ble avbildet. I tillegg ble næringsprøver innsamlet av Norsk Polarinstitutt analysert for å sammenlikne med data fra viltkameraene. Byttedyrartene som ble avbildet på viltkameraene var lodde (*Mallotus villosus*), tverrhalet langebarn (*Leptoclinus maculatus*), sil (*Ammodytes sp.*) og torskefisk (*Gadinae*). Torskefisk ble ikke funnet i næringsprøvene, derimot ble det funnet sild (*Clupea harengus*). Gjennomsnittlig lengde på avbildet fisk var 58.3 mm, mens antall fisk per levering var 3.2. Antall fisk per levering avtok med økende lengde på byttefisk. Lengde på fisken og antall fisk per levering ble brukt til å beregne byttedyrmasse og masse per levering. For leveringer fanget på bilde var gjennomsnittlig vekt per levering 5.6 g, mens innsamlede prøver hadde gjennomsnittsvekt på 6.6 g. Gjennomsnittlig antall leveringer per dag var 1.4. Til sammenlikning varierte antall leveringer på Hornøya i Finnmark fra 5.5 til 10.3 leveringer daglig. Med Hornøya som referanse betyr dette at viltkameraene i beste fall fanget opp en av fire leveringer. Sesongvariasjon i diett tydet på en forbedring i næringstilgang fra 2015 til 2016. Klekkedato for lunden på Bjørnøya varierte fra 27. juni til 10. juli. Det ble ikke funnet noe døgnmønster i foreldrenes matleveringer. Forut for dette studiet visste man lite som lundens diett på Svalbard. På grunn av begrenset datagrunnlag bør resultatene som presenteres her tolkes med varsomhet, men metoden som er brukt demonstrerer potensialet som ligger i å bruke viltkamera ved overvåking av kolonihekkende sjøfugl.

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Introduction

Seabirds live in an environment with fluctuating food quality and quantity, and need to adapt to these changes in order to breed successfully (Kadin et al. 2016). Mobile animals divide their time between foraging and resting, and spend considerable time inactive during favorable feeding conditions (Herbers 1981). Due to flexible time-budgets, more time can be allocated to foraging when feeding conditions are deteriorating (Litzow & Piatt 2003). Seabirds are flexible in chick investment (Erikstad et al. 1997), and are able to compensate for changes in food quality by changing feeding rates (Eilertsen et al. 2008) and prey load composition, i.e. prey size, mass, energy content and number of fish per load (Barrett 2002; Kadin et al. 2016). Chick provisioning pose a high metabolic cost for adult birds (Davoren & Burger 1999; Gabrielsen 2009), yet it is advantageous to increase parental effort in the current breeding season as long as own survival and future reproduction is not jeopardized (Erikstad et al. 1997; Kadin et al. 2016). During the breeding season, all seabirds are central place foragers depending on adequate food resources within foraging range from the colony (Harris & Wanless 2011), and provisioning should be optimized (Ydenberg 1994) in order to maximize adult bird fitness (Pyke 1984). According to central place foraging theory, energy gain is dependent on travel cost and travel time, and animals are expected to select larger prey with increasing travel distance (Pyke 1984 and references therein). The ability of auks to travel far from the colony without too much energy loss is limited by high cost of flight due to high wing-loading as a consequence of adaptations to both flight and maneuverability under water (Nettleship & Birkhead 1985).

The Atlantic puffin (*Fratercula arctica*, hereafter referred to as puffin) is a pelagic diving alcid (Fauchald et al. 2015a) endemic to the North Atlantic Ocean (Harris & Wanless 2011). Being a boreal species (Gabrielsen 2009), the puffin is associated with a southerly distribution. Due to a warmer climate, the species' distribution range is expected to move to the north coinciding with a northward shift in prey species, and puffin numbers are already increasing in the Barents Sea (Fauchald et al. 2015b). Of the European puffin population, 27 % breed in Norway (Anker-Nilssen et al. 2015), providing Norway with an international conservation responsibility. Due to a population decline, the puffin is considered vulnerable (VU) on the Norwegian Red List, while the Svalbard population has status least concern (LC) (Henriksen & Hilmo 2015). The knowledge about the basic breeding biology of puffins in Svalbard is scarce, despite c. 50 colonies with

estimated 10 000 breeding pairs (Strøm 2006). Population census data for puffins on Bjørnøya indicate a breeding population of roughly 600 breeding pairs (Anker-Nilssen et al. 2007). Puffins usually breed in burrows dug out in soil, commonly deep and with several entrances (Harris & Wanless 2011). In the lack of loose soils, puffins at Svalbard breed in holes between rocks and crevices (Strøm 2006), often with one single entrance, which makes camera monitoring applicable. In puffins, incubation normally lasts for 40-45 days (Myrberget 1962), and fledging occur 38-44 days after hatching (Harris & Wanless 2011). Both adults provide the chick with small, schooling fish (Strøm 2006). Puffins catch prey fish by pursuit diving down to maximum 68 m (Burger & Simpson 1986). Foraging ranges extend tens of kilometers offshore from the colony, with increasing feeding ranges under poor feeding conditions (Harris et al. 2012).

With short food webs and few key species on each trophic level, the Barents Sea is a simple ecosystem with tight links between trophic levels (Sakshaug et al. 1994; Theisen 1997). Due to fluctuating recruitment and constantly changing fish populations, prey fish available to seabirds vary between years (Furness & Camphuysen 1997). Because seabird diet composition reflects prey availability (Furness & Camphuysen 1997; Barrett 2002; Durant et al. 2009), long-term seabird diet studies can be used as an indicator of marine fish stocks and ecosystem status (Durant et al. 2009). Diving depth, duration of dives and prey fish size is shorter for puffins than for larger seabirds (Barrett 2002), limiting their ability to compensate for deteriorating food availability. Changes in feeding conditions is expected to force a rapid switch in diet composition in small-bodied seabirds (Furness & Camphuysen 1997), making the puffin an excellent study species (Barrett 2002).

Investigation of chick diet by observation in the colony is possible because puffins carry one or more fish crosswise in the bill back to the burrow (Harris & Wanless 2011). In addition to direct observation with binoculars (eg. Barrett 2002; Eilertsen et al. 2008) or telescope (Rodway & Montevecchi 1996), mist-netting (Rodway & Montevecchi 1996; Barrett 2002) and catching fish-carrying adults with noose-poles and collecting prey fish (Eilertsen et al. 2008) are previously used methods to monitor puffin chick diet during the breeding season. Examining content of stomachs, regurgitations and excrements, collection of dropped fish and biochemical analysis are other methods used to sample seabird diet (Barrett et al. 2007). Observation is often combined with collection of food samples for calibration of observations (Barrett 2002; Eilertsen et al.

2008; Gaglio et al. 2016), but is not a feasible method at Bjørnøya due to the topography of the colony (Hallvard Strøm pers.comm.). Methods that require catching of adult birds and confiscating food loads are obviously disturbing (Cutler & Swann 1999) and should be avoided when possible. Additionally, visual sampling is associated with low verifiability and possible observational bias. To make monitoring less invasive and more time-efficient, I introduce remote photography as an alternative monitoring method of puffin chick diet. Remote photography is defined by Cutler & Swann (1999) as “the photography (...) of wild animals in the absence of the researcher”, and has enabled temporally high resolution observations of prey delivered to chicks during breeding (Steen et al. 2012; Sonerud et al. 2014). Photo trapping is simple and requires a minimum of fieldwork, hence it is cost-effective compared to traditional monitoring methods (Steen 2009; Cox et al. 2012). Also, data are verifiable and can be corrected for observational bias (Cutler & Swann 1999).

To the best of my knowledge, camera traps have not previously been used to monitor chick diet in the Atlantic puffin. The aim of my study was (1) to examine if camera traps are suitable for monitoring daily activity and parental food provisioning in the Atlantic puffin, and (2) to describe parental provisioning in the puffin at the northern range of its distribution.

Material and methods

Study area

The study was conducted in Nordhamna at the north side of Bjørnøya (74.30° N, 18.55° E, figure 1), where there is midnight sun from 30 April until 12 August. The entire island and the surrounding 12 nautical miles is protected as a nature reserve (Forskrift om fredning av Bjørnøya naturreservat 2002). Steep cliffs surround the island, making an excellent breeding habitat for seabirds. The polar front, where warm Atlantic currents meet cold Arctic currents, is located near Bjørnøya, making the waters surrounding the island among the most productive in the Barents Sea. The climate of Bjørnøya is Arctic oceanic (Theisen 1997), with relatively mild winters and cold summers. Average air temperature in the coldest and warmest months are -8.1 °C in January and 4.4 °C in August, respectively, and annual mean temperature is -2.4 °C (Norwegian Meteorological Institute 2017).

Bjørnøya holds one of the largest seabird breeding colonies in Europe (Theisen 1997), and is one of few places where all the six Atlantic auk species breed (Strøm & Bakken 2004). Trends in seabird populations found at Bjørnøya are representative for seabirds both in the northern and southern Barents Sea (Systad & Strøm 2012; Anker-Nilssen et al. 2015), which is why Bjørnøya has been chosen as a key location for seabird monitoring in the SEAPOP program (Anker-Nilssen et al. 2015). Puffins breeding in Norway are not monitored north of Hjelmsøya, Finnmark (71.03° N, 24.43° E), located more than 400 km southeast of Bjørnøya.



Figure 1: Bjørnøya is located halfway between Spitsbergen and mainland Norway in the western Barents Sea (Cherel et al. 2001). The study area, Nordhamna, is marked with a hatched rectangle.

Remote photography

The fieldwork was conducted in July 2015 and in June-August 2016 (table 1). In 2015, a pilot project was conducted to investigate whether camera traps at puffin burrow entrances would provide useful data. Employees at the Norwegian Polar Institute (NP) deployed five camera traps at puffin burrow entrances. SD-cards and batteries were not changed during the 2015 breeding season. Three cameras were still running when removed, while two cameras stopped recording on 18 July and 27 July, respectively, most likely due to discharged batteries. On 27 June 2016, camera traps were deployed at six puffin burrow entrances. Four cameras were controlled on 2 July make minor changes in setup if necessary. Batteries and SD-cards were changed on 13 July by NP employees. Cameras were removed from burrows with failed breeding. At burrows with

successful breeding, camera monitoring continued until 1 August. None of the burrows monitored in 2015 were monitored in 2016.

Table 1: Start and end date for monitoring, and total number of images recorded, for each of the eleven cameras set up to monitor Atlantic puffin burrows at Bjørnøya.

Year	Camera/burrow ID	Monitoring period	No. of images
2015	1	18 July - 27 July	39 542
	2	17 July - 27 July	23 137
	3	5 July - 18 July	30 176
	4	17 July - 27 July	40 135
	5	5 July - 27 July	144 017
2016	1	27 June - 13 July	6 191
	2	27 June - 1 August	67 483
	3	27 June - 13 July	14 834
	4	27 June - 1 August	21 574
	5	27 June - 1 August	20 978
	6	27 June - 13 July	32 590
Total			440 657

In 2016, cameras were deployed before hatching, except for the camera at burrow 3, where hatching occurred the day the camera was deployed (27 June). Date of first recorded fish load delivery was used as a measure of hatching date (Harris & Wanless 2011). In burrow 2, pieces of eggshell were observed at the entrance before the first recorded fish load delivery, and date of first eggshell recording was thus set as hatching date. In 2015, cameras were deployed after hatching for all successful burrows, and data on chick age was not obtained. In lack of better estimates, the mean hatching date in 2016 was set as hatching date for all burrows in 2015. The mean (\pm SD) was based on the three successful burrows in 2016, and calculated to be 6 July \pm 3.2 days.

Cameras were deployed at burrows where breeding was confirmed either by presence of a live chick or a warm egg. Cameras were deployed at burrows which seemed to have only one entrance. Given the natural constraints at each site, camera traps were placed attempting to record adult birds facing the camera when returning with prey load deliveries (figure 2). Care was taken to minimize triggering by neighboring or passing birds, as well as to avoid sea spray and rain covering the lens. Depending on the properties of the burrow entrance, camera traps were mounted on tripods (Joby Gorillapod SLR-ZOOM, DayMen Canada Acquisition ULC) and supported by rocks for stability and camouflage.



Figure 2: Camera traps were placed to capture adult Atlantic puffins returning to the burrow with prey load deliveries.

The camera traps used were Reconyx HyperFire Professional PC900 (Reconyx Inc., Holmen, WI, USA). These cameras are specially designed for research, i.e. to function under harsh conditions and to be very reliable (Wellington et al. 2014). The camera traps had passive infrared sensors (PIR), which triggered recording when changes in heat radiation (i.e. object surface temperature) were detected (Welbourne et al. 2016). Triggered shots were stored on 32 GB SD-cards (Sandisk SDHC class 4, Western Digital Technologies, Inc., CA, USA) as JPEG files. Cameras were powered by 12 AA lithium batteries (Energizer Ultimate Lithium, Energizer Holdings, Inc., MO, USA). Trigger speed (i.e. time interval between animal movement and first recorded image) was 0.2 s, maximum two images were recorded per s and number of images per trigger was programmable (Reconyx Inc. 2013). In 2015, the cameras were set to take three

images per trigger. In 2016, they were set at two images per trigger, because three images per trigger did not contain extra information. Date and time were automatically recorded for all images.

Image analysis: prey load deliveries

Images stored on SD-cards were transferred to an external hard drive. The image management software Reconyx MapView™ Professional was used for image analysis. Approximately 10 000 images were reviewed per day during image analysis, demanding four weeks to review all images from successful burrows. Considerable time was also spent reviewing images from unsuccessful burrows, even if this work progressed faster. All images with prey load deliveries were kept for further analysis. In addition, I got access to a small sample of puffin prey fish collected by NP employees during fieldwork at the colony at Bjørnøya in 2012-2014. Samples were frozen and analyzed by technicians at NP. For camera trap images, prey species, number of fish per load, and prey length were determined when possible. The initial aim was to get results comparable to other puffin diet studies. In lack of standardized field instructions for observation of seabird provisioning (Robert Barrett, pers.comm.), methodology for analysis of prey fish used in this thesis is described in detail in the following section.

When possible, prey fish were identified to the lowest taxonomic level. Hallvard Strøm (NP) and Robert Barrett (University of Tromsø), both of which are seabird experts involved in the SEAPOP project, conducted species identification. For 46 deliveries, number of fish per load was estimated both by me and Hallvard Strøm (NP) independently. When exact number of fish per load was not possible to determine, a minimum certain number of fish was counted (e.g. when a load contained at least three fish, it was classified as 3+). The minimum certain number of fish per load was used in further analysis (in this example three fish). In cases of disagreement about species identification and number of fish per load, emphasis was put on Strøm's perception, because he knows the local conditions at Bjørnøya after years of seabird research at the island.

The length of prey fish brought to the burrow by adult puffins was measured on images where one or more fish and the entire puffin bill were visible. Fish length measurements were performed in the image analysis software ImageJ Basics version 1.38 (Rasband 1997-2016). Fish length was measured as multiples of the puffin bill depth, and images were scaled using the known depth of the bill (figure 3). Weighted average of bill depths measured by Barrett et al. (1985) were used (37.1 ± 0.4 mm). For each image, I zoomed in to get the bill and the prey load as large as possible. For dark images, ImageJ was used to adjust brightness and contrast to improve visibility.

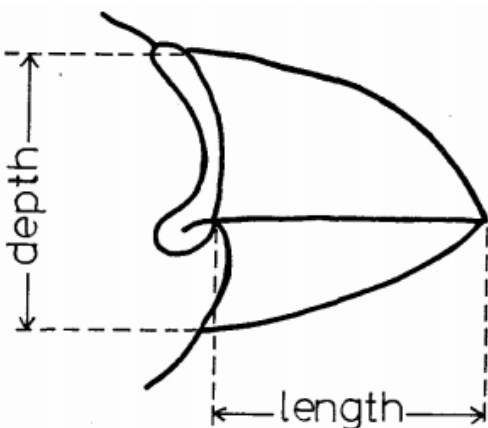


Figure 3: Illustration of Atlantic puffin bill. Bill depth was measured as the length on the highest point (Corkhill 1972).

Puffins carry prey fish crosswise in the bill, with fish tail protruding on one side and fish head protruding on the opposite side. Most images with prey load deliveries only depicted one side of the bill, i.e. only parts of the fish. From the images, it was not possible to predict how much of the fish body was protruding on the opposite side of the bill. The tail end of fish was measured along a segmented line drawn adjacent to the side of the fish, providing a relative measure of fish length (hereafter referred to as relative fish length or RFL). To calculate total fish length (hereafter referred to as absolute fish length or AFL), head and tail end percentages were calculated and added to the measured RFL. Total fish length, length of head end, and length of tail end were measured on images of prey-carrying puffins where the entire fish could be seen. Head-tail relationships were calculated separately for small fish (including larvae) and large fish. For small fish and larvae, ten fish length measurements on eight different online images were conducted. For large fish, two fish length measurements on two different images recorded by camera traps at Bjørnøya were conducted. For small fish and larvae, head end percentage (\pm SD)

was 32.2 % (± 14.2 %) and tail end percentage was 67.8 % (± 14.2 %). For large fish, head end percentage (\pm SD) was 15.6 % (± 0.37 %) and tail end percentage was 84.4 % (± 0.37 %). For 20 prey load deliveries, the length of prey fish was estimated both by me and seabird expert Robert Barrett independently, to quantify effect of observer on AFL estimates.

Prey mass was determined using length-mass relationships (table 2 and figure 4). Length-mass relationship for lesser sandeel (*Ammodytes marinus*) was used for all fish of the genus sandeel, according to species identification of puffin prey conducted by Barrett et al. (1987). Mass was estimated for prey load deliveries where both fish species, number of fish and AFL were known. In loads where only one fish length was measured, all the other fish was assigned the same length. If several fish in the same load were measured, the mean length of the measured fish was assigned to all fish. For two deliveries, prey loads consisted of two different fish species, and length measurement was possible only for individuals of one of the two species. Mass of the unmeasured species was then set as mean mass of other specimens of the same species.

Table 2: Length-mass relationship for fish provided by Atlantic puffins and recorded by camera traps. W denotes mass (g), while L denotes length (mm for gadids, cm for capelin, daubed shanny and sandeel).

Fish species	Length/mass relationship	Reference
Daubed shanny	$W = 0.00389 \times L^{3.12}$	} Froese et al. (2014) Froese & Pauly (2017)
Capelin	$W = 0.00398 \times L^{3.12}$	
Sandeel	$W = 0.00251 \times L^{3.13}$	
Gadids	$W = 133.6 \times 10^{-6} \times L^{2.33}$	Elliott & Gaston (2008)

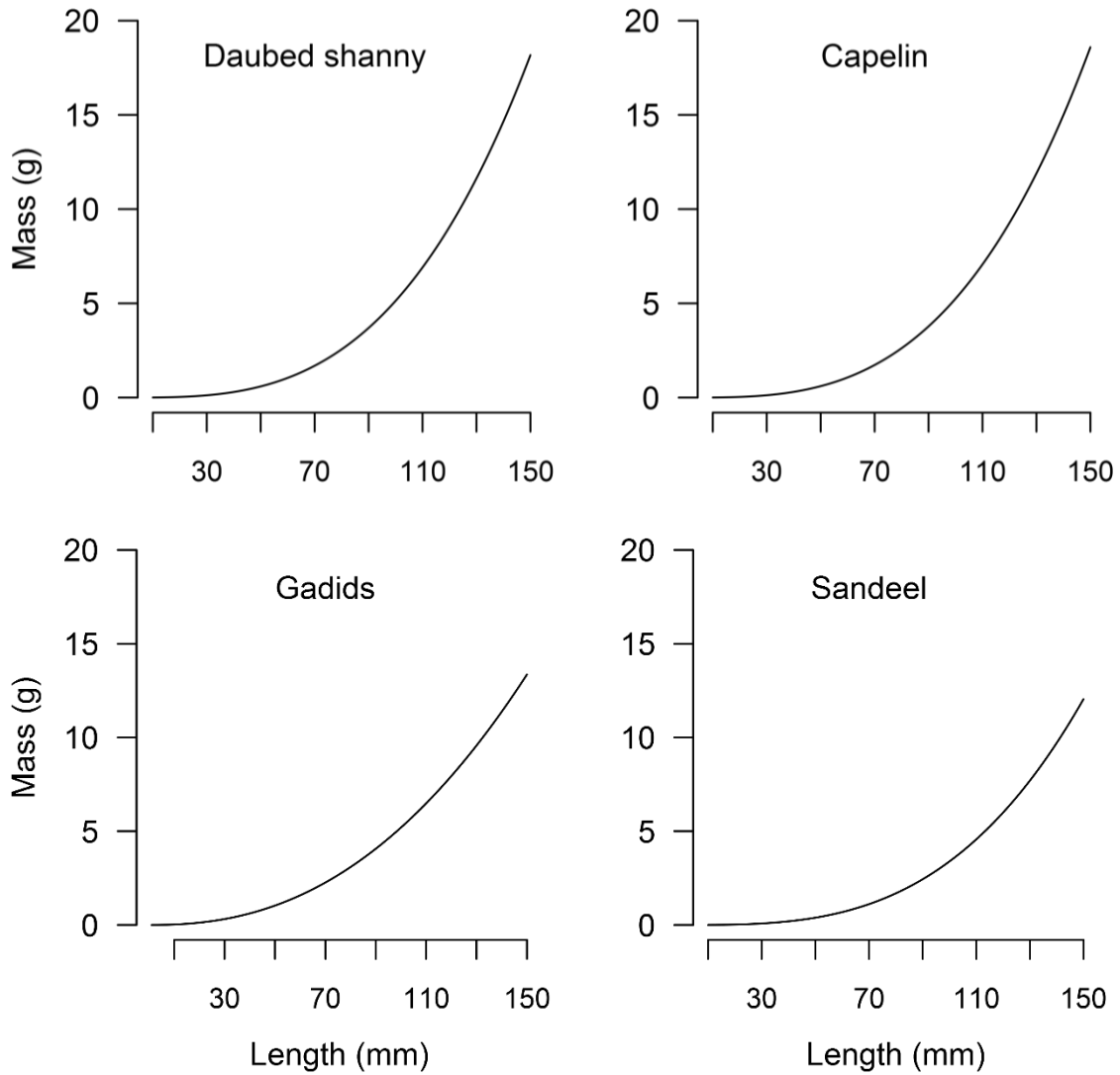


Figure 4: Length-mass relationship for prey fish brought to the burrow by adult Atlantic puffins. References are listed in table 2.

For fish with estimated mass, the energy content (kJ wet weight) was calculated based on data in Elliott & Gaston (2008). The energy content for Polar cod (*Boreogadus saida*) was used for all gadids.

Statistical analysis

Camera monitoring periods were divided into hour blocks (i.e. each day was divided in 24 unique hour blocks). Hour blocks with at least 50 minutes of recording were included. This resulted in 2566 hour blocks of recording from the six successful burrows (figure 5).

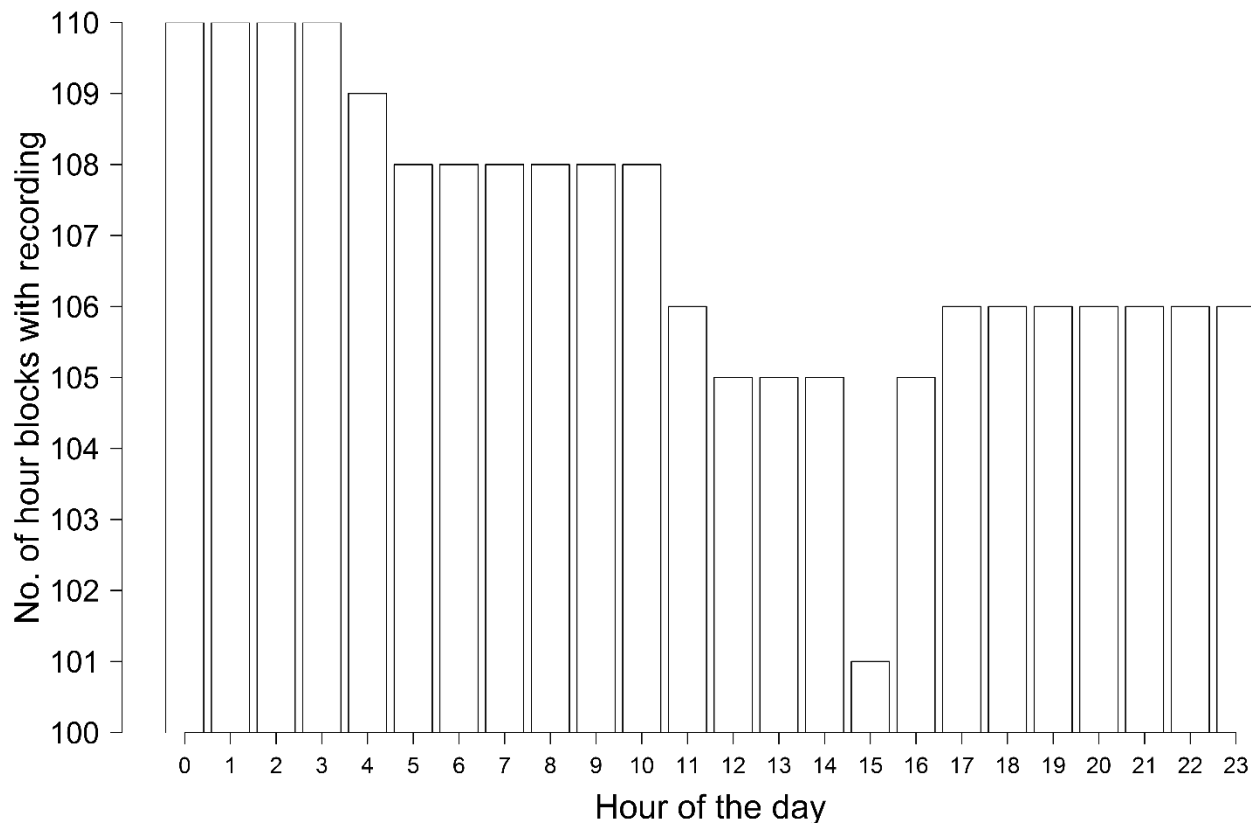


Figure 5: Distribution of recording hours during the day (N = 2566, range 101-110). Hour 0 lasts from 0000-0100, hour 1 from 0100-0200 etc.

Each hour block was given a score depending on whether at least one prey load delivery occurred (1) or not (0) within the given hour block. Statistical analysis was conducted in R version 3.2.2. Generalized linear mixed models from the package ‘lme4’ (R Development Core Team 2014) were used in the analysis of diurnal activity patterns. Pairs of sine and cosine functions (Nelson et al. 1979; Pita et al. 2011) represented the periodic component of time series used in the models (Pinheiro & Bates 2000). The response variable was whether or not there was a prey load delivery within the hour block (logistic regression and binomial distribution). Deliveries at the six successful cameras (N = 159 deliveries) were included in the analysis. Two deliveries within the

same hour block occurred twice. These were scored as a delivery in the same way as one delivery, thus prey load deliveries were recorded in 157 different hour blocks.

The explanatory variable ‘time of day’ was fitted with 24 h as the fundamental period (i.e. 0 to 23 hours, $k = 1$) combined with one (i.e. 12 hour cycles, $k = 2$) and two (i.e. 8 hour cycles, $k = 3$) harmonies, and tested for by using the cosinor method (Nelson et al. 1979; Pita et al. 2011). Days since hatching (‘*DaysDiff*’) was added as explanatory variable in M₄-M₇ (table 3). To control for differences between burrows, ‘burrow ID’ was included as a random variable (Pinheiro & Bates 2000).

Table 3: Models of diurnal activity patterns where x represent ‘time of day’, ϵ is random effect ‘burrow ID’, f is the probability for delivery at hour x , a_0 is the intercept, and k is the number of harmonies (one, two or three sinusoidal components). Full models are listed in appendix I.

Model no.	General activity model
M ₀₋₃	$\text{logit}(f(x)) = a_0 + \sum_{i=1}^k \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \epsilon$
M ₄₋₇	$\text{logit}(f(x)) = a_0 + \sum_{i=1}^k \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \text{DaysDiff} + \epsilon$

All fitted models (M₁-M₇) were compared to M₀, which contained the random term only. All models were ranked based on their AICc values. To separate the best model, a difference in AICc (ΔAICc) of 2.0 was set as a critical value (Burnham & Anderson 1998; Burnham 2002). The model with lowest AICc was considered the best. For all statistical models and tests, $\alpha = 0.05$ was used as significance level.

Results

Prey load deliveries

In 2015, breeding was successful in three of the five burrows monitored, resulting in 94 recorded prey load deliveries. In 2016, breeding was successful in three of the six burrows monitored, resulting in 66 recorded prey load deliveries. Overall, 160 prey load deliveries were recorded by the camera traps set up at puffin burrow entrances (table 4). Due to few recorded prey load deliveries, quantification of prey consumption was not possible. Instead, data were used to qualitatively describe diet composition and feeding patterns in puffins at Bjørnøya.

Table 4: Number of recorded prey load deliveries for each of the eleven cameras deployed at Atlantic puffin burrow entrances at Bjørnøya. Successful breeding (yes/no) indicate whether there were live chicks in the burrow at the end of the monitoring period. Burrows without live chicks were considered unsuccessful.

	Burrow ID	No. of recorded prey load deliveries	Successful breeding
2015	1	38	Yes
	2	17	Yes
	3	0	No
	4	39	Yes
	5	*	No
2016	1	0	No
	2	7	Yes
	3	1	No
	4	28	Yes
	5	30	Yes
	6	0	No
Total		160	

* Not analyzed due to poor image quality

Of all prey load deliveries, 58 contained adult fish only (36 % and 73 % of deliveries with identified prey in 2015 and 2016, respectively), 41 contained fish larvae only (52 % and 17 % of deliveries with identified prey in 2015 and 2016, respectively), while 13 loads contained both adult fish and larvae. Prey identification was not possible in 48 of the recorded prey load deliveries. There was a significant difference in proportion of adult fish and fish larvae in prey loads between years (Pearson's chi-squared test: $N = 112$, $\chi^2 = 16.47$, $df = 2$, $p < 0.01$). Identification to species, genus or family level was possible for 69 specimen in 29 prey load deliveries (table 5). Load mass was determined for 19 prey load deliveries. Mean load mass (\pm SD) pooled for both seasons was 5.6 ± 3.2 g (range 1.2-14.9 g, see also table 7). There was no significant difference in load mass between the two seasons (median (first and third quartile) load mass in 2015 and 2016 was 5.5 g (4.5 and 6.0 g, $N = 9$) and 5.4 g (2.8 and 6.5 g, $N = 10$), respectively. Wilcoxon rank sum test: $W = 46$, $p = 0.97$).

Of identified prey fish, daubed shanny (*Leptoclinus maculatus*) was the most numerous species, and constituted the largest percentage of both total mass (g) and total energy (kJ wet weight). Mass and energy content per fish was highest for sandeel (*Ammodytes spp.*) and capelin (*Mallotus villosus*), and lowest for gadids and daubed shanny, respectively (ranked from highest to lowest mass and energy per fish).

Table 5: Composition of prey fish brought back to the burrows by Atlantic puffins at Bjørnøya during the 2015 and 2016 breeding seasons pooled. Energy content is given with \pm SD.

	N	% by N	Mass (g)	% by mass	Energy (kJ)	% by energy
Sandeel	3	4.3	17.5	16.4	88.5 ± 1.9	16.8 ± 2.2
Daubed shanny	45	65.2	40.4	37.8	200.7 ± 6.9	38.2 ± 3.4
Capelin	8	11.6	30.1	28.2	147.4 ± 4.8	28.1 ± 3.3
Gadids	13	18.8	18.9	17.7	88.8 ± 3.6	16.9 ± 4.0
Total	69		106.9		525.4	

Daubed shanny dominated both load mass and fish number in 2015 (figures 6 and 7). Daubed shanny was the main constituent of fish number also in 2016. Sandeel was not recorded in puffin chick diet in 2015, but dominated load mass in 2016 together with capelin. Note that for both figures, sample size is small.

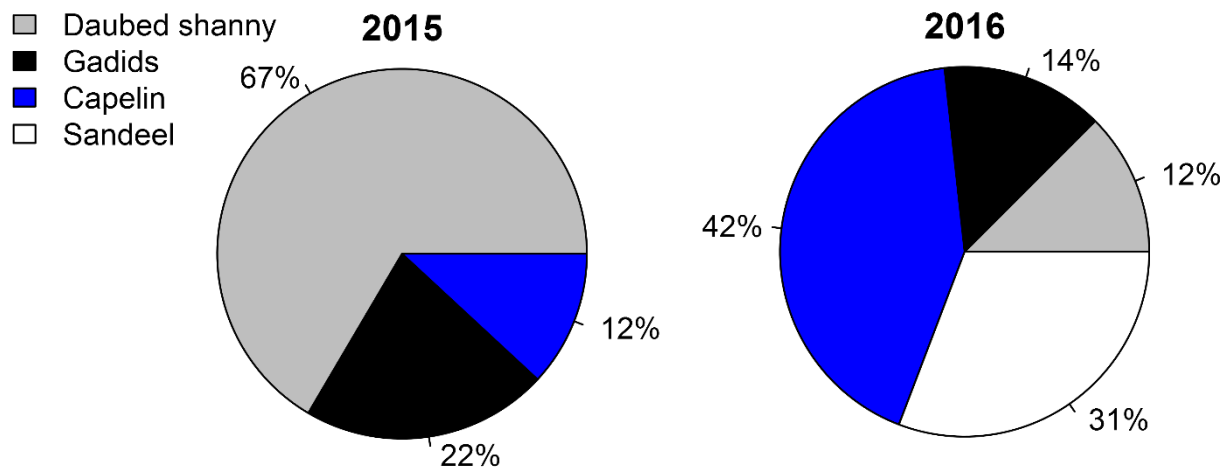


Figure 6: Prey species composition of Atlantic puffin chick diet at Bjørnøya as percentage of total mass delivered in the two seasons 2015 and 2016. Note that mass estimation was possible for relatively few prey loads (69 fish in 19 deliveries weighed 50.0 g in 2015 and 56.8 g in 2016).

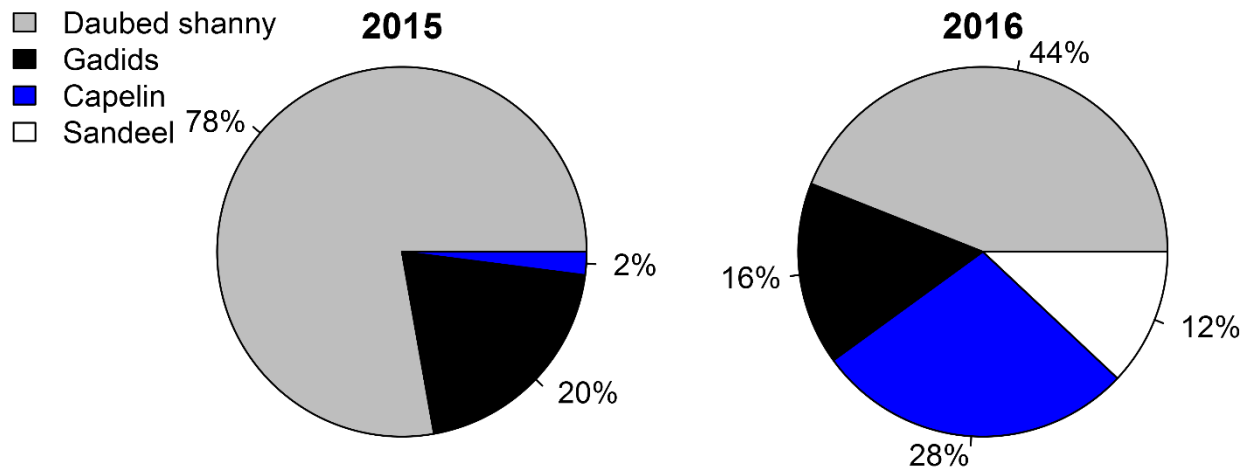


Figure 7: Prey species composition of Atlantic puffin chick diet at Bjørnøya as percentage of total number of fish delivered in the two seasons 2015 (N = 44) and 2016 (N = 25).

Length of prey fish was measured three times to minimize risk of measurement error. Mean (\pm SD) difference in the three repeated RFL measurements was 2.97 ± 2.34 mm (range 0.21-11.8 mm, table 6 and figure 8). High R^2 for all three regressions (0.97, 0.97 and 0.98 for regression A, B and C, respectively) indicate little variation between measurements.

Table 6: Parameter estimates from simple linear regressions fitted to repeated RFL measurements.

Regression A: length1 as a function of length2. Regression B: length1 as a function of length3. Regression C: length2 as a function of length3. For all regressions $N = 94$ and $df = 92$.

Regression	Variable	Estimate	SE	t	p
A	Intercept	0.01	0.86	0.01	0.99
	Length2	1.02	0.02	56.88	<0.01
B	Intercept	-1.21	0.89	-1.36	0.18
	Length3	1.02	0.02	56.46	<0.01
C	Intercept	-0.82	0.66	-1.25	0.21
	Length3	0.10	0.01	74.24	<0.01

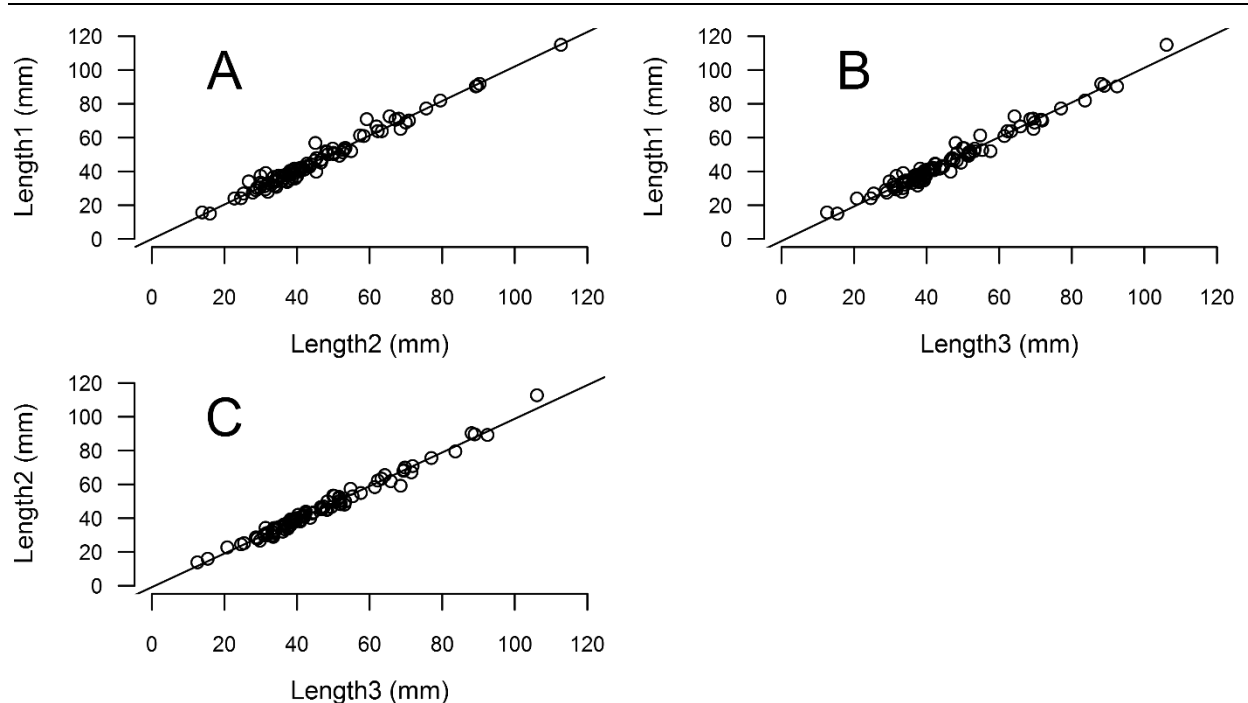


Figure 8: Precision of repeated RFL measurements ($N = 94$, $df = 92$) of prey fish delivered at the burrow of Atlantic puffins at Bjørnøya. Parameters for regression lines are given in table 6.

RFL provided a relative measure of fish length, only measuring the visible part of prey fish. RFL measurements were possible for 69 out of 160 prey load deliveries. In loads with multiple prey, one or more fish were measured, resulting in 94 unique fish measurements (distribution in appendix II). For all fish where RFL was measured, AFL was estimated by adding a percentage of measured RFL as described in the methods section (distribution in figure 9). Pooled for both breeding seasons, mean (\pm SD) AFL was 58.3 ± 18.5 mm (range 18.6-128.6 mm). There was a significant difference in AFL between the two seasons (median (first and third quartile) AFL in 2015 and 2016 was 51.2 mm (44.8 and 59.6 mm, N = 67) and 74.9 mm (57.0 and 81.3 mm, N = 27), respectively. Wilcoxon rank sum test: $W = 393$, $p < 0.01$).

Species/genus/family was determined for 27 of the 94 fish with estimated AFL. Sandeel and capelin had mean AFL (\pm SD) 110.3 ± 18.3 mm (N = 2) and 89.2 ± 13.2 mm (N = 7), respectively. Gadids and daubed shanny were noticeably smaller, with mean (\pm SD) AFL 51.6 ± 5.7 mm (N = 6) and 53.3 ± 11.8 mm (N = 12), respectively.

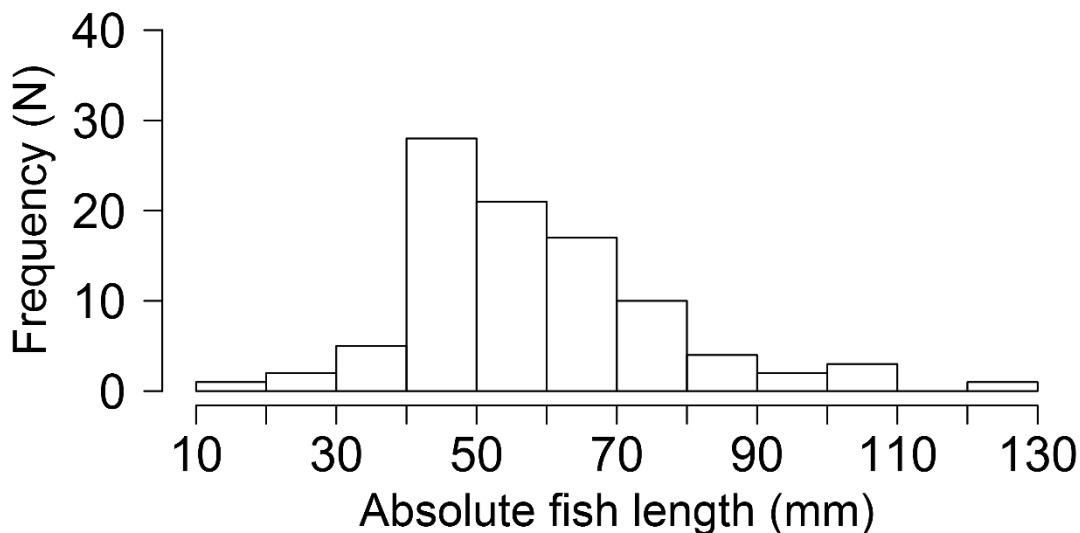


Figure 9: Frequency distribution of AFL of fish brought back to the burrow by adult Atlantic puffins at Bjørnøya (N = 94).

To quantify effect of observer on fish length estimates, two parties estimated AFL independently for 20 images. When fish length was adjusted for, percentage difference in length estimates revealed larger observation error for large fish compared to small fish (figure 10). A low R^2 (0.32) indicated contrasting length measurements between observers.

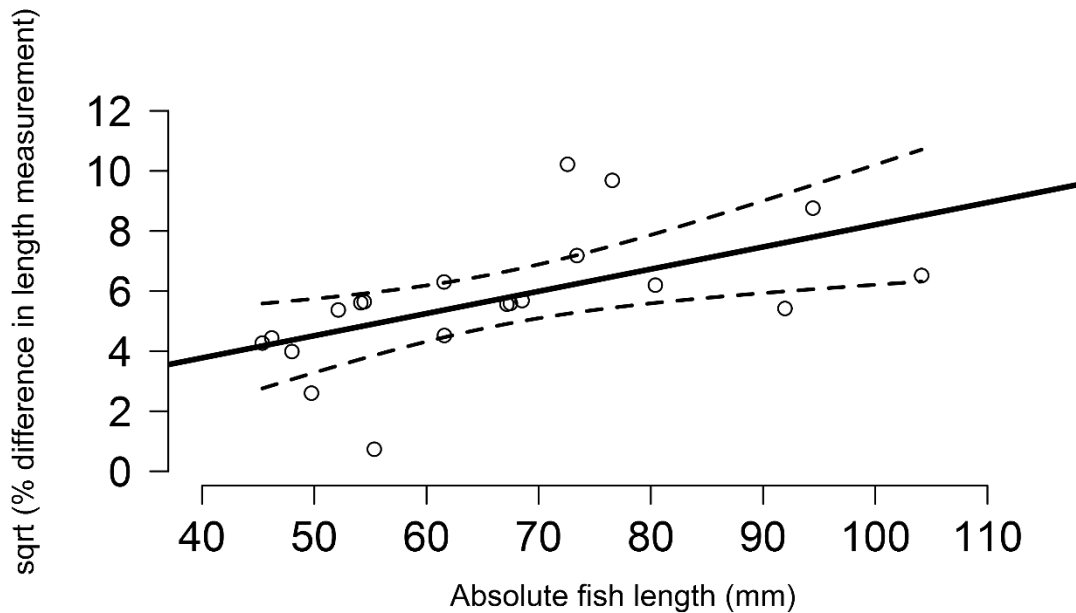


Figure 10: Square root transformed difference between fish length measurements conducted by myself and Robert Barrett. My length measurements (AFL) were used as reference level. Y-axis represent square-root transformed percentage difference between the two measurements (difference as percentage of AFL). Regression equation: $\text{sqrt}(y) = 0.82 (\pm 1.73) + 0.07 (\pm 0.03) * \text{AFL}$ ($N = 20$, $t = 2.92$, $df = 18$, $p = 0.01$, $R^2 = 0.32$). Dashed lines represent the 95 % confidence interval.

Number of fish per load was determined when possible, i.e. for 110 of 160 deliveries (figure 11). Pooled for both breeding seasons, mean number (\pm SD) of fish per load was 3.2 ± 1.8 (range 1-8, see also table 7). There was a significant difference in number of fish per load between the two seasons (median (first and third quartile) number of fish per load in 2015 and 2016 was 3 (3 and 5, $N = 65$) and 2 (1 and 3, $N = 45$), respectively. Wilcoxon rank sum test: $W = 2148$, $p < 0.01$).

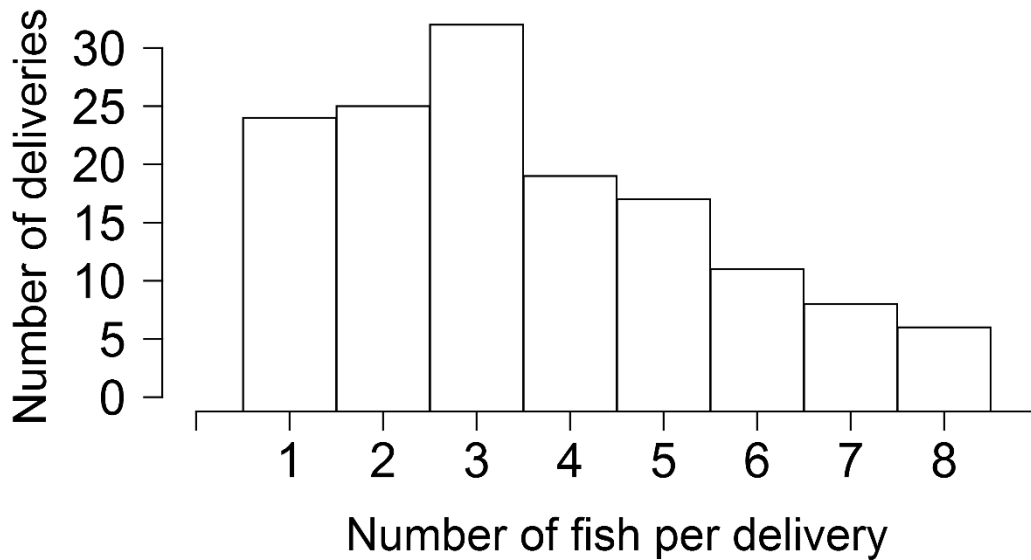


Figure 11: Distribution of number of fish per prey load delivery recorded at Atlantic puffin burrow entrances at Bjørnøya during the 2015 and 2016 breeding seasons (N = 110).

For the 46 prey load deliveries where Hallvard Strøm and I estimated number of fish per load independently, differences ranged from none to three. For 37 (80 %) of the deliveries, estimated number of fish were the same. For the nine deliveries (20 %) where numbers were in disagreement, seven differed by one fish (15 %), one estimate differed by two (2 %) and one estimate differed by three fish (2 %). There was no significant difference in estimated number of fish per load between the two observers (paired student's t-test, N = 46, $t = -0.44$, $df = 45$, $p = 0.66$). Number of fish per load decreased significantly with increasing AFL (figure 12). Number of fish per load increased significantly with increasing load mass (figure 13).

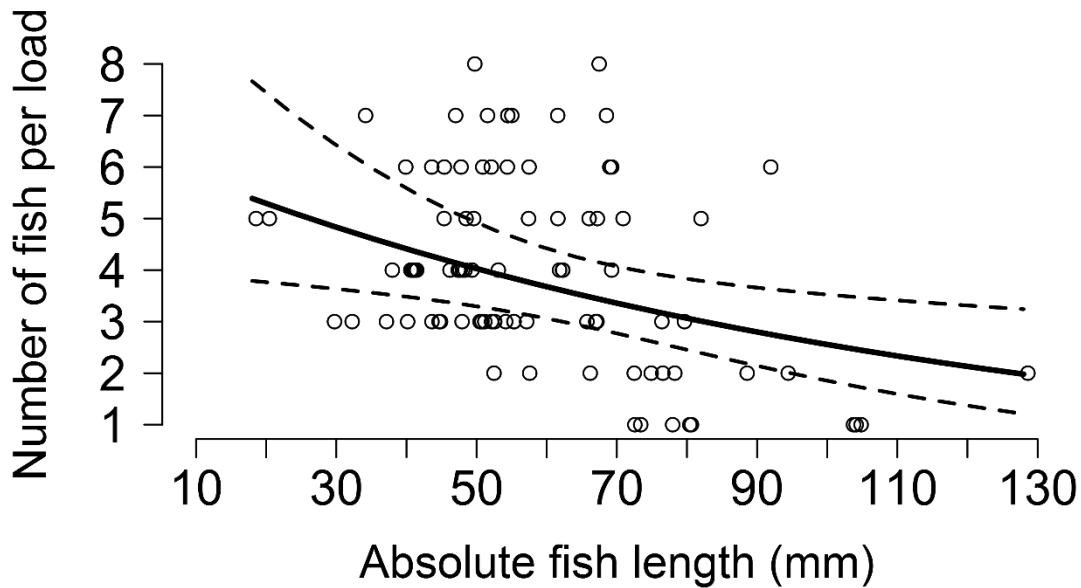


Figure 12: The relationship between number of fish per load and AFL in prey loads delivered at the burrow by Atlantic puffins at Bjørnøya. Regression equation: number of fish per load = $1.85 (\pm 0.24) - 0.01 (\pm 0.00) * AFL$ ($N = 90, z = -2.59, df = 87, p = 0.01$). Random factor (burrow ID) = 6. Dashed lines represent the 95 % confidence interval.

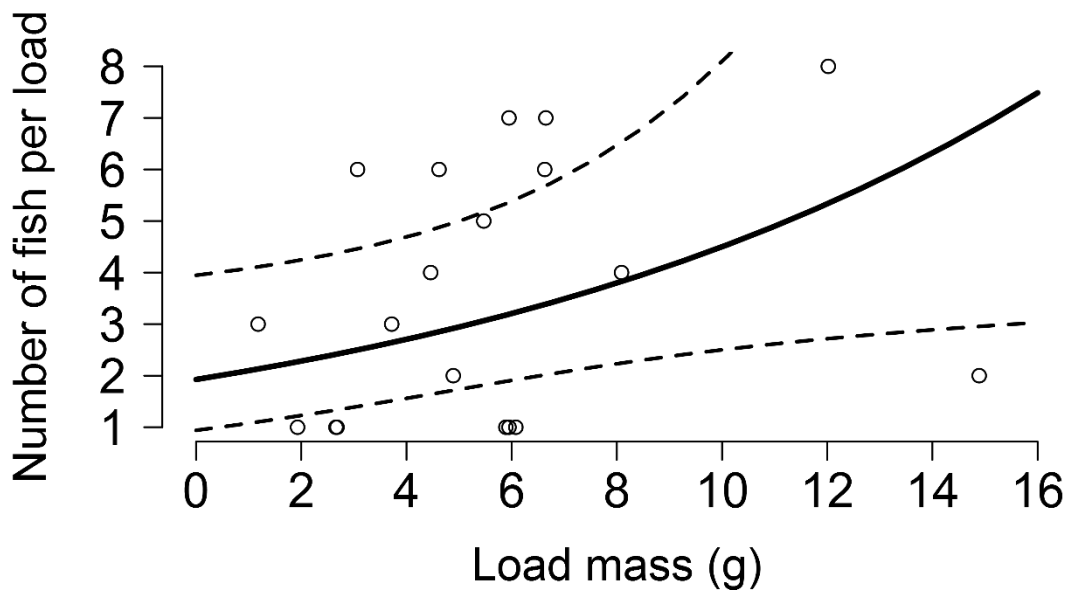


Figure 13: The relationship between number of fish per load and load mass (g) in prey loads delivered at the burrow by Atlantic puffins at Bjørnøya. Regression equation: number of fish per load = $0.66 (\pm 0.37) + 0.08 (\pm 0.04) * load\ mass$ ($N = 19, z = 2.15, df = 16, p = 0.03$). Random factor (burrow ID) = 6. Dashed lines represent the 95 % confidence interval.

Food samples collected at Bjørnøya

Puffin prey loads collected at Bjørnøya during fieldwork were compared to data acquired by camera traps. Sample size of collected prey was small, and prey species identification was reputedly challenging, but the following four species/genera were identified: capelin (N = 1), daubed shanny (N = 1), sandeel (N = 1) and Atlantic herring (*Clupea harengus*, N = 6). Both mean load mass and mean number of fish per load were larger for collected samples, compared to data acquired by camera traps (table 7).

Table 7: Load mass (g) and number of fish per load found in Atlantic puffin prey load deliveries collected by the Norwegian Polar Institute (NP, N = 13) and by camera trap recordings (CT) at Bjørnøya.

		N	Min	Max	Mean	SD
NP	Load mass (g)	6	4.05	12.36	6.60	2.90
	No of fish per load	12	1	12	5.83	3.05
CT	Load mass (g)	19	1.18	14.89	5.62	3.24
	No of fish per load	107	1	8	3.25	1.75

Feeding frequency

When only days with recorded prey load deliveries (N = 71) were included, mean number (\pm SD) of recorded feeds per burrow per day were 2.2 ± 1.5 . For all monitoring days after hatching (N = 112), mean number (\pm SD) of recorded feeds per burrow per day were 1.4 ± 1.6 (range 0-7, figure 14). On 41 of the monitored days after hatching, no prey load deliveries were recorded. Only the six successful burrows were included in this analysis.

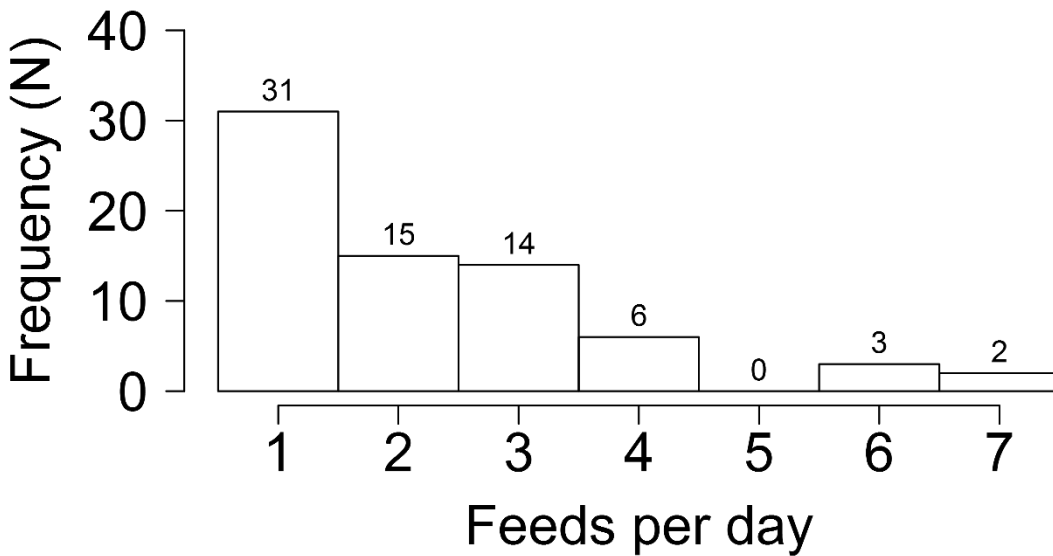


Figure 14: Distribution of number of recorded feeds per day (N = 159) at Atlantic puffin burrows at Bjørnøya. Number on each bar indicate number of days with associated number of feeds. Only successful burrows were included (N = 6).

Breeding phenology

Hatching dates were estimated for the successful burrows in 2016 (table 8). Hatching date for burrow 3 is also known, since it occurred while cameras were mounted.

Table 8: Estimated laying date, hatching date and fledging date for Atlantic puffins breeding at Bjørnøya, based on data from the 2016 breeding season.

	Burrow 2	Burrow 3	Burrow 4	Burrow 5
Laying date	26 - 31 May	13 - 18 May	21 - 26 May	20 - 25 May
Hatching date	10 July	27 June	5 July	4 July
Fledging date	17 - 23 August	4 - 10 August	12 - 18 August	11 - 17 August

Sex difference in feeding rate

In one burrow (no. 5, 2016) one of the adult birds had two rings, one steel ring marked NOS_5109544, and one plastic ring marked BT2. This was a female bird, ringed by NP 6 August 2014, when it was at least four years old. Out of totally 30 recorded prey load deliveries at this burrow, 22 were delivered by the ringed female and three by the male. It was not possible to determine which of the adult birds delivered the remaining prey load deliveries.

Daily activity pattern

Multicosinor models did not reveal any significant circadian activity pattern in puffin prey load deliveries at Bjørnøya. None of the models were significant, leaving M_0 as the best model (table 9), suggesting that hour of the day and days since hatching were not important for predicting prey load delivery. Probability of delivery was constant during the day, with 6 % ($e^{-2.71} = 0.06$) probability of delivery within a given hour block.

Table 9: The two best models explaining daily activity pattern in prey load deliveries in the Atlantic puffin at Bjørnøya. Models were ranked by $\Delta AICc$. Only models with $\Delta AICc < 2.0$ are listed. Remaining models are listed in appendix III.

Model	Rank	df	AICc	$\Delta AICc$
M_0	1	2564	1106.0	0.0
M_7	2	2563	1107.9	1.9

Models M_2 and M_3 were ranked as number 4 and 7, respectively. Yet, these two models suggested a pattern of two daily peaks of delivery, with one peak in the morning and one peak in the evening (table 10 and figure 15). Even if these models were not significant, comparing the models to the plotted raw data of prey load deliveries during the hour of the day pooled for both breeding seasons, it indicated a pattern (figure 16).

Table 10: Parameter estimates for M_0 - M_3 of daily activity patterns in Atlantic puffins at Bjørnøya based on generalized linear mixed models fit by maximum likelihood. Random factor (burrow ID) = 6, N = 2566. For M_0 - M_3 , df was 2564, 2562, 2560 and 2558, respectively.

Model	Variable	Estimate	SE	z	p
M_0	Intercept	-2.71	0.38	-7.11	<0.01
M_1	Intercept	-2.71	0.38	-7.10	<0.01
	$I(\cos(2 * \pi * \text{Hour}/24))$	-0.06	0.12	-0.54	0.59
	$I(\sin(2 * \pi * \text{Hour}/24))$	0.00	0.12	0.03	0.98
M_2	Intercept	-2.71	0.38	-7.12	<0.01
	$I(\cos(2 * \pi * \text{Hour}/24))$	-0.07	0.12	-0.55	0.58
	$I(\sin(2 * \pi * \text{Hour}/24))$	0.00	0.12	0.04	0.97
	$I(\cos(2 * 2 * \pi * \text{Hour}/24))$	-0.14	0.12	-1.21	0.23
	$I(\sin(2 * 2 * \pi * \text{Hour}/24))$	0.10	0.12	0.88	0.38
M_3	Intercept	-2.72	0.38	-7.12	<0.01
	$I(\cos(2 * \pi * \text{Hour}/24))$	-0.07	0.12	-0.55	0.59
	$I(\sin(2 * \pi * \text{Hour}/24))$	0.00	0.12	0.01	0.99
	$I(\cos(2 * 2 * \pi * \text{Hour}/24))$	-0.14	0.12	-1.21	0.23
	$I(\sin(2 * 2 * \pi * \text{Hour}/24))$	0.10	0.12	0.87	0.38
	$I(\cos(3 * 2 * \pi * \text{Hour}/24))$	-0.02	0.12	-0.14	0.89
	$I(\sin(3 * 2 * \pi * \text{Hour}/24))$	-0.04	0.12	-0.32	0.75

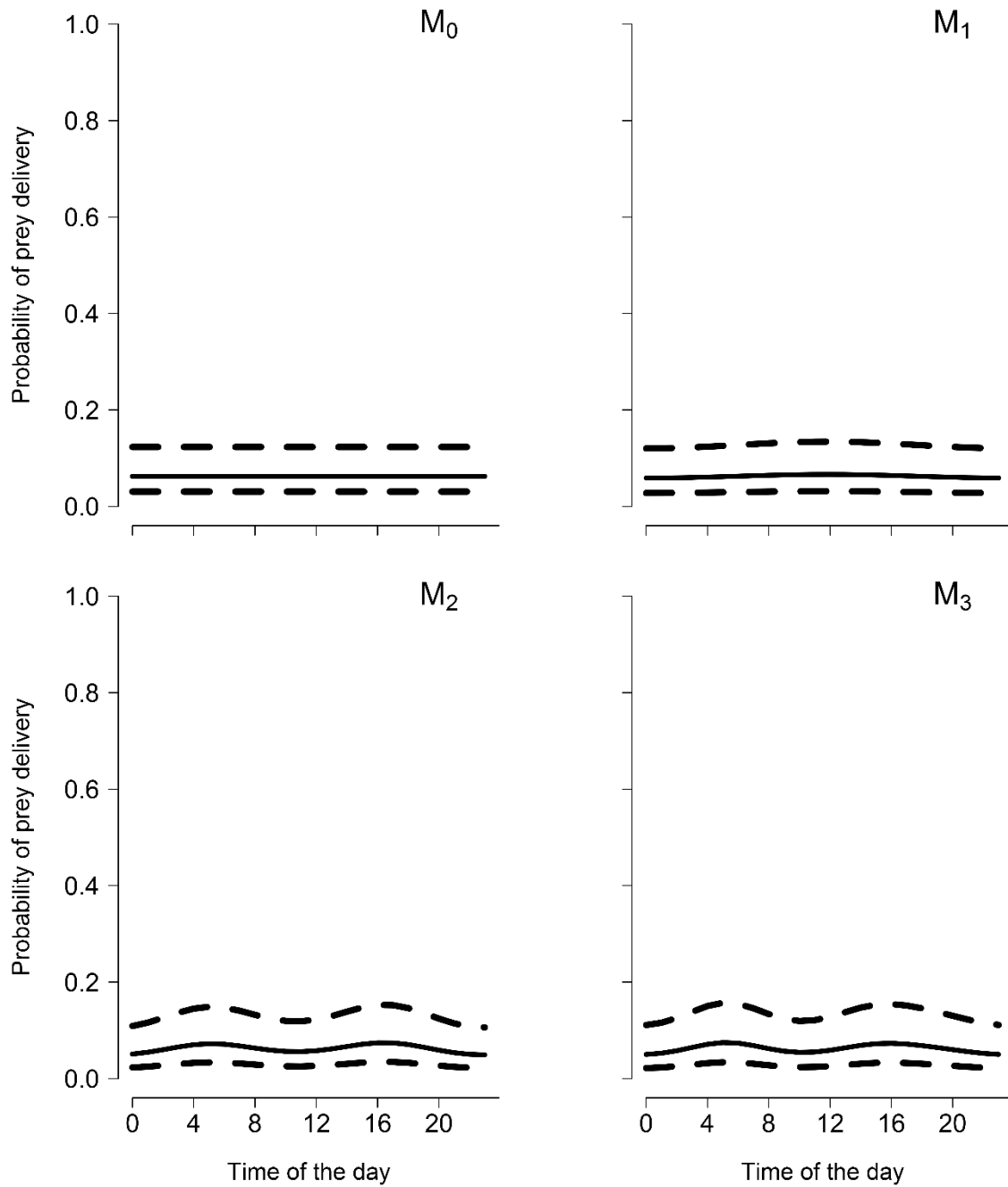


Figure 15: Plotted models explaining daily activity pattern in prey load deliveries in the Atlantic puffin at Bjørnøya. Parameter estimates are given in table 10. Enlarged figures in appendix IV.

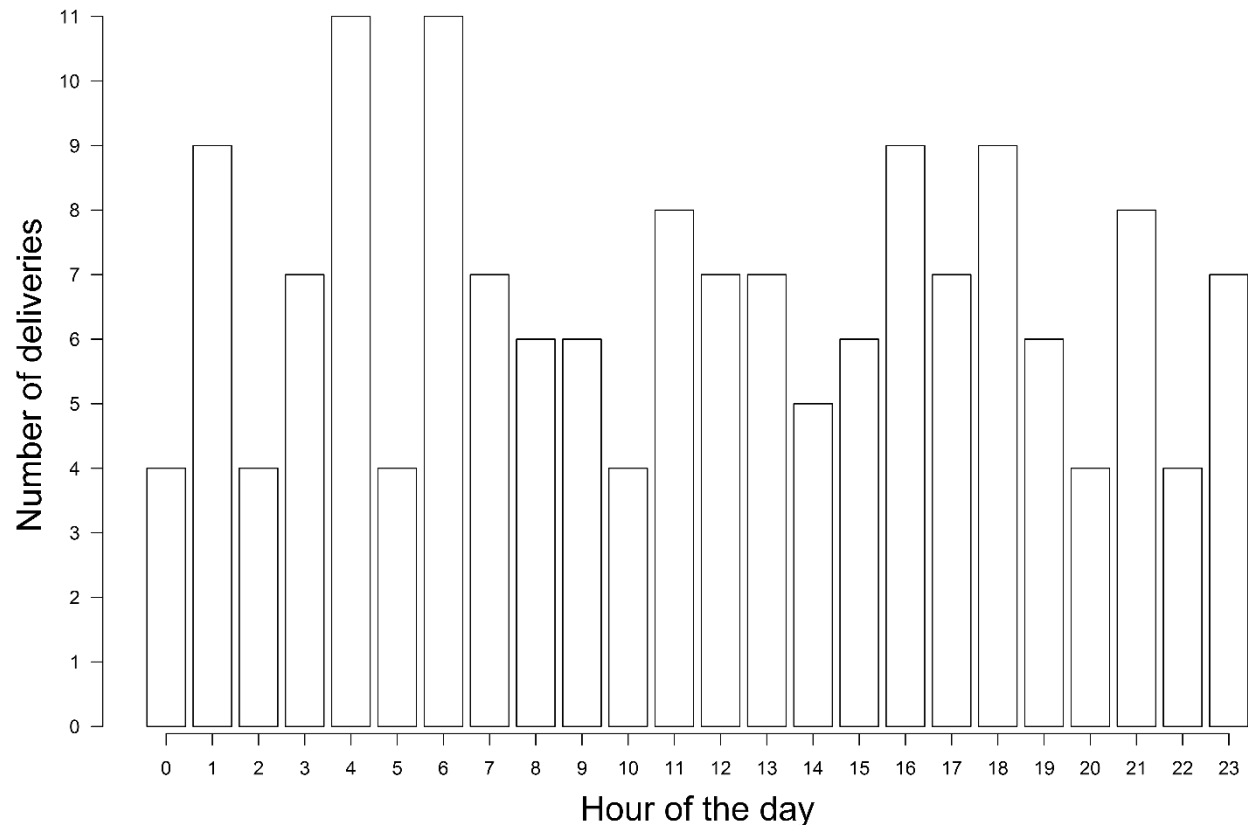


Figure 16: Raw data of recorded prey load deliveries at Atlantic puffin burrows at Bjørnøya during the hour of the day in the 2015 and 2016 breeding seasons pooled (N = 160, range 4-11). Hour 0 lasts from 0000-0100, hour 1 from 0100-0200 etc.

No analysis was run on seasonal activity patterns, due to small sample size of deliveries at each nest. Deliveries over the two respective seasons were pooled for all burrows and presented in appendix V.

Discussion

Prior to my study, little was known about puffin diet at Svalbard (Anker-Nilssen et al. 2000, Hallvard Strøm pers.comm.). The results presented here should be interpreted cautiously since they are based on relatively few prey load deliveries. A larger study is needed to confirm my findings, but the method presented here demonstrates the potential of using camera traps to monitor parental food provisioning in the Atlantic puffin. Like most other seabird diet studies (Barrett et al. 2007), this study investigated chick diet in the breeding season. It is important to emphasize that diet of adult breeders, diet of non-breeders and diet outside the breeding season may differ from the diet provided to chicks (Hedd et al. 2010).

Prey load composition

In my study, poor image quality made species identification difficult, and identification to species/genus/family level was possible only for 69 fish in 29 prey loads recorded by camera traps. Even for collected prey samples, species identification was difficult due to loss of color and structure in the freezing process (Hallvard Strøm pers.comm.). According to Duffy & Jackson (1986), a large sample size is needed to determine the exact proportion of different prey species in seabird diets. In lack of better data, I assume that fish identified to species/genus/family level in my study are representative of actual prey load composition. Capelin, daubed shanny and sandeel were found both in prey loads recorded by the camera traps and in collected food samples. The occurrence of capelin in the puffin's diet was expected, since capelin dominates diet of other seabirds breeding at Bjørnøya (Barrett et al. 1997; Cherel et al. 2001). I found that fish larvae constituted a relatively large proportion of puffin chick diet, which is interesting considering that loads consisting of many small fish have low energy content compared to loads of the same weight containing few large fish (Barrett 2002). Atlantic herring was only found in the collected samples, while gadids were found only in prey loads recorded by camera traps. At first, herring found in collected samples were mistaken to be gadids. It is possible that herring and gadids were mistaken when identifying prey species from camera trap images as well. Any misidentification of fish species would have further implications for calculation of fish mass and energy content.

I found a mean daily delivery rate of 1.4 deliveries per day for the successful burrows, ranging from none to seven. Feeding frequency on Hornøya, Finnmark ranged from 5.5 to 10.3 deliveries

per day (Eilertsen et al. 2008). Assuming similar feeding frequencies at Bjørnøya, one out of four deliveries were recorded by the camera traps at best. It is likely that more deliveries were actually recorded, but because puffins dive straight down into the burrow when returning with a delivery (Harris & Wanless 2011), prey fish were not visible on the images even with 0.2 s trigger speed. Harris & Wanless (2011) counted events where adult birds jumped quickly into the burrow as prey load deliveries, even if prey was not observed, claiming that such behavior only occur when adult birds carry prey. However, I included only episodes where prey loads were visible. With constant monitoring over time, I assume that the probability of detection was equal for all deliveries despite of periods with reduced image quality due to rain and sea spray on the lens. Any possible negative effect of weather on prey load delivery could have been explained either by lower prey load detectability due to reduced image quality, or by reduced feeding success during rainy and windy weather. Studies investigating the effect of weather on pursuit diving auks have shown contrasting results, providing evidence both for and against weather effects on feeding behavior (Birkhead 1976; Finney et al. 1999). Because it would not be possible to distinguish whether an effect of weather was caused by reduced image quality or reduced feeding success, weather was not included as an explanatory variable for prey load delivery in my study.

When estimating fish length on images, fish can be measured relative to both bill length (e.g. Eilertsen et al. 2008) and bill depth (e.g. Creelman & Storey 1991). I chose to measure prey relative to bill depth because this gave less perspective issues. If not for this, bill length would have been a better measure, since bill length is relatively constant while bill depth vary with sex and age (Barrett et al. 1985). Prey fish will flex when held in the puffin bill (Gaglio et al. 2016). Because prey load deliveries in my study were depicted from only one angle, it was challenging to correct for perspective when measuring prey length. Robert Barrett estimated fish lengths from images using traditional seabird monitoring methods in order to calibrate my measurements. Barrett noted that estimating fish length when observing is easier, since birds move and can be seen from different angles while holding the prey load in the bill. Length estimates derived from direct observation combined with mist-netting are found to be reliable (Rodway & Montevecchi 1996; Eilertsen et al. 2008), yet traditional methods of measuring fish length require considerable experience and may be associated with observer bias with no possibility of later confirmation (Rodway & Montevecchi 1996). I would thus argue that the method used to measure fish length in my study might be an adequate supplement to traditional methods. When comparing fish

length measurements conducted by myself and Robert Barrett, percentage difference in length estimates (corrected for fish length) increased with increasing fish length, which implied that length measurements were uncertain, especially for larger fish. Decreasing accuracy with increasing prey size was also found by Lee & Hockey (2001) when investigating biases in field estimation of shorebird prey. Direct length measurements from images tend to underestimate fish length (Gaglio et al. 2016), and any underestimation would have further implications for calculation of fish mass and energy content.

I found the mean number of fish per load recorded by camera traps to be 3.2. In collected food samples, the mean number of fish per load was 5.8. In comparison, Eilertsen et al. (2008) found the number of fish per load at Hornøya to be 7.5 and 8.2 in 2002 and 2003, respectively, while Barrett et al. (1987) found number of fish per load to range from two to 24 in 1980-82. In the latter study, one fish or a few relatively large ones per load were most common. In my study, fish number was easier to determine in food loads with few fish, which might have caused an overrepresentation of loads with few fish. The number of fish per load was based on conservative estimates, which might have caused an underestimation of number of fish per load. Hallvard Strøm estimated number of fish per load independent of my estimates. No difference between the estimates suggests that an underestimation was less likely. Any underestimation in number of fish per load may have caused error in calculation of fish mass and energy content. There was an effect of fish length on number of fish per load. Because the mean number of fish per load was low, mean fish size was expected to be relatively large (> 100 mm).

For prey load deliveries recorded by camera traps, I found mean load mass to be 5.6 g, compared to 6.6 g for collected food samples. Yearly mean load mass found at Hornøya, Finnmark ranged from 7.3 to 14 g (Eilertsen et al. 2008), while yearly means at Isle of May, Scotland ranged from 5.8 to 11.4 g (Harris & Wanless 2011). Load masses in the literature referred to above were found by catching adult birds, confiscating and weighing prey loads. In comparison, it may seem like food loads at Bjørnøya were lighter, but since the methodologies differ, comparisons should be interpreted carefully. Contrary to Harris & Wanless (2011) and Eilertsen et al. (2008) who found that load mass decreased with increasing number of fish per load, I found that load mass increased with increasing number of fish per load. Because the sample size was small and variation was large, my result is disputable even if the regression was significant.

Nutritional composition of fish vary with fish length, maturity, time of the season, species, location and year (Lawson et al. 1998). When calculating the energy content of puffin prey loads, it would have been preferable to use energy content calculated for fish nearby the study location. Because such data were not available for Bjørnøya, energy content of prey fish was calculated using data found for Brünnich's guillemot (*Uria lomvia*) prey fish in the Canadian Arctic (Elliott & Gaston 2008). I have chosen to use the study by Elliott & Gaston (2008) as a reference because it included all species identified on my camera trap images, and because the methodology was consistent for calculation of energy content. According to Elliott & Gaston (2008), capelin contained least energy (4.9 kJ/g) and sandeel most (5.1 kJ/g) of the four prey species identified in my study. In comparison, Lawson et al. (1998) found capelin to have the highest energy content (8.4 kJ/g) and sandeel to have the lowest energy content (4.4 kJ/g) of the four fish species. Choice of reference would thus greatly affect the estimation of energy content of prey fish.

In the results discussed above, data from the two camera-monitoring seasons were pooled to increase sample size. Inter-annual difference in prey load composition was investigated as well. Large sample size is recommended when comparing diet between years (Duffy & Jackson 1986), and results on inter-annual variation should in my case be interpreted with caution. I found no difference in load mass between the two years of monitoring. Prey load deliveries contained less fish larvae and median AFL was larger in 2016 than in 2015. In 2016, median number of fish per load was smaller and the proportion of large prey species (i.e. capelin and sandeel) was higher. Decreased number of fish per load together with increasing prey size is associated with favorable feeding conditions (Barrett et al. 1987; Eilertsen et al. 2008), suggesting that feeding conditions were better in 2016 than in 2015. No difference in load mass despite change in feeding conditions supports the theory that puffins are able to buffer fluctuating feeding conditions by changing feeding behavior (Barrett 2002).

Breeding phenology

Timing of reproduction is a key factor for successful breeding (Dunn 2004), yet laying date and hatching date is still unknown for some Norwegian seabirds (Barrett 2001). I found mean estimated hatching date for Atlantic puffins at Bjørnøya to be 6 July. In puffins, breeding is relatively constant between years and colonies (Nettleship & Birkhead 1985; Burr et al. 2016). The incubation and chick-rearing period is long in puffins compared to other seabird species

(Nettleship & Birkhead 1985), and early breeding onset is crucial for successful reproduction (Barrett 2001). Burr et al. (2016) reported a mean hatching date for black-legged kittiwake (*Rissa tridactyla*), common guillemot (*Uria aalge*) and Brünnich's guillemot at Bjørnøya to be 4 July, 2 July and 6 July, respectively. With incubation lasting 24-32 days for kittiwakes, 32 days for the two guillemot species (Strøm 2006), and 40-45 days for puffins (Myrberget 1962), puffins at Bjørnøya have to lay their eggs 8 to 21 days prior to the other species if hatching is to occur on the same day. Seabird hatching is delayed at higher latitudes to match peak prey availability (Burr et al. 2016). Burr et al. (2016) found that puffin hatching was delayed by 1.7 days for each degree increase in latitude. Using this delay when comparing hatching date at Bjørnøya with mean hatching date at Hornøya (70.22° N, 31.08° E, mean hatching date 29 June), estimated hatching at Bjørnøya would be delayed by 6.8 days, i.e. occur on 6 July, which is in accordance with my findings.

Estimation of hatching date was based on the first recorded fish delivery at two of the four burrows where hatching date was determined. Using the first fish delivery as a measure of hatching date is common in puffin research (Harris & Wanless 2011) to avoid disturbance associated with burrow examination. The chick is not always fed on the day of hatching (Harris & Wanless 2011), which may cause one day error in the hatching date estimate. In my case, it is also likely that one or more deliveries occurred before first delivery recorded by the camera trap, causing additional error in the hatching date estimate.

Sex difference in feeding patterns

In monomorphic bird species like the Atlantic puffin, it is not possible to tell the sexes apart visually, but I was able to investigate the sex difference in feeding patterns for one burrow where the female bird was ringed. The female delivered 73 % of all recorded deliveries at this burrow, while the male delivered 10 %. This is in accordance with Creelman & Storey (1991), which found that female puffins provided more food loads than male puffins throughout the breeding season. Camera trap monitoring might have recorded more female deliveries by chance, but with equal sampling effort throughout the breeding season, male and female deliveries were assumed to have the same detectability. Female-biased food provisioning has been found in several auk species, such as crested auklet (*Aethia cristatella*) (Fraser et al. 2002), common guillemot (Wanless & Harris 1986), Brünnich's guillemot and razorbill (*Alca torda*) (Paredes et al. 2006).

In guillemots and razorbills, female-biased feeding rate is explained by an intermediate development strategy with early fledging and only males caring for the chick after colony departure. During the period of biparental care, males thus spend more time covering their own needs (Thaxter et al. 2009). In puffins, females feed the chick more often than males, while the latter spend considerable time in the colony defending the burrow during the chick-rearing period (Creelman & Storey 1991). Equal weight loss for both sexes during the chick-rearing period (Barrett et al. 1985) indicates that the energy expenditure is similar despite of female-biased feeding rate in puffins.

Daily activity pattern

The best model explaining daily activity in puffins at Bjørnøya showed no diurnal pattern in chick provisioning. This is in accordance with Barrett et al. (1997), which also failed to find any diurnal variation in chick feeding patterns for Brünnich's guillemot and common guillemots breeding north of the Arctic Circle. Most seabirds are visual predators (Schreiber & Burger 2001), and forage during hours of daylight. In the Arctic summer, daylight lasts around the clock (midnight sun), allowing seabirds to forage continuously throughout the 24-h day. Such continuous activity may be an adaption to maximize delivery rate in order to successfully raise offspring during the short polar summer season (Steiger et al. 2013). Few studies have investigated the response of wild animals to continuous daylight, but a lack of rhythmicity is found in both polar residents and non-residents breeding in the Arctic (Reierth & Stokkan 1998; Steiger et al. 2013). In comparison, puffin chicks at lower latitudes are not fed at night (Nettleship & Birkhead 1985). Instead, chick provisioning peaks in early morning, with a smaller peak in the evening (Myrberget 1962; Harris & Wanless 2011). I found no significant circadian activity pattern in puffin prey load deliveries, yet non-significant models of daily activity showed a similar pattern with peak activity in the morning and in the evening. Diurnal feeding patterns occur in seabirds that depend on prey species conducting diel vertical migration (Hays 2003). The lack of a distinct day and night during the Arctic summer may prevent vertical migration in prey fish (Regular et al. 2010), which again may explain why I failed to detect any daily pattern in prey load deliveries.

Methodological limitations and opportunities

The effect of disturbance on breeding puffins vary geographically and temporally, with largest impact during the onset of breeding and around the time of hatching (Rodway et al. 1996). I have investigated camera traps as a less invasive alternative to traditional monitoring methods. During the fieldwork, efforts were made to avoid unnecessary disturbance. After recommendation by Cutler & Swann (1999), as little time as possible was spent in the colony, and modification of burrow entrances were minimal. When images were reviewed, it was evident that puffins responded to the camera traps, looking directly at the camera and curiously investigating it. Meek et al. (2016) found that camera traps affected animal behavior, as animals responded to emission of light and sound, or simply just the presence of a foreign object. Although being referred to as a less invasive method, equipment effect of camera traps should not be disregarded (Cutler & Swann 1999; Meek et al. 2016).

Because prey size, prey type, orientation of prey in the bill, light conditions and distance from the camera affect prey detectability on camera trap images (Lee & Hockey 2001), all images from the 2015 breeding season were reviewed prior to the 2016 breeding season to adjust camera setup and optimize image quality. In spite of this, prey identification was challenging due to variable image quality. Misjudging the number of fish per load or misidentifying fish species are common errors when observing seabird diet (Rodway & Montevecchi 1996; Barrett et al. 2007), and fish larvae and small fish are difficult to identify even when collected (Eilertsen et al. 2008, Hallvard Strøm pers. comm.). When using camera traps, images can be stored, re-analyzed and confirmed by experts (Gaglio et al. 2016) to avoid observational bias. In my study, two independent parties estimated both number of fish per load and fish length measurements. Estimates on number of fish per load coincided between observers, while fish length measurements did not. In cases where observations were not uniform, observation differences could be used as a measure of preciseness.

When using observation to investigate seabird diet, fieldwork is often conducted on one or a few 24-h watches during the breeding season, monitoring several burrows simultaneously (e.g. Barrett et al. 1987; Barrett et al. 1997; Eilertsen et al. 2008). In contrast, camera traps monitor only one burrow entrance at a time. Because seabird diet vary between days, seasons, sexes and individuals (Duffy & Jackson 1986), constant camera trap monitoring over time is more likely to

detect variance in diet compared to direct observation. Camera traps are referred to as a less time-consuming method than continuous video recording (Cutler & Swann 1999), yet I spent considerable time processing approximately 300 000 images, ending up with only 160 recorded prey load deliveries. A better camera setup could minimize unwanted recordings (Hamel et al. 2013), which again would have reduced review time, power consumption and storage capacity used. Longer intervals between battery and SD-card change would have caused less disturbance to the birds.

Prey load detectability in camera traps depends on camera position, trigger speed, sensitivity of IR motion detector and environmental conditions (Wellington et al. 2014). Reconyx camera traps are designed to record small-bodied animals and have a relatively fast trigger speed (Wellington et al. 2014). Failing to depict what seemed like possible prey load deliveries, an even faster trigger speed would be desirable. In addition, to determine the reliability of the motion detection camera, camera traps could have been combined with continuous camera monitoring (Steen 2009; Steen & Aase 2011; Steen 2017). Continuous camera monitoring systems are commonly powered by heavy 12 V batteries (Cox et al. 2012), and transportation issues prevented me from bringing such heavy equipment to Bjørnøya.

Conclusion

My study illustrates the potential of using camera traps to monitor seabirds in colonies where traditional monitoring methods are unsuitable, providing useful information on diet composition, breeding phenology, sex differences in feeding rate and diurnal activity patterns in a burrow-nesting auk. Due to small sample size, further studies are needed to conclude on breeding habits for Atlantic puffins breeding at Bjørnøya. Like all other monitoring methods, camera traps have both advantages and shortcomings (Cutler & Swann 1999; Barrett et al. 2007; Cox et al. 2012). In summary, camera traps required minimal fieldwork, data were verifiable, monitoring effort was constant throughout the breeding season and disturbance of breeding birds was minimal. Difficulty to identify prey due to unsatisfactory image quality, few recorded prey load deliveries and very time-consuming image review were disadvantages of using camera traps. With enhanced camera technology, the method presented here should be developed further to improve image quality, decrease time required to process images and thus making image review less time-consuming and more cost-effective. Future studies should ensure sufficient sample size by setting up more camera traps, as well as quantifying the detectability rate of camera traps, e.g. by the use of concurrent continuous video recording. Placing camera traps inside the burrow should be considered in order to reduce unwanted triggering, and to obtain information on chick development and activity. I do believe that camera traps may provide a valuable contribution to seabird research in the future, although camera traps can probably not substitute traditional monitoring methods at present.

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Appendix I

Table I: Full models of diurnal activity patterns. x represent ‘time of day’ and ε is random effect ‘burrow ID’. f is the probability for delivery at hour x . a_0 is the intercept.

Full model	
M_0	$\text{logit}(f(x)) = a_0 + \varepsilon$
M_1	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \varepsilon$
M_2	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2 * 2\pi x}{24} + b_2 \sin \frac{2 * 2\pi x}{24} \right) + \varepsilon$
M_3	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2 * 2\pi x}{24} + b_2 \sin \frac{2 * 2\pi x}{24} \right) + \left(a_3 \cos \frac{3 * 2\pi x}{24} + b_3 \sin \frac{3 * 2\pi x}{24} \right) + \varepsilon$
M_4	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \text{DaysDiff} + \varepsilon$
M_5	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2 * 2\pi x}{24} + b_2 \sin \frac{2 * 2\pi x}{24} \right) + \text{DaysDiff} + \varepsilon$
M_6	$\text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2 * 2\pi x}{24} + b_2 \sin \frac{2 * 2\pi x}{24} \right) + \left(a_3 \cos \frac{3 * 2\pi x}{24} + b_3 \sin \frac{3 * 2\pi x}{24} \right) + \text{DaysDiff} + \varepsilon$
M_7	$\text{logit}(f(x)) = a_0 + \text{DaysDiff} + \varepsilon$

Appendix II

Mean (\pm SD) RFL was 45.7 ± 16.8 mm (range 14.0-111.3 mm).

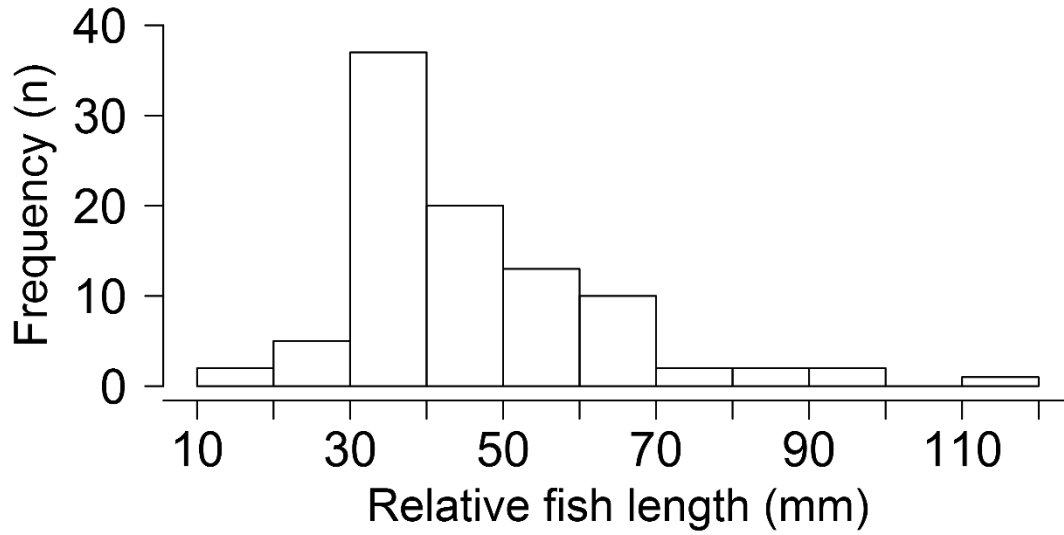


Figure II: Frequency distribution of RFL of fish brought back to the burrow by adult Atlantic puffins at Bjørnøya (N = 94).

Appendix III

Table III: All models included in the daily activity analysis. Full models are listed in appendix I. Degrees of freedom (df), Akaike information criterion (AICc) and difference in AICc from the best model (Δ AICc) are listed. Models are ranked based on Δ AICc.

Model	Rank	df	AICc	Δ AICc
M ₀	1	2564	1106.0	0.0
M ₇	2	2563	1107.9	1.9
M ₁	3	2562	1109.7	3.7
M ₂	4	2560	1111.5	5.5
M ₄	5	2561	1111.6	5.6
M ₅	6	2559	1113.4	7.4
M ₃	7	2558	1115.3	9.3
M ₆	8	2557	1117.3	11.3

Appendix IV

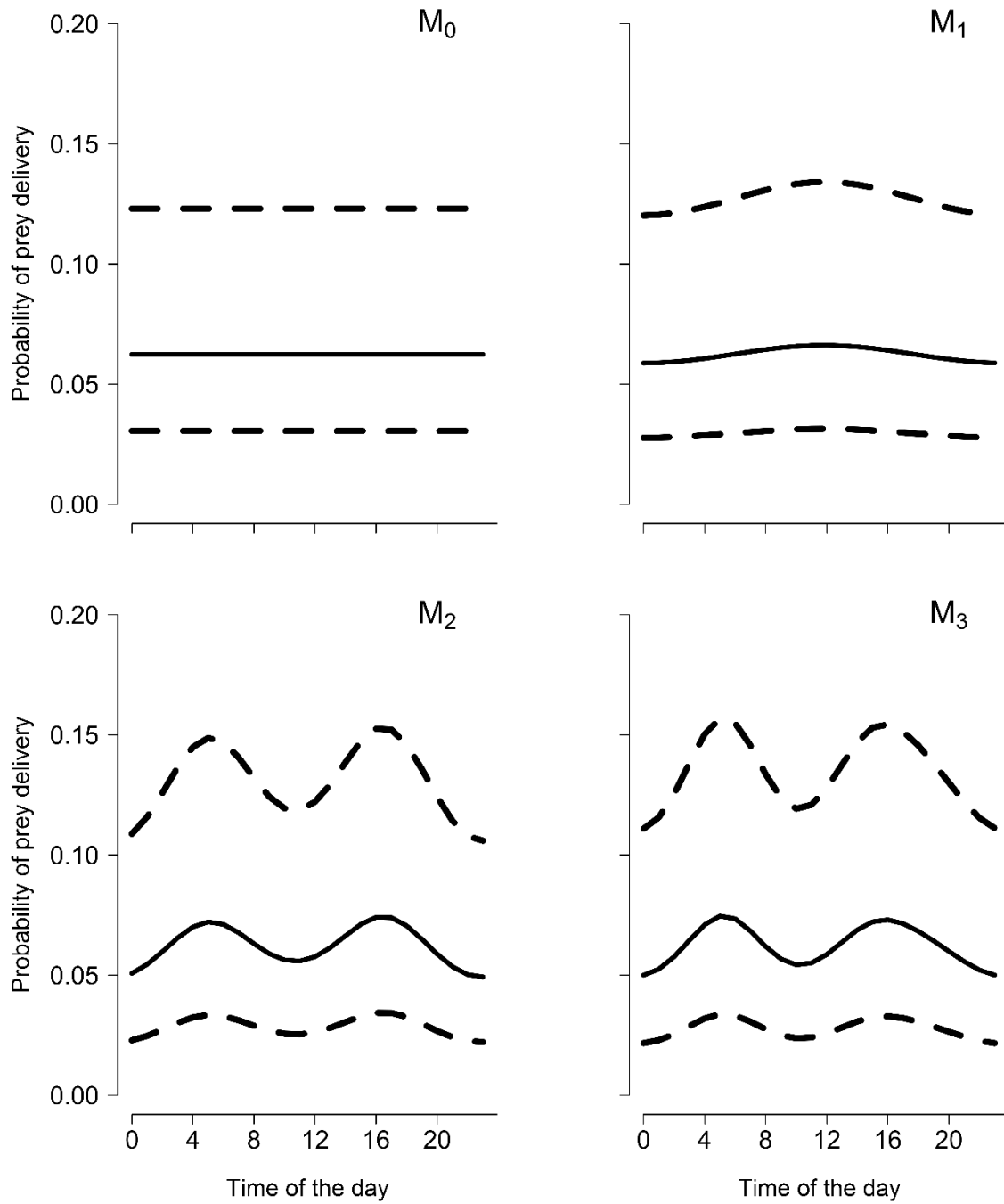


Figure IV: Plotted models explaining daily activity pattern in prey load deliveries in the Atlantic puffin at Bjørnøya. Parameter estimates are given in table 10. Full models in appendix I.

Appendix V

Seasonal activity patterns in the two seasons monitored. Delivery data from all breedings within the same season are pooled and presented in the same figure. Due to small sample size for each burrow, it was not possible to run further analysis on seasonal activity patterns.

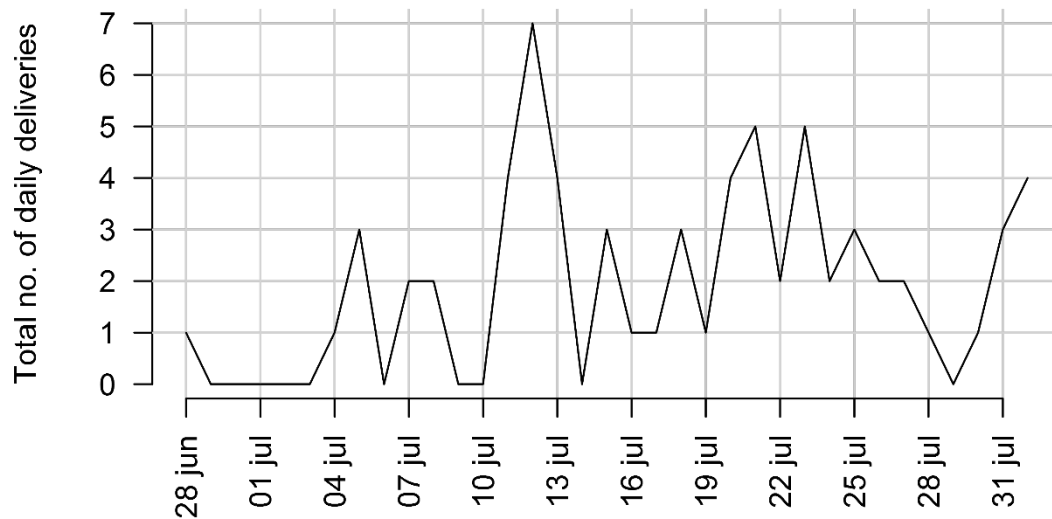


Figure V-I: Total number of prey load deliveries recorded by camera traps at four different Atlantic puffin burrow entrances at Bjørnøya during the 2016 breeding season (N = 66). One breeding was unsuccessful, and only one prey load delivery was recorded at this burrow.

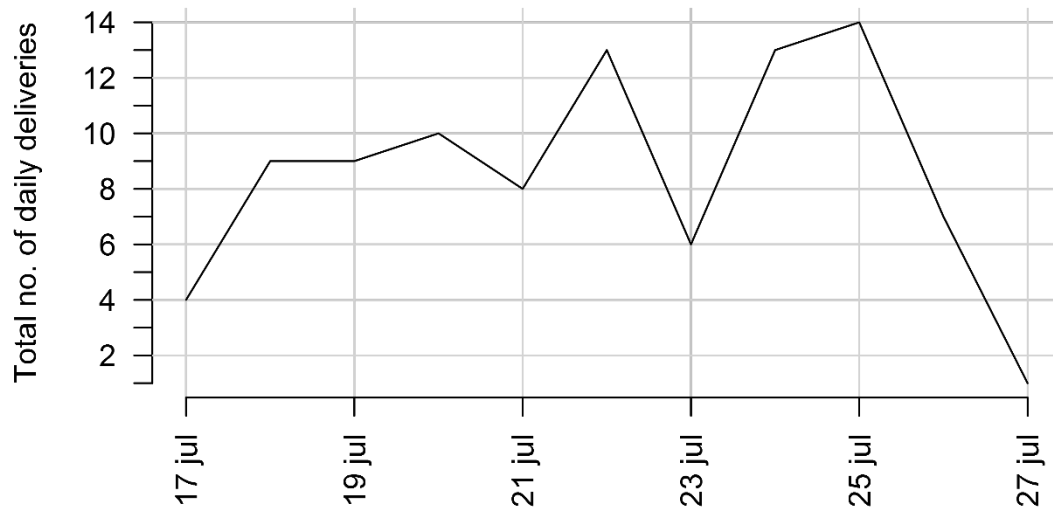


Figure V-II: Total number of prey load deliveries recorded by camera traps at three different Atlantic puffin burrow entrances at Bjørnøya during the 2015 breeding season (N = 94).



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