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Should I Stay or Should I Go? Geolocators reveal different winter home ranges and -foraging patterns in sympatrically breeding razorbills (*Alca torda*)

Magne Hestem

Master of Science in Natural Resource Management

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Supervisors:

Tone K. Reiertsen, Kjell Einar Erikstad, Per Fauchald, Manuel Ballesteros

- Norwegian Institute for Nature Research (NINA)

Thron O. Haugen

- Norwegian University of Life Sciences (NMBU)



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“A razorbill in the hand is better than ten on the roof”

Cover photo by Magne Hestem

Razorbill (*Alca torda*) captured during breeding season at Hornøya

PREFACE

I would like to start by thanking my team of supervisors; Tone K. Reiertsen, Kjell Einar Erikstad, Per Fauchald and Manuel Ballesteros at NINA and Thron O. Haugen at NMBU. A special thanks to Tone and Kjell Einar for guiding me through the mysterious world of seabirds; to Manuel for leading me into the world of spatial data-analyses in R; and especially to Per and Thron for believing in me when I came to you in the fall of 2018 and said I wanted to take on a master-project in Tromsø, a mere 1172 km (great circle distance) from campus Ås (Sørhellinga). A commute which is nearly the same as that undertaken by the winter-migrating razorbills from Hornøya. Well, they say you should try to know your (study-) species... I also wish to thank the Norwegian Institute of Nature Research (NINA) and the SEAPOPOP-project for funding the study and providing me with an office in Tromsø.

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Magne Hestem
Tromsø, December 2019

ABSTRACT

Annual migration between breeding- and wintering grounds is a common behavior that is found in a range of taxa, including many seabird-species such as alcids. Within-population-differences in migration strategies, including high or low fidelity in routes, wintering destination and timing, might have a strong impact on survival and later breeding success due to potential differences in e.g. threat exposure and environmental conditions during the inter-breeding season. Knowledge of such is therefore crucial in order to understand the population dynamics of a taxa as well as to improve conservation strategies within environmental management. Through the usage of light based geolocators equipped with saltwater immersion sensors, this study investigated spatial distribution and activity patterns of razorbills breeding in the southern Barents Sea during their non-breeding season of 2018/19. The razorbills were found to divide into at least two main groups depending on their choice of wintering destination. One group migrated south to overwinter in Skagerrak while the other stayed resident in the Barents Sea. The razorbills wintering in the Barents Sea significantly lowered their activity during the main winter-months, spending less time foraging and in flight. The razorbills wintering in Skagerrak did not lower their activity to the same extent, leading to a seasonal difference of time spent foraging and in flight, depending on migration strategy. No difference on body condition between the two groups was found during the following breeding season, suggesting that both strategies might be a viable alternative. However, further research is needed in order to establish an understanding of consistency and drivers of migration in the Barents Sea razorbills as well as any possible long term-fitness consequences.

Keywords:

Activity-data, GLS, Inter-breeding season, Migration, Razorbill, Wintering destination

ABSTRAKT

Årlig migrasjon mellom hekke- og overvintringsområder er et fenomen kjent i en rekke arter, inkludert sjøfugl. Forskjellige migrasjonsstrategier innad i en populasjon kan gi variasjon i eksponering for forskjellige farer som e.g. predasjon og forurensning, samt naturlige miljøforhold. Dette kan igjen ha stor innvirkning på årlig overlevelse og senere hekkesuksess, derfor vil slik informasjon være av stor betydning for å forstå populasjonsdynamikken innad i en art samt forbedre strategier for vern og forvaltning. Gjennom bruk av lysloggere (GLS) utstyrt med saltvannssensorer, har denne studien undersøkt områdebruk og aktivitetsmønstre for alke hekkende i det sørlige Barentshavet gjennom vintersesongen 2018/19. Det ble funnet at alkene kunne deles inn i minst to hovedgrupper basert på overvintringsområde, hvor den ene gruppen migrerte sørover til Skagerak-området mens den andre ble igjen i det sørlige Barentshavet. Alkene som overvintret i Barentshavet senket aktiviteten midtvinters og brukte mindre tid på furasjering og flyvning under denne perioden. Alkene som dro til Skagerrak senket ikke aktiviteten i samme grad, hvilket ledet til en signifikant sesongbasert forskjell i tid brukt på furasjering og flyvning, avhengig av overvintringsområde. Det ble ikke funnet noen forskjeller i kroppskondisjon mellom de to gruppene i den påfølgende hekkesesongen, hvilket kan antyde at begge alternativene er fungerende strategier. Flere studier er allikevel nødvendig for å undersøke om disse mønstrene er gjentakende over flere sesonger, bakenforliggende årsaker (drivere) samt kunne fastslå hvordan valg av overvintringsområde eventuelt påvirker kondisjon og eventuelt hekkesuksess i et langtidsperspektiv.

Nøkkelord:

Aktivitets-data, Alke, GLS, Migrasjon, Vinter-område

LIST OF ABBREVIATIONS

DF	Degrees of Freedom
G	Gram
GLS	Global Location Sensor
HR	Home Range
KG	Kilogram
KM	Kilometers
LMM	Linear Mixed effect Model (regression)
LSCV	Least Squares Cross Validation
MPA	Marine Protected Area
MSE	Mean Squared Error
PBS	Phosphate buffered saline
PELT	Pruned Exact Linear Time
RB	Razorbill
SD	(sample) Standard Deviation
SE	(sample) Standard Error

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INTRODUCTION

Annual migration (i.e. seasonal movement between breeding- and wintering-grounds) are a common trait found in a range of taxa including seabirds (Dingle & Drake, 2007; Jessopp et al., 2013). Migrative behavior can occur on a population-wide scale where all individuals from a population take part in a more or less unison movement into a new area or individuals might disperse into different areas showing high or low fidelity in routes, stop-over sites and/or destination (Delord et al. (2017); Fayet et al. (2016a); Yamamoto et al. (2010) and references therein). The drivers behind dispersive migration might be various and are not fully explored or understood (Guilford et al., 2009), however main theories include competition, age and/or sex-related segregation and adaption of parental behavior (Fayet et al., 2016a). Intraspecific competition might lead individuals to seek resources further away from the colony either because of a large population size (density-dependent) or due to pressure from more dominant individuals (quality-dependent) (Gunnarsson et al., 2005). Alternatively, the extra effort needed to reach the more favorable areas could be in an order that only the strongest individuals have the surplus energy needed to undertake the journey (Blake et al., 2013). Segregation might also be sex-specific, where morphologically different genders exploit different ecological niches, or as age-specific, where adults and younglings separate into different areas (Dolbeer, 1982; Phillips et al., 2011; Riotte-Lambert & Weimerskirch, 2013). Dispersal can also happen on a completely individual level, either as a result of individual specialization happening through exploration in early life stages or eventually at a completely random pattern, although the latter is suggested to be a viable strategy only under the circumstances where resources also have a random or homogenous spatial occurrence (Fayet et al., 2016a; Guilford et al., 2011; Phillips et al., 2011).

Variations in migrative strategies within a population might make way for differences in inter-breeding activity patterns, access to resources, threat exposure as well as to modify the timing of arrival back to the breeding grounds, which in turn might affect survival rate and/or subsequent breeding success (Bogdanova et al., 2017; Delord et al., 2017; McFarlane Tranquilla et al., 2014; Reiertsen et al., 2014; Sorensen et al., 2009) and references therein). Therefore, knowledge of within-population differences in use of space during the inter-breeding period as well as related activity patterns, will lead to better understanding of population dynamics within a taxa (Delord et al., 2017; Desprez et al., 2018; Guilford et al., 2009). For environmental management purposes, such information might also be essential to understand how a population might be exposed to different threats such as uptake of environmental contaminants, oil spills, fisheries bycatch, wind farms and

more (Baerum et al., 2019; Drewitt & Langston, 2006; Leat et al., 2013; Montevecchi et al., 2012), potentially having decisive impact on environmental management decisions (Guilford et al., 2009).

Uncovering strategies of migration in birds were for a long time dependent solely on ringing, a method depending on coincidental re-findings of individuals and ring-number reported to the researcher. Consequently, data could take many years to receive and could easily be deficient, providing biased and possibly spurious results (Huettmann & Diamond, 2000). However, during the last decades, technical improvements have facilitated the emerge of miniature geolocators (Geolocation Light Sensors) weighing less than 2 grams and providing long lasting battery capacity (typically a year or more). Such devices have proven ideal for movement tracking of several seabird-species, such as alcids (Burger & Shaffer, 2008; Merkel, 2019). Through regular measure and recording of light levels, the loggers can -when retrieved- provide data that can be used to derive latitudinal and longitudinal positions on specific dates throughout a migration-cycle. Many geolocators have also been equipped with saltwater-immersion-sensors, providing sequential records on whether the logger were dry or in touch with water. This data (often referred to as activity-data) have in later years been used in several studies as a proxy for seabird-activity during the non-breeding season (Cherel et al., 2016; Dean, 2013; Mattern et al., 2015; Ramírez et al., 2013). Although the use of geolocators still relies on recapture of the tagged individual and are not perfect in sense of margin error (± 186 km, (Phillips et al., 2004)), these data have now helped to reveal complete migratory movements as well as inter-breeding activity patterns in a range of seabird-species (see for instance Desprez et al. (2018); Dias et al. (2016); Fayet et al. (2017); Kubo et al. (2018) and McKnight et al. (2011)).

The current study focused on the razorbills (*Alca torda*). A medium to large-sized alcid, breeding in colonies over most of the North Atlantic waters as far north as the southern boundaries of the Barents Sea. Like many alcids, the razorbills are believed to spend their time constantly at sea during the non-breeding period, making it difficult to follow and monitor, hence little is known about its behavior during this period (Linnebjerg et al., 2018; St John Glew et al., 2018). Consequently, most knowledge on razorbills comes from the breeding period when they gather in coastal breeding colonies, typically nesting in crevices or behind scree found on steep rock cliffs, raising up to one chick per mating pair (Barrett, 2015; Harris & Wanless, 1989). During the breeding season the razorbill feeds primarily on pelagic fish such as capelin (*Mallotus villosus*) or sandeel (*Ammodytes spp.*), and its foraging strategy relies heavily on diving (Barrett, 2003; Lilliendahl, 1997; Linnebjerg et al., 2015). Being morphometrically adapted for diving efficiency generally come with a trade off

in regards of efficiency in flight, with diving typically favoring from a heavier body compared to wing-size, while flying would favor the opposite (Watanabe et al., 2011), hence flight is seen as a costly behavior of many seabird-species including the razorbills (Thaxter et al., 2010). Still, several studies have reported that the razorbills sometimes undertake relatively long flights during the non-breeding season in order to overwinter in areas distant from their breeding sites (Brown, 1985; Clarke et al., 2010). Earlier ringing recoveries have for instance revealed that razorbills from the Russian part of the Barents Sea have migrated as far as the southern parts of the Scandinavian peninsula and even the Gulf of Finland (Cherenkov et al., 2016). Similar types of behavior have been detected among the razorbills breeding in the Norwegian parts of the Barents Sea waters, where parts of the breeding population spend their wintering period as far south as Skagerrak, while other stay in the waters closer to the breeding colony (Reiertsen, Erikstad et al., unpubl.). Why the Barents Sea-razorbills seem to opt for different strategies during the non-breeding season and how this might affect activity patterns and fitness levels are still unknown.

Through the usage of miniature geolocators equipped with saltwater-immersion sensors, the aim of this study was to investigate spatial distribution and activity patterns of the razorbills from Hornøya during their non-breeding period in order to identify potential differences in intraspecific migration strategies. The birds migrating further away from the colony were expected to spend more time foraging due to a need to compensate for the extra energy-expenditure associated with migration. Subsequently, potential differences in activity were predicted not to be evident during periods prior to autumn-migration and post spring-migration, when the birds spend their time in the same areas. Measures of birds body metrics was taken both during deployment and recapture of the geolocators in order to investigate potential impact of migration strategy on body condition.

METHODS

STUDY SITE

The small (0.4 km²) island of Hornøya (70° 23' N, 31° 09' E), is located in the south-western part of the Barents Sea approximately 0.5 nautical miles outside of Vardø, Norway (Figure 1). The climate is defined as arctic, with a mean summer temperature of less than 10 ° C (Murray et al., 1998; SSB, 2013).



Figure 1: Map showing the geographical location of Hornøya (marked in red). Map produced by Magne Hestem using package ‘ggplot2’ in program R (Wickham, 2016).

Hornøya houses known breeding seabird colonies and have been home to research and monitoring of seabird populations for several decades, with some time-series extending back to the 1980s (Barrett, 2001). Common species on the island are Atlantic puffin (*Fratercula arctica*), common guillemot (*Uria aalge*), Brünnichs guillemot (*Uria lomvia*), black legged kittiwake (*Rissa tridactyla*), European shag (*Phalacrocorax aristotelis*), herring gull (*Larus argentatus*) and great black-backed gull (*Larus marinus*), in addition to the razorbill. The population of razorbills on the island were estimated to be around 500 breeding pairs in 2008 (R. Barrett, unpubl.). There are no annual counts, but there is an impression that the population is increasing (T. K. Reiertsen, pers. comm.).

FIELDWORK AND DATA SAMPLING

GLS-loggers were deployed on adult razorbills (n=30) during June - July 2018. The loggers were of type Mk4083 (Biotrack) weighing 1.9 grams, equivalent to $< 0.01\%$ of mean body weight of the razorbills (mean bird body weight in 2018: $712.2 \pm \text{SD } 75.4$ grams) and thus well below earlier suggestions on recommended limits on tag weight (Phillips et al., 2003; SEATRACK, 2018; Vandenabeele et al., 2011). The birds were captured using remote-controlled foot-snares and ringed with a both metal and a plastic identification ring. Loggers were mounted on the plastic ring using plastic cable ties, self-adhesive tape and glue (SEATRACK, 2018). At the time of logger deployment, body mass, tarsus-length, culmen-length, head-bill-length and wing-length were recorded. The loggers were retrieved at recapture of the birds during June and July 2019, providing year-round-data (summer-to-summer). At the time of recapture, body mass was recorded once more by use of hand-held scales (Pesola), and blood was sampled for sex determination. Before release, new loggers (Biotrack Mk3006, weighing 2.5 grams (SEATRACK, 2018)) were mounted for sampling of data during the coming year. All field work was carried out with permission from management authorities and the Norwegian Food Safety Authority.



Figure 2: Picture illustrating fieldwork on Hornøya. A razorbill has recently been captured using remote-controlled foot-snares. Photo: Ditte Lyngbo Kristensen.

ANALYSIS OF GEOLOCATOR DATA

Determining spatial distribution

Raw data from the geolocators were downloaded in the field and then decompressed using ‘BAS Geolocator Decompressor’ (British Antarctic Survey). Some of the loggers ($n = 6$) failed to download in the field and were sent to Lotek UK Ltd. for recovery of data. Light data were analysed following Lisovski and Hahn (Lisovski et al., 2012a) using the package ‘Geolight’ in program R (3.5.2) (R Core Team, 2018). Light-level data from the geolocators were used to estimate daily twilight-events from the period of deployment. Positioning was done by computation of latitude from estimated length of day and longitude from the timing of local midday or midnight. Twilight-events were defined by using a threshold-method for solar angle (Lisovski et al., 2012b). For the resident individuals, Hornøya was used as geographic location to derive most suitable solar angle, while more relevant locations (Kattegat: $57^{\circ} 53' N$, $11^{\circ} 26' E$; Brønnøysund: $65^{\circ} 87' N$, $12^{\circ} 12' E$), were used for the migrating individuals in order to overcome potential error caused by the change of habitat, improving the accuracy of positioning (Bridge et al., 2013). Estimations of twilight events could be strongly influenced by an adverse number of coincidental shading effects, ultimately resulting in false positioning (Lisovski et al. 2012b). To improve the accuracy of positioning, data were filtered twice by using the functions [loessFilter] and [distanceFilter] (loess-quartile = 1, max. speed threshold of 40 km/h) (Lisovski et al., 2015; Phillips et al., 2004). In order to examine geographic distribution and use of habitat through the non-breeding period, four different seasons were defined out from expected changes in use of habitat (Table 1). The seasonal home-ranges of the razorbills were then estimated as LSCV-smoothed kernel density contours (1000 x 1000 pixel grid) by using the R-package ‘adehabitatHR’ and visualised on map using ‘ggplot2’ (Calenge, 2006; Calenge, 2015; Wickham, 2016). 50 and 95 % kernels were considered to represent core- and main distributions, respectively (Fieberg & Kochanny, 2005) and references therein). Latitude positions are prone to high inaccuracy around the time of the equinoxes due to more or less equal day length around the globe, making safe estimations nearly impossible (Fox, 2010; Phillips et al., 2004; Wilson et al., 2002). Some of the season were therefore limited in time in order to avoid a period of minimum 10 days before and 25 days after fall equinox and 20 days prior to spring equinox. This is a little wider window than what has earlier been suggested (see Wilson et al. (2002) and references therein), and were applied as a result of manual inspection of the datasets (Bridge et al., 2013), providing a fixed restriction in time that could be applied to the tracks of all individual birds.

Table 1: Time intervals of the defined seasonal periods used for geographical mapping of home-ranges for razorbills from Hornøya through the non-breeding period.

Seasonal period	Time interval	Expected phenology of the razorbills
Post breeding	Aug 1 – Sep 10	Including the autumn moult-period.
Late autumn	Oct 15 – Nov 30	Period of expected end of moult and start of migration ^{1) 2)}
Winter	Dec 1 – Jan 31	Expected period of winter-residency.
Late winter	Feb 1 – Mar 1	Expected period of start of return-migration.

Referenced by: ¹⁾ (St John Glew et al., 2018) ²⁾ (Cherenkov et al., 2016). Parts of the time intervals was restricted to avoid the periods around the equinoxes, where geolocator data are incomplete (Wilson et al., 2002).



Figure 3: Geolocator of type Mk4083 (Biotrack) mounted on to the plastic identification ring wrapped around the leg of a razorbill. Photo: Magne Hestem

Foraging and flight times during the non-breeding season

Saltwater-immersion data from the geolocators were used to investigate activity patterns of the razorbills during the non-breeding season by an approach similar to studies done by Cherel et al. (2016), Fayet et al. (2016a) and Shoji et al. (2015). Mk4083-loggers measure saltwater immersion every three seconds and makes sequential records of this for every 10 minutes. For analysis, each 10-minute interval were assigned to one out of three categories depending on their percentage of wet/dry-time: “Sitting-time” (logger being 100 % wet), “Flight-time” (logger being 0 % wet / completely dry) and “Foraging-time” (logger being between 1 and 99 % wet). It has earlier been some debate about where to set the thresholds for the different categories (Mattern et al., 2015). In the present study, it was chosen to use what has been described as “conservative threshold-values”, meaning that only exclusively wet or dry intervals have been considered as “Sitting-time” or “Flight-time” (Cherel et al., 2016). To investigate activity patterns for the different months of the non-breeding season, for each individual bird, the number of different 10-minute interval-categories were counted, summarised and transformed into minutes before computing a monthly average of time spent on each category of activity for each hour of the 24-hour cycle. The average time proportions for the different migrative groups were later computed as the mean of the birds from the respective groups.

Timing of migration events

Estimating day of departure from breeding colony

When the razorbills are leaving the colony after the breeding season, they experience a period of feather moulting where they are unable to fly and are, as a consequence, spending their time constantly on the water (Harris & Wanless, 1990). This distinct shift in behaviour can be detected in the saltwater-immersion data from the loggers as there is a marked shift in the amount of recorded dry/wet time, thus making it possible to estimate individual departure dates for the birds similarly as to what has previously been done on common guillemots (Erikstad et al., 2018). The saltwater-immersion data values were summarised for each day of the relevant period and the departure date where then identified by using a changepoint analysis on the resulting time-series. The analysis were performed with the package ‘changepoint’ in R using Pruned Exact Linear Time (PELT) in the function [cpt.meanvar] (Killick et al., 2012; Killick & Eckley, 2014; R Core Team, 2018). The method is useful to look for multiple changepoints in mean and variance in a dataset and returns a vector with values of identified changepoints.

Estimating date of arrival to breeding colony in spring

The razorbills arrival to the colony after the return-migration happened close to the spring equinox when safe estimations of latitude positions are not available (Wilson et al., 2002). By using only longitudinal positions from unfiltered geolocation data sets (Cherel et al., 2016), it was still possible to follow the birds movement along the east-west oriented coastline of Northern-Norway. Two requirements were set in order to define arrival day at the colony: Firstly, the longitudinal position should have reached that of the colony within the average error of 1.82° (Phillips et al., 2004). Secondly, the plotted curve of a birds longitudinal positions should stabilize around the longitudinal position of the colony, indicating that the bird had settled in the area for the upcoming breeding season. If more than one position were available per day, the data were smoothed by computing one mean position and obvious outliers (deviation > 500 km from the core distribution) were filtered out from the data-sets. A changepoint-analyses following Killick and Eckley (2014) were done in order to objectively recognize periods of stable longitudinal positions. An example plot for illustration is to be found in Figure 4. A similar approach was done in order to recognize stop-over periods during autumn and spring migration.

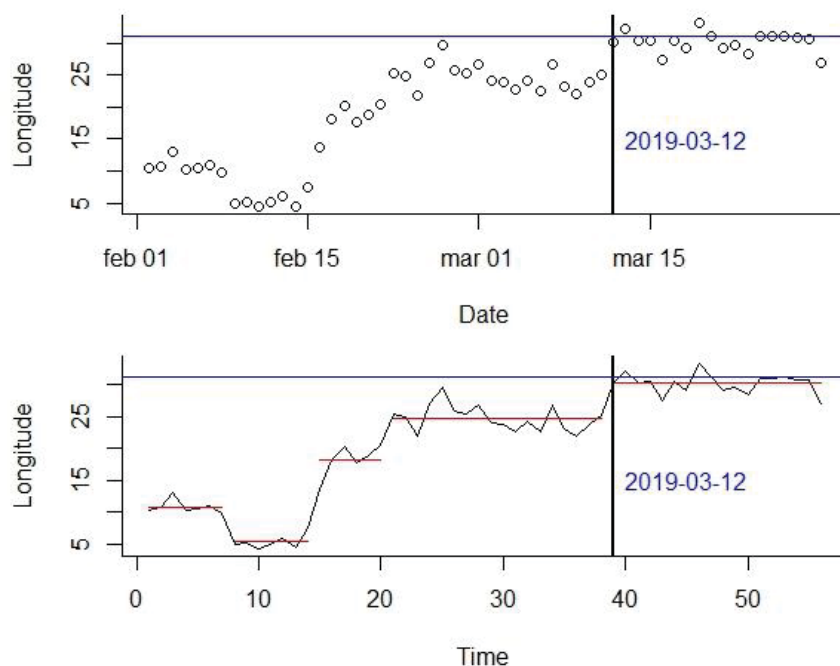


Figure 4: Illustrational graphs for estimation of individual arrival time for razorbills at colony-area using longitude-positions. *Upper:* Plot of longitudinal positions for one example bird after date. *Lower:* Example of returned output-plot from changepoint-analysis after Killick & Eckley (2014). Red horizontal lines indicate periods of stability. *Both graphs:* Black vertical lines are added to indicate point of arrival to the colony-area. Blue horizontal lines are added to indicate longitudinal position of colony.

Estimating time of other migration events

Arrival date in the winter-habitat was defined as the first day a bird was located within the outer latitudinal and longitudinal boundary of the winter home-range derived from the 50 % Kernel density contour. Similarly, the start of the spring migration was defined as the first day the bird left the boundaries of their home-range, not to return again. The duration of the transition-stage, between autumn and winter home-ranges were defined as the number of days used to move from the post-breeding area to the arrival in the winter-habitat. As some irregularities were seen in how some of the birds moved in and out of their core post-breeding home-range, a bird was considered to have started their southward migration when they crossed the 25th parallel, avoiding a bias in the data (similar to the estimation of spring arrival time (above), only longitudinal positions were used, as parts of the period under consideration overlapped with the equinox-period). Start of return-journey for one bird were determined using only longitude-data due to departure close to spring equinox.

SEX-DETERMINATION

Razorbills are a monomorphic species, hence accurate determination of sex cannot be done by visual observation alone (Grecian et al., 2003). Sexing was therefore done using a DNA-based technique following Griffiths et al. (1998) by technicians at Nord University in Bodø. In brief, DNA was extracted from the blood samples of razorbills by using a Phusion Blood Direct PCR Master Mix kit (Thermo Scientific) after being diluted 10 times in phosphate-buffered saline (PBS) (pH 7.2; Gibco). Polymerase chain reaction (PCR) was performed to amplify the sex-related CHD-W and CHD-Z genes using P2 (5'-TCT-GCA-TCG-CTA-AAT-CCT-TT-3') and P8 (5'-CTC-CCA-AGG-ATG-AGR-AAY-TG-3') as forward and reverse primers respectively (total volume of 20 µL, containing 2 µL of blood). Sex was determined by visualizing the samples, together with controls, on a 1.5 % agarose gel. Males are recognized by having one (CHD-Z) and females two bands (CHD-Z and CHD-W). For further details on the method, see Griffiths et al. (1998).

STATISTICS

The saltwater-immersion data from the loggers was used to test for differences in activity-level of the migrating and resident razorbills. Razorbill-activity was expected to vary depending on season as well as migration strategy and it was therefore chosen to test for an interaction-effect between the two variables. Differences in foraging and flight times were tested for independently by fitting two linear mixed-effect models (LMMs) using time of year (month), wintering destination and the interaction of the two as fixed factor variables, always including individual birds as a random factor.

Both models were fitted using a maximum-likelihood-approach. Statistics on foraging included the entire non-breeding season from the beginning of October (although effectively leaving out most of the molting period, when the Razorbills spend their time constantly on the water (Harris & Wanless, 1990; St John Glew et al., 2018)) to the end of March, hence including the time when the razorbills came back to the colony. Data from March was kept out of the statistics done on flight time as colony attendance was expected to infer with the immersion data, causing a large amount of false flight time.

T-tests (equal variances assumed) were conducted to test for differences in body-metrics, body condition, home-range size as well as arrival and departure time to and from the colony. (Differences in variance were tested for by using Fisher's F-test, assuming equal variances if $p > 0.05$.) As a measure of body condition, residuals from a linear model of body mass explained by another body-size measure were used instead of body mass alone, in order to account for differences in size between the birds. The explaining variable to body mass in the regression was chosen by fitting several bivariate linear regression models with length of wing, tarsus, head-bill and culmen as explanatory variables on body mass. The preferred model was the one with least unexplained variation to the recorded observations of body weight, which was examined using R^2 and MSE-values (appendix A).

All statistical computation were done using R version 3.5.2 (R Core Team, 2018). LMMs were computed using the 'nlme'-package (Pinheiro et al., 2019). R^2 values on LMMs were computed by the 'MuMIn'-package following a method designed for use on mixed effect models (Barton, 2019; Nakagawa et al., 2013; Nakagawa et al., 2017). Home range sizes were computed from shapefiles containing respective kernel densities by the 'geosphere'-package (Hijmans, 2017). A percentage of two-dimensional spatial overlap in home-ranges (HR) were computed directly in the 'adehabitatHR'-package following the formula $[HR_{i,j} = A_{i,j} / A_i]$, where A_i is the total area covered by animal (or group) 'i' and $A_{i,j}$ is the area where animal 'j' overlaps with animal 'i' (Calenge, 2006). This method of estimating home-range overlap is 'directional' (i.e. depending on whether the measure is of animal i 's HR overlapped by animal j or *vice versa*). The results were therefore averaged in order to provide a single statistic of overlap that is reported together with the values of $HR_{i,j}$ and $HR_{j,i}$ (Fieberg & Kochanny, 2005).

RESULTS

RECAPTURE OF BIRDS AND LOGGERS

Out of the 30 birds equipped with GLS-loggers in 2018, 28 returned to the colony the following year and 24 of them were recaptured. In total, data from 18 loggers were successfully retrieved and included in the analyses. Four loggers failed to download data (also after being returned to manufacturer for recovery) and two of the loggers had stopped logging already during the fall of 2018. Hence making it impossible to determine the wintering habitat of these birds, and they were therefore excluded from the study.

SPATIAL DISTRIBUTION DURING THE NON-BREEDING SEASON

All the birds were still present in the Barents-sea region in the period between middle of August to middle of September (including -at least parts of- the molting-period (St John Glew et al., 2018)). Some of the birds stayed relatively close to Hornøya ($n = 9$) while others went as far east as the area outside of the Kola- and Kanin-peninsula in Russia ($n = 9$) (Figure 5). There was no evidence that choice of habitat for the early autumn-period was linked to either sex or later choice of wintering habitat. Core home ranges (area under 50% kernel contours) of male and female razorbills overlapped during the early autumn with an average of 62% ($HR_{\text{male,female}} = 0.71$; $HR_{\text{female,male}} : 0.54$) while the home ranges of birds that later migrated south to Skagerrak and those residing in the Barents Sea overlapped with an average of 71% ($HR_{\text{SK,BA}} = 0.60$; $HR_{\text{BA,SK}} = 0.82$).

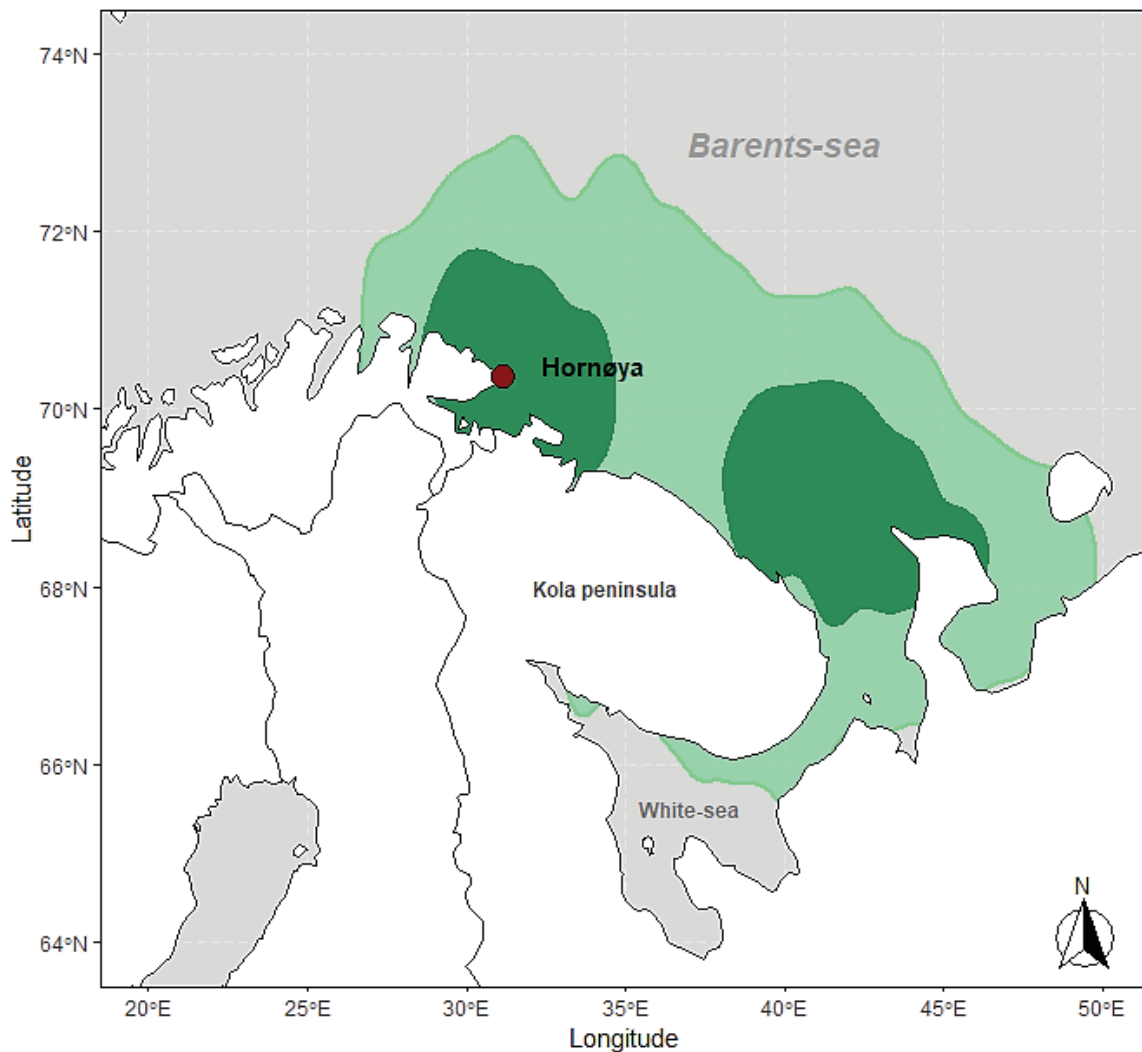


Figure 5: Geographical distribution of Hornøya-Razorbills during the early autumn/post-breeding-period displayed as 95 and 50 % kernel density contours (main and core home-ranges, respectively).

During the period between mid-October and beginning of November, the birds were arriving in their wintering habitat where they stayed during the two main winter months (December and January). Seven of the birds stayed in the Barents-sea region during this period while the remaining 11 migrated further south. Most of the migrating birds ($n = 10$) went on to winter in the straits of Skagerrak and Kattegat, between Denmark, Sweden and Norway, while one stayed in the Norwegian-sea outside the coast of Helgeland and Nord-Trøndelag, Norway (Figure 6). As it was not considered plausible to connect the one bird wintering in the Norwegian-sea to either of the two other migrative groups it was excluded from further statistical analyses. However, relevant information obtained on the individual is still reported where applicable. Both males and females were present in the two main wintering habitats (Table 2). During the winter-period, the average core home range of the Skagerrak-birds was significantly larger when compared to that of Barents-sea birds ($t_{15} = -3.86$, $p < 0.01$) (Table 2).

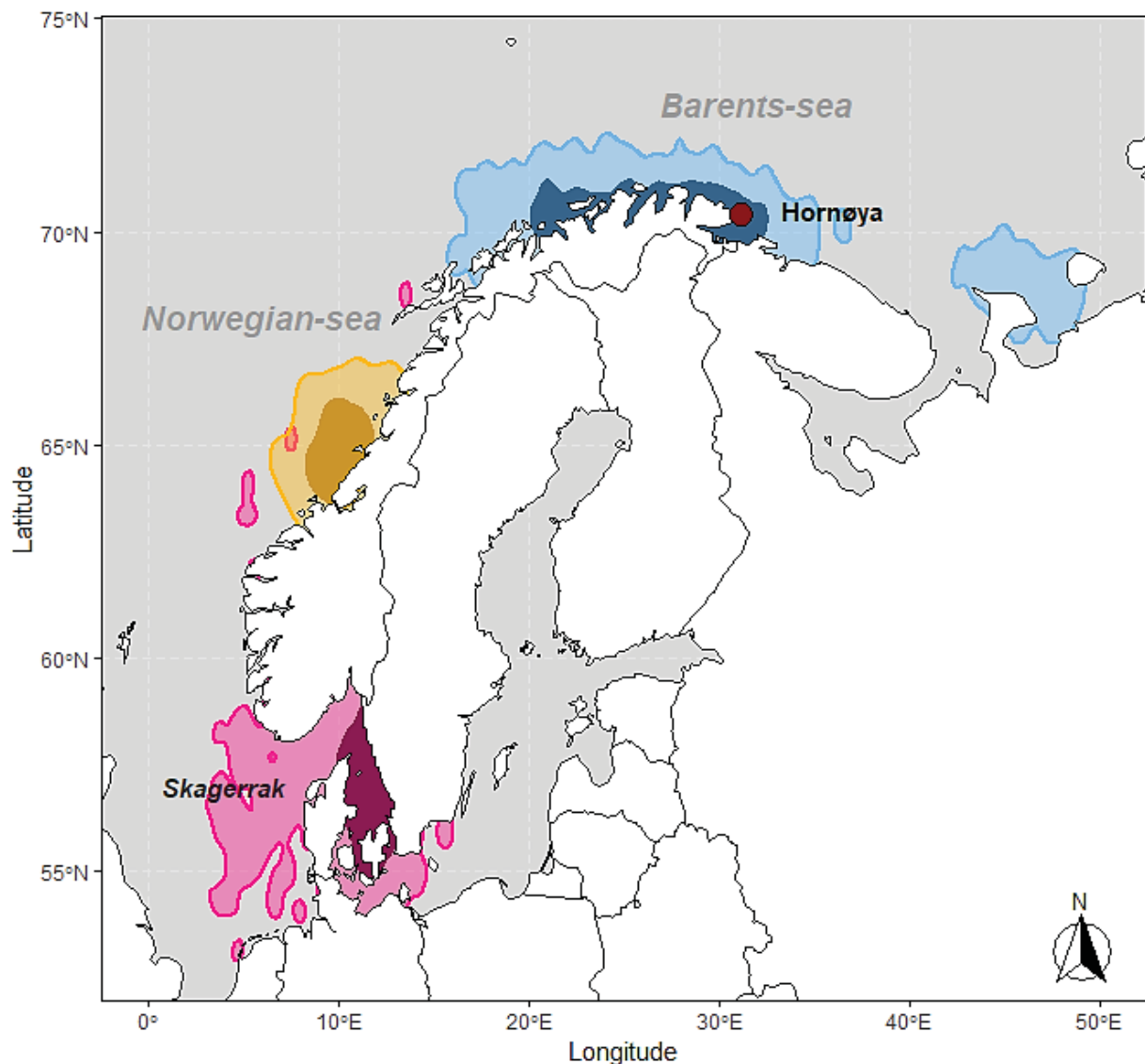


Figure 6: Geographical distributions of Hornøya-Razorbills during the main wintering period (December-January) displayed as 95 and 50 % kernel density contours (main and core home-ranges, respectively). Blue color: Birds wintering in the Barents-sea region (resident). Brown color: Migrative bird wintering in the Norwegian-sea. Red color: Migrative birds wintering in the Skagerrak-region.

Most of the migrating razorbills began their return journey in the beginning of February and arrived in the colony during early to mid-March. The Skagerrak-razorbills used between 13 to 48 days on their return migration while in comparison, they were found to use only between 8 and 13 days on the outbound migration in the autumn (Table 2). There was no significant difference in arrival time between the birds that had wintered in Skagerrak and the birds that wintered in the Barents-sea ($t_{15} = -0.48$, $p = 0.64$). Similarly, there was no evidence that departure time from the colony differed for any of the two groups ($t_{15} = 0.82$, $p = 0.43$).

Table 2: Estimated times of migration-events and wintering home ranges of razorbills breeding on Hornøya after their choice of wintering destination. All values are given in means \pm SD where applicable.

	Barents Sea (n = 7)	Skagerrak (n = 10)	Norwegian Sea (n = 1)
Male/Female	5/2	5/4 (1 unknown)	0/1
Departure date from breed. colony	26/7 \pm 4	24/7 \pm 6	29/7
Start of southward migration	-	19/10 \pm 6	27/10
Date of arrival in winter-HR	-	28/10 \pm 5	31/10
Transfer time to winter-HR (days)	-	10.5 \pm 2	5
Departure date from winter-HR	-	9/2 \pm 14	11/2
Date of return to breed. colony	6/3 \pm 5	7/3 \pm 9	8/3
Transfer time spring migration (days)		27.4 \pm 12.2	26
Centroid position of winter-HR (population-estimate, 50 % kernel)	N70° 17', E28° 55'	N56° 58' E11° 46'	N64° 49' E10° 5'
Mean size of individual winter-HR in km ² (50 % kernel)	25 388 \pm 18 969 *	64 634 \pm 21 643 *	32 406

* indicates significant ($p < 0.05$) differences between destination-groups. As there was only one bird wintering in the Norwegian Sea, it was omitted from further analyses due to sample size, hence only descriptive statistics are presented. Timing of winter migration were not found applicable for the birds that resided in the Barents Sea.

ACTIVITY OF THE RAZORBILLS DURING THE NON-BREEDING SEASON

Foraging activity

Razorbill foraging times varied with both time of year and with choice of migration strategy. The razorbills wintering in the Barents Sea significantly lowered their foraging activity during the winter months, with a minimum occurring in December. The razorbills wintering in Skagerrak did also lower their foraging activity during the winter months, but the activity did not decrease to the same extent as the birds wintering in the Barents Sea. As a result, the razorbills migrating to Skagerrak spent on average more time foraging during the winter months than the birds that resided in the Barents Sea. In February and March, both groups increased their foraging times and there were only minimal differences between them (Figure 7). Overall, the fitted model including the variables time of year (month) and wintering destination could account for 52% of the observed variation in razorbill foraging time. Within the model, time of year significantly contributed to explain razorbill foraging time ($F_{5,75} = 67.56$, $p < 0.001$) while wintering destination as a single effect was not significant ($F_{1,15} = 0.36$, $p = 0.56$). Still, the interaction term of the two were significant, indicating that time of the year had a different impact on foraging time in the two wintering destinations ($F_{5,75} = 16.16$, $p < 0.001$) (parameter estimates are listed in table 3). Foraging activity also varied within the 24-hour cycle with more time spent foraging during morning twilight-hours for both migrating and resident razorbills. Further investigations of this pattern were out of bound for this study, but information on this topic can be found from figures in Appendix B.

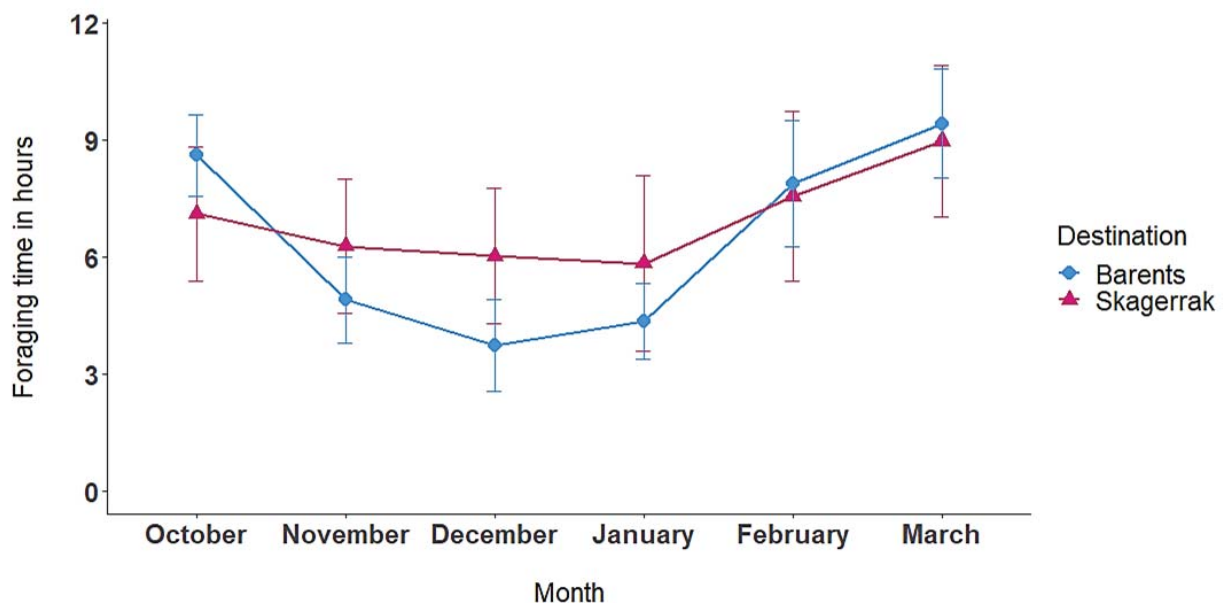


Figure 7: Mean daily foraging time \pm SD after month for razorbills wintering in the Barents Sea- ($n = 7$) and Skagerrak ($n = 10$) regions. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

Table 3: Predicted estimates, slope estimates, SE, df, t- and p-values for daily foraging time in razorbills during their non-breeding season (October - March) depending on their wintering destination. The model included time of year (month), wintering destination and an interaction of the two as fixed effects. Individual birds were included as a random effect. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

	Parameter	Pred. est.	Estimate	Std. Error	DF	t-value	p-value
Barents Sea	October (intercept)	8.609	8.609	0.639	75	13.477	< 0.001
	November	4.904	-3.705	0.426	75	-8.697	< 0.001
	December	3.752	-4.857	0.426	75	-11.401	< 0.001
	January	4.356	-4.254	0.426	75	-9.985	< 0.001
	February	7.887	-0.722	0.426	75	-1.695	0.094
	March	9.422	0.813	0.426	75	1.908	0.060
Skagerrak	October	6.891	-1.718	0.833	15	-2.063	0.056
	November	6.326	3.140	0.555	75	5.653	< 0.001
	December	6.145	4.111	0.555	75	7.402	< 0.001
	January	5.922	3.285	0.555	75	5.914	< 0.001
	February	7.533	1.364	0.555	75	2.456	0.016
	March	8.801	1.098	0.555	75	1.976	0.052
Simplified model syntax:		Foraging time ~ month * destination					
Model R ² marg./cond.:		0.52 / 0.89					
Random effects SD intercept / residual:		1.399 / 0.749					

R²s are given as marginal (only fix. eff.) and conditional (incl. rand. eff) values following Nakagawa (2013; 2017).
The table is written following R programming language although modified for readability (R Core Team, 2018).

Flight time

In the fitted model for prediction of razorbills flight time (Table 4), time of year significantly contributed to the prediction ($F_{4, 60} = 18.12$, $p < 0.001$) while wintering destination alone was not significant in the model ($F_{1, 15} = 2.32$, $p = 0.15$). The interaction term was significant ($F_{4, 60} = 2.57$, $p < 0.05$), indicating that time of year had a different effect depending on the choice of migration strategy also for prediction of flight time. Similar to what was observed for foraging times, the Barents Sea razorbills lowered their time spent in flight during the winter months with a minimum occurring in December. Also the Skagerrak-birds spent less time in flight during the winter months, but generally more time than the birds in the Barents Sea. Still, the difference was smaller than what was observed regarding time spent foraging and was only significant during the month of December. In February, both groups had again increased their flight times and it was not possible to detect any difference between them (Figure 8). Overall, time of year and wintering destination could explain 34% of the observed variation in razorbills flight time during the non-breeding season.

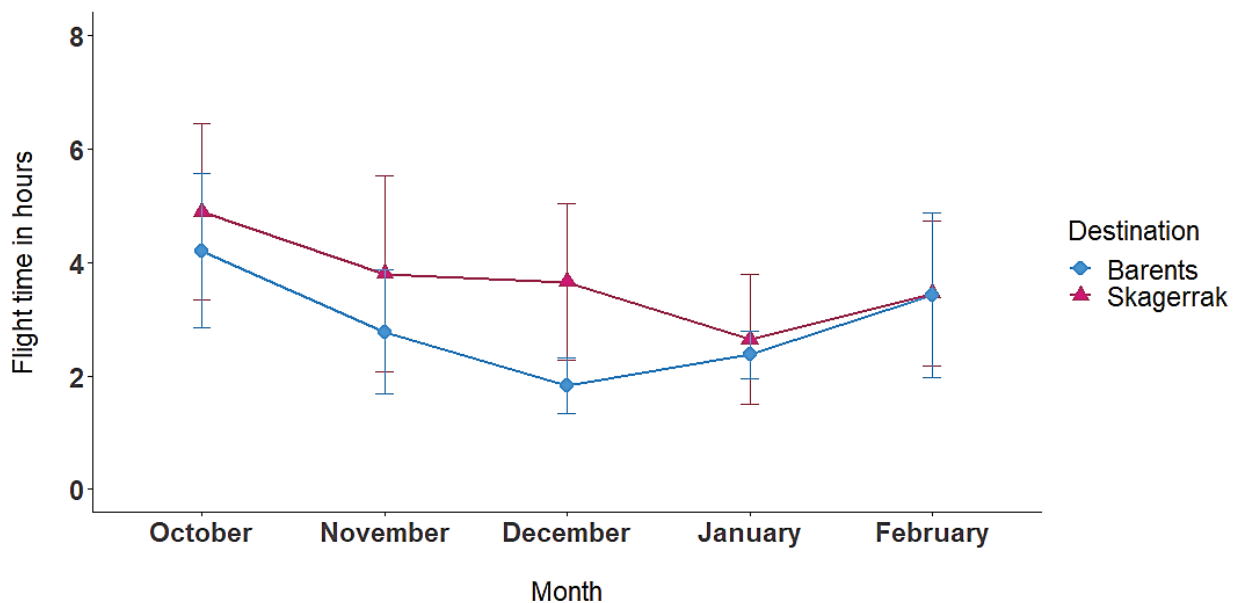


Figure 8: Mean daily level of flight time \pm SD after month for razorbills wintering in the Barents Sea- and Skagerrak regions. Flight time were defined as the sum of all 10-minute intervals registered by the geolocators as being completely dry.

Table 4: Predicted estimates, slope estimates, SE, df, t- and p-values for daily flight time in razorbills during their non-breeding season (October - February) depending on their wintering destination. The model included time of year (month), wintering destination and an interaction of the two as fixed effects. Individual birds were included as a random effect. Flight time was defined as the sum of all 10-minute intervals registered by the geolocators as being completely dry.

	Parameter	Pred. est.	Estimate	Std. Error	DF	t-value	p-value
Barents Sea	October (intercept)	4.207	4.207	0.489	60	8.601	< 0.001
	November	2.907	-1.299	0.411	60	-3.162	0.003
	December	1.829	-2.377	0.411	60	-5.784	< 0.001
	January	2.214	-1.992	0.411	60	-4.848	< 0.001
	February	3.194	-1.013	0.411	60	-2.464	0.017
Skagerrak	October	4.883	0.677	0.638	15	1.061	0.305
	November	3.796	0.212	0.536	60	0.396	0.694
	December	3.652	1.145	0.536	60	2.138	0.037
	January	2.684	-0.207	0.536	60	-0.387	0.700
	February	3.448	-0.423	0.536	60	-0.789	0.433
Simplified model syntax:		Flight time ~ month * destination					
Model R ² marg./cond.:		0.34 / 0.77					
Random effects SD intercept / residual:		0.978 / 0.722					

R²s are given as marginal (only fix. eff.) and conditional (incl. rand. eff) values following Nakagawa (2013; 2017). The table is written following R programming language although modified for readability (R Core Team, 2018).

BODY CONDITION AND SIZE-MEASURES

Average body size-measures were in general a little higher for the birds that wintered in Skagerrak compared to the ones that wintered in the Barents Sea, although the differences were only significant in regards of culmen-length ($t_{15} = -2.97$, $p < 0.01$). It was not possible to claim a significant difference in the case of neither mass ($t_{15} = -1.34$, $p = 0.20$), wing-length, ($t_{15} = -0.38$, $p = 0.71$), head-bill-length ($t_{15} = -1.93$, $p = 0.07$) or tarsus length ($t_{15} = -1.17$, $p = 0.26$) (Table 5).

The measures of head-bill (length from tip of the beak to back of the head) were the best explanatory variable for body mass ($\beta = 14.8 \pm 3.3$, $R^2 = 0.57$, $F_{1,20} = 20$, $p < 0.001$) (see appendix A) for table of candidate models) and were used to calculate body condition of the razorbills. There were no evidence that the choice of wintering destination had any impact on body condition during the following breeding season neither between the two sample groups ($t_{15} = 0.06$, $p = 0.96$) or between years (Skagerrak birds: $t_{18} = 0.52$, $p = 0.61$; Barents-sea birds: $t_{12} = -0.52$, $p = 0.61$).

Table 5 : Body-metrics in millimeters (except b. mass given in gram) for Hornøya-razorbills after wintering destination. Values reported are given in mean \pm SD where applicable. * indicates significant ($p < 0.05$) differences between destination-groups.

	Barents-sea (n=7)	Skagerrak (n=10)	Norwegian-sea (n=1)
Wing	212.4 \pm 4.4	213.4 \pm 5.6	208
Head-bill	94.6 \pm 3.1	97.1 \pm 2.4	95
Tarsus	34.7 \pm 1.4	35.5 \pm 1.3	34.1
Culmen	33.9 \pm 1.3 *	35.7 \pm 1.2 *	35.3
Body mass 2018	710 \pm 65.7	730 \pm 50.4	730
Index of body cond. 2018 ¹⁾	12.37 \pm 40.78	-10.11 \pm 48.17	-
Body mass 2019	709.3 \pm 73.4	745.5 \pm 37.8	715
Index of body cond. 2019 ¹⁾	0.62 \pm 43.16	-0.43 \pm 34.12	-

¹⁾ Averaged values of residuals obtained from a model of razorbills body mass on head-bill-length.

DISCUSSION

Differences in migratory strategies and spatial distribution within a population can have strong impacts on resource availability and threat exposure for the individuals, which in turn might affect population survival-rate and breeding success (Bogdanova et al. (2017); Delord et al. (2017); McFarlane Tranquilla et al. (2014); Reiertsen et al. (2014); Sorensen et al. (2009) and references therein). Results showed that the razorbills breeding in Hornøya were found to occupy similar areas during the times of post- and pre-breeding, but separated into at least two main wintering destinations, one in the Barents Sea and one in Skagerrak. The birds migrating to Skagerrak met the predictions of spending more time foraging and in flight. However, there was found to be no difference in body condition related to choice of wintering destination. Neither on timing of departure and arrival to the colony before and after the winter-season.

SPATIAL DISTRIBUTION

Early autumn (post breeding)

Migration to the wintering habitats did not start immediately as all razorbills had a stop-over period immediately after leaving the colony. During this period, the razorbills occupied an area located between Hornøya in the west and the Kanin-peninsula (Russia) in the east. This is different behavior than what has been earlier reported for the closely situated Russian razorbill breeding colonies in the White Sea. In fact, Cherenkov et al. (2016) reported that razorbills from the Russian colonies began their migration to their wintering habitats immediately after leaving the colonies in the late summer. On the contrary, in this study, razorbills directly moved a considerable distance eastwards from the breeding colony. A possible explanation to the observed differences in these studies might be that Cherenkov et al. (2016) based this part of their study on visual observations (mainly from the Onega Bay, in the inner part of the White Sea) and not on geolocators of any kind. Any observation of the razorbills from these colonies moving out of the White Sea area could easily be interpreted as the start of a direct southward migration, although they might in fact have had a stop-over period similar to that observed in this study. However, it is also possible that the spatial distribution of the razorbills during the autumn might differ both between different breeding populations as well as between years. Further studies, preferably with geolocator data from several colonies and seasons, would be needed in order to investigate for fidelity in timing of migration and stop-over sites used by razorbills from the different colonies along the coast of Northern Norway and North-west Russia. It is not clear what drives parts of the breeding population on Hornøya to

move eastwards during the autumn period, but it is suggested that spatial distribution and occurrence of seabirds is closely linked to the presence of their prey (Fauchald et al., 2011). A similar eastward movement during the autumn has also been detected in both Brünnich's and common guillemots breeding on Hornøya and it was suggested that this was driven by the occurrence of capelin as well as larvae of spawning polar cod (*Boreogadus saida*) that drifts northwards from an area between Novaja Zemlja and the Kanin-peninsula during the late summer and autumn (Steen et al., 2013). Razorbills molt their feathers directly after leaving the colony (leaving them flightless) and males nourish their chicks at sea during this period (Elliott et al., 2017; Linnebjerg et al., 2018; St John Glew et al., 2018). Given these limitations, it is possible that the razorbills are minimizing their costs of foraging by following the current of Atlantic water that flows east along the coastline of Finnmark and the Kola Peninsula (Carscadden et al., 2013) bringing with it a potentially stable food source of 0-group Atlantic cod (*Gadus morhua*) that is coming from the spawning grounds in Finnmark during the same period (Ottersen et al., 2014).

Winter

Two main strategies of migration were evident in the razorbills during the winter. One group of razorbills resided in the Barents Sea ($n = 7$) while other migrated south to Skagerrak ($n = 10$). The razorbills wintering in Skagerrak inhabited an area ranging from the eastern part of the North Sea to the beginning of the western part of the Baltic Sea, most of them having their core wintering home ranges east of the Skagen peninsula (Denmark). This confirms earlier ringing recoveries that have suggested Skagerrak and Kattegat as wintering habitats for Barents Sea razorbills (Brown, 1985; Cherenkov et al., 2016). It would also imply that Hornøya-razorbills probably overlap in site use with individuals from other breeding colonies situated in both the North West Atlantic and the Baltic Seas (Brown (1985); Cherenkov et al. (2016); Heubeck et al. (2011) and references therein). Earlier studies undertaken on ringing recoveries seem to have focused on Skagerrak as the main wintering area of the Barents Sea breeding razorbills. Brown (1985) for instance; refers to those residing up north as 'stragglers'. This is in contrast to the results of the present study, where both alternatives seemed reasonably 'equally attractive' with regards to the number of individuals opting for either alternative. Such intraspecific differences in migration strategy (also known as partial migration) are known in a range of other taxa and have in later years also been reported in other seabird-species such as black-legged kittiwakes, European shag and common diving petrels (*Pelecanoides urinatrix*) (Cherel et al., 2006; Grist et al., 2014; McKnight et al., 2011). A study conducted on Brünnich's- and common guillemots have demonstrated that both southward migration and residency might be equally viable alternatives of life-history-strategies also of species experiencing Arctic conditions

(Fort et al., 2013). Indeed, it was not successful to detect any difference in body condition between the migrating and resident birds included in the current study, indicating that both strategies could be successful strategies also in case of the razorbills. However, this study only included data from a single migration-cycle. Alcids are long-lived species that seem highly adaptable to sudden and random changes in their environment (Gaston & Woo, 2008; Shoji et al., 2014). Studies conducted over several seasons is therefore recommended in order to detect any long-term consequences that life-history variations might have on population dynamics (Sydeman et al. (2017) and references therein).

POSSIBLE DRIVERS OF MIGRATION

It is currently not known what drives the razorbills from Hornøya to opt for several different migration strategies, although a range of possible explanations to partial migration is to be found in literature and include segregation due to sex- or age-differences, intraspecific resource-competition and cultural inheritance (Chapman et al. (2011); Fayet et al. (2016a) and references therein). Sex- and/or age-differences have been found to cause intraspecific segregation in birds (see for instance Dolbeer (1982)). Cherenkov et al. (2016) did explain sightings of razorbills in the Onega Bay during late autumn as young individuals that had missed out on the main movement of birds going south. However, all razorbills included in the present study were adult individuals and established breeders, effectively leaving out age as an explanation. Neither were there any sign of segregation due to sex, as both males and females were present in both Skagerrak and the Barents Sea. Segregation in foraging areas due to intraspecific competition for resources have been found evident in seabirds (Lewis et al., 2001) and a recent study found that density dependent resource-competition were a strong driver of migration in Atlantic puffins (Fayet et al., 2017). In populations where partial migration is driven by density dependence, differences in body size have often been detected between migrant and resident individuals. Smaller-sized individuals might be less dominant and therefore more likely to migrate further (Chapman et al., 2011; Gunnarsson et al., 2005). In addition, larger individuals might be more likely to stay resident due to a naturally higher tolerance of winter conditions (higher ratio of body volume to -surface and better ability to store energy reserves) (Chapman et al., 2011; González-Solís et al., 2007). However, there were no evidence that the residing razorbills were of larger body size. On the contrary, the migrating razorbills had higher recordings of all recorded body-measures. Apart from the case of culmen-length, it was not successful to prove the differences statistically, but this might be due to the relative small sample size available for the study. Migratory behavior can also be inherited either genetically or culturally

(i.e. learned from family members) (Harrison et al., 2010; Helbig, 1991). Alcids have the special life-history trait of male parents following their younglings to sea and nourishing them for a period of up to two months (Harris & Wanless, 1990; Linnebjerg et al., 2018). There seems to be no available knowledge on the behavior of the chicks after this period but it has been suggested that this male biased parenting might affect life history-traits such as dispersal (Insley et al., 2003). Unfortunately, any further investigation of such a link were out of the bounds for the present study. However, inheritance of migratory behavior could potentially explain the highly significant difference in culmen length observed between the migratory groups through favoring or maintaining different traits in body-morphometrics. Indeed, it has earlier been suggested that wintering destination rather than breeding site might determine body size of little auks (*Alle alle*) (Wojczulanis-Jakubas et al., 2010).

ACTIVITY PATTERNS DURING THE NON-BREEDING SEASON

Activity data obtained from geolocators equipped with saltwater-immersion sensors were used to test whether migration strategy impacted activity level of the razorbills, by investigating patterns of foraging and flight time during their non-breeding season. For the analysis of the activity-data, earlier studies on seabird-species have chosen to interpret each 10-minute data-interval into a category of the birds state of activity, (see for instance Fayet et al. (2016a); Phalan et al. (2007) and Ramírez et al. (2013)). Dry intervals have typically been interpreted as flight time and wet intervals have been interpreted as the bird sitting on the water surface. In addition, the intermittent values (logger registering both dry and wet sequences during an interval) have by some been assigned to a category of type “foraging-activity” (see for instance Fayet et al. (2016b); Fayet et al. (2017) and Shoji et al. (2015)). Arguably, some of the time-intervals might in reality belong to a different category than what has been assigned. Typical examples has been the habit of many auk-species to tuck their leg up during resting periods, resulting in dry intervals and “false” flight time (Fayet et al., 2016a) or a bird stretching or scratching themselves in the water, potentially leading to intermittent values and “false” foraging-time (McKnight et al., 2011). It is still believed that this sort of data provides a justifiable proxy for measuring activity-patterns in seabirds (Cherel et al., 2016; Mattern et al., 2015; McKnight et al., 2011). Given the assumption that this sort of disturbance, or “white noise”, is equal among groups of the birds under investigation, it will indeed be useful to compare relative activity-levels between groups of birds as well as identify activity-patterns that might occur during a 24-hour- or seasonal cycle.

All animals need to balance gain and effort to optimise their foraging strategy (see for instance Erwin (1983)). It is believed that migrating individuals need to compensate for the extra energetic cost of movement by increasing their energy uptake during the period of winter residency (Dingle & Drake, 2007). The migrating razorbills were therefore predicted to spend more time foraging and in flight compared to those residing in the Barents Sea. The results showed that the razorbills wintering in the Barents Sea significantly lowered their activity during the main winter months, spending less time foraging and in flight. The birds wintering in Skagerrak did not lower their activity to same extent. This led to a significant seasonal difference in activity depending on choice of wintering destination, where razorbills wintering in Skagerrak did spend more time foraging and flying during the mid-winter period, hence meeting the predictions. This result is in clear support of the findings of an earlier study on migration performed on Atlantic puffins (Fayet et al., 2016a). Similar to the razorbills, the puffins were found to lower their foraging-times during the winter-period, but longer-distance migrants did not lower their effort as much as those staying within a closer distance to the breeding colony. However, establishing a causal link between increased foraging times and migration distance might prove difficult, as there are several other possible explanations to the observations. The observed differences in foraging times could also reflect a variation in density of available resources, alternatively the potential energy gained per item of prey (Fayet et al., 2016a; Sydeman et al., 2017). In addition, environmental conditions such as local variations in weather and sea-surface temperature (SST) are likely to impact metabolism and thus the need to forage (Fort et al., 2009). Further studies on the topic should therefore preferably include both an estimation of energy expenditure and diet. Direct assessment of winter-diet might prove difficult, but analyses of the composition of stable carbon and nitrogen isotopes in feathers ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have proven to be a valuable proxy for this in several earlier studies (Bearhop et al., 2006; Quillfeldt et al., 2005; St John Glew et al., 2018). Razorbills are diving foragers, hence deploying a time-depth recorder (TDR) at the same time as the geolocators would help to provide more detailed knowledge of their foraging patterns. Both providing information on actual foraging effort of the razorbills, as well as providing better means for estimating energy-expenditure compared to saltwater-immersion data alone.

It is interesting that the differences in foraging time observed in this study were not a result of a general increase in foraging times of the migrants but rather a much sharper decrease of the foraging times of those residing during the mid-winter. This is in clear contrast to the findings of other studies carried out on high-latitude seabird-species, that have claimed foraging times to increase during winter as a consequence of availability of resources, higher energetic demands as

well as limitations due to poorer visual guidance (Daunt et al., 2006; Fayet et al., 2017; Fort et al., 2013). An optimal foraging strategy should try to balance gain and effort; this might indicate that the period of mid-winter represent a ‘bottleneck-situation’ for the Barents-sea wintering razorbills where available prey is scarce or difficult to come by. A somewhat similar trend can perhaps be detected in common guillemots also wintering in the Barents-sea. Fort et al. (2013) demonstrated that even though their foraging levels generally increased during the non-breeding season, common guillemots peaked their effort before the onset of the polar-night. This was interpreted as an attempt to ‘stock up’ their energy reserves prior to facing a more challenging winter-period. Further studies, including a modelling of daily energy expenditure in the razorbills might provide valuable insights to how seabirds balance their foraging effort depending on different life-history strategies.

CONCLUSIVE REMARKS

To the knowledge of the author, this is the first study to investigate spatial distribution and activity patterns of razorbills breeding in the southern Barents Sea (Hornøya) using geolocators equipped with saltwater immersion sensors. Results showed that razorbills breeding in Hornøya were found to use at least two different migration strategies during their non-breeding season of 2018/19. One group migrated to winter in the waters close to Skagerrak, the other staying in the Barents Sea-area. The birds migrating to Skagerrak met the predictions of spending more time foraging and flying during the winter season compared to those residing in the Barents Sea. It was not possible to detect any impact on body condition related to choice of migration strategy during the following breeding season, implying that both alternatives might be a viable and consistent strategy within the breeding population. However, further research on consistency and drivers of migration in the razorbills on Hornøya, as well as long term assessment of fitness impacts are needed in order to make any further assumptions or conclusions on this topic.

Currently, we are witnessing an increasing interest in the use of both Nordic and sub-Arctic coastal areas for both commercial and political interests in e.g. fisheries and renewable energy from wind-farming (Faglig forum for norske havområder, 2019). Knowledge and understanding of how anthropogenic use of marine areas might impact the present fauna-populations are therefore crucial in order to improve areal management planning (Lewison et al., 2012). For a migrating population, vulnerability and needs of protective measures might vary over the seasons and detailed knowledge of behavior and distribution are therefore needed in order to improve conservational strategies such as for instance use of Marine Protected Areas (MPAs) across time and space (Perrow et al. (2015);

Montevecchi et al. (2012); St John Glew et al. (2019) and references therein). Research on razorbills have earlier been strongly biased towards the breeding season, leading to a knowledge-gap concerning the rest of their annual cycle. The present study has investigated spatial use and activity patterns during the non-breeding season of razorbills breeding in the low Arctic. Thus, hopefully contributing to a better understanding of the taxa as well as increasing the knowledge base used for decision making within marine environmental management.

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APPENDIX A

To investigate individual body condition of the razorbills, differences in body size were corrected for by using residuals from a linear model of body weight on a representative of body size instead of weight alone. Several bivariate regression models were fitted in order to select the one that best could account for body weight. I.e. choosing the one with that best could explain the observed variability in body weight (tightest fit of the residuals). Table A1 summarises key values of the candidate models.

Table A1 : Test statistics used to compare candidate models for explaining body mass in Razorbills from Hornøya. Body mass (weight) is used as dependent variable in all models. Preferred model in italics.

Independent variable	R ²	MSE	DF	F-value	p-value
<i>Head-bill-length</i>	<i>0.57</i>	<i>1444.3</i>	<i>1, 15</i>	<i>19.99</i>	<i>< 0.001</i>
Culmen-length	0.41	1980.4	1, 15	10.52	< 0.01
Tarsus-length	0.31	2328.5	1, 15	6.71	< 0.05
Wing-length	0.13	2949.2	1, 15	2.14	0.16

APPENDIX B

Figures showing variations in foraging activity over during the 24-hour cycle for birds wintering in Skagerrak and the Barents Sea during the months October to March. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

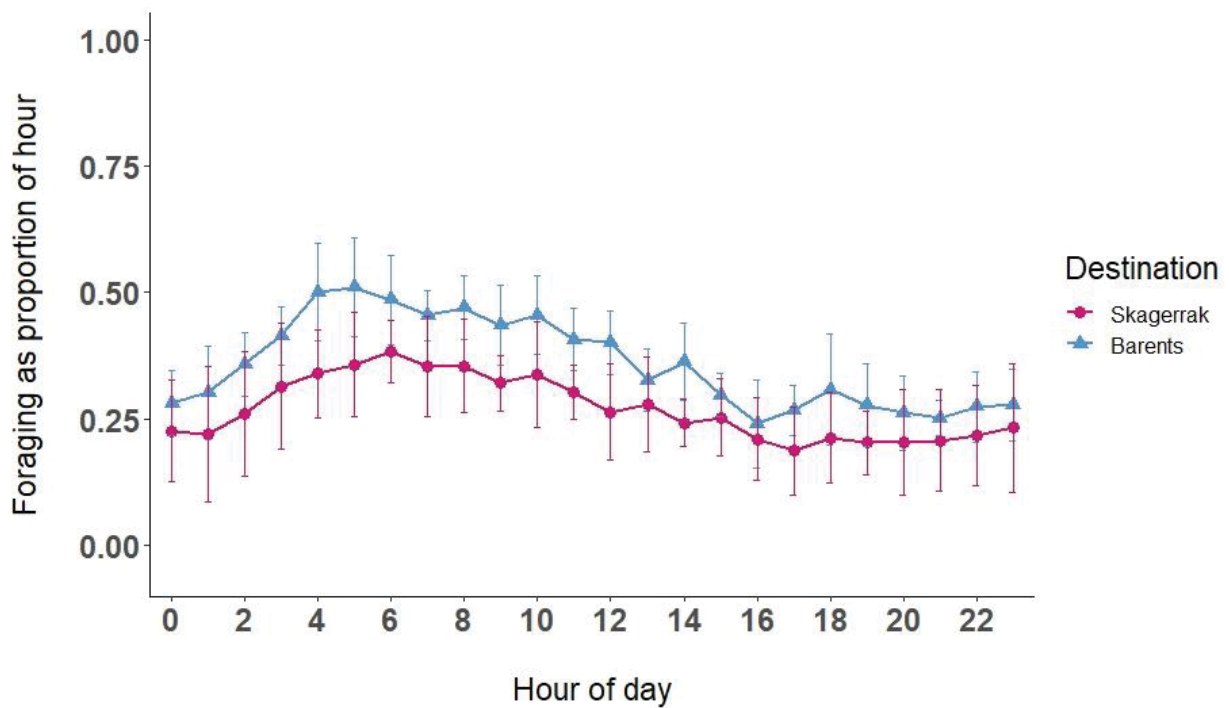


Figure B1: Daily pattern of razorbill foraging in October depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

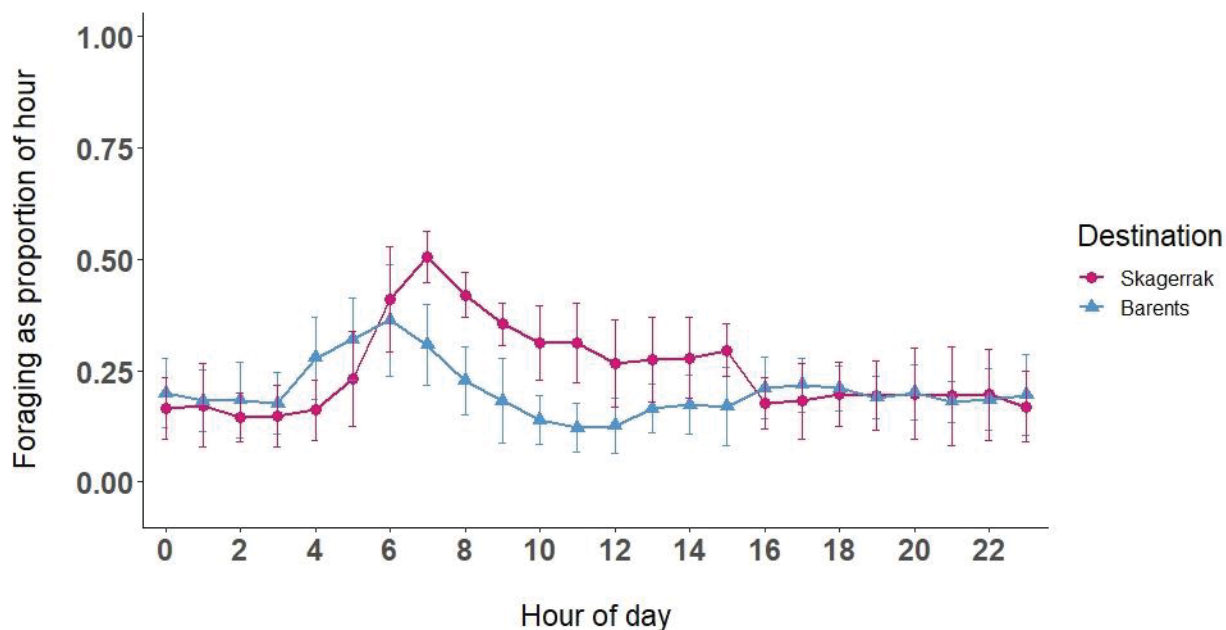


Figure B2: Daily pattern of razorbill foraging in November depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

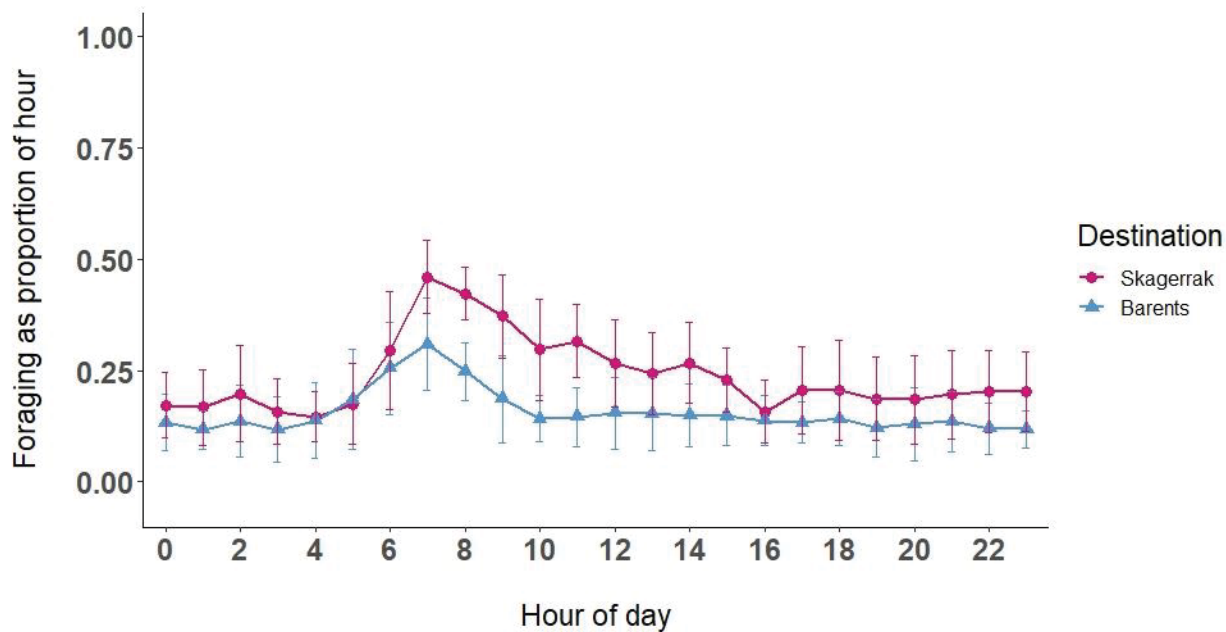


Figure B3: Daily pattern of razorbill foraging in December depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

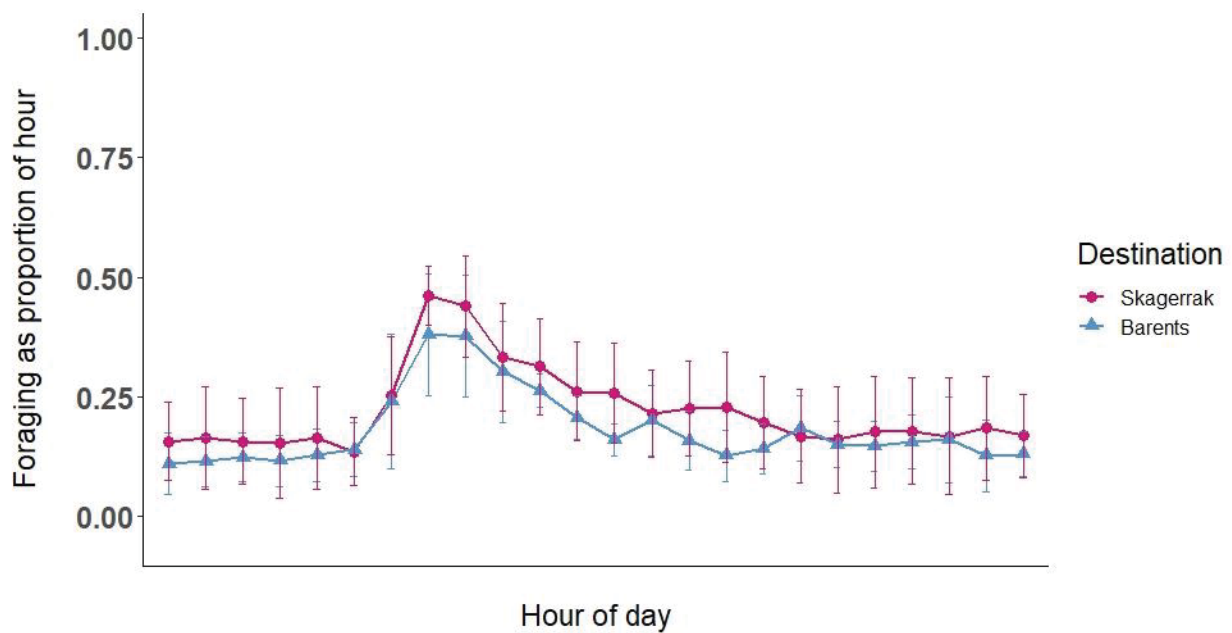


Figure B4: Daily pattern of razorbill foraging in January depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

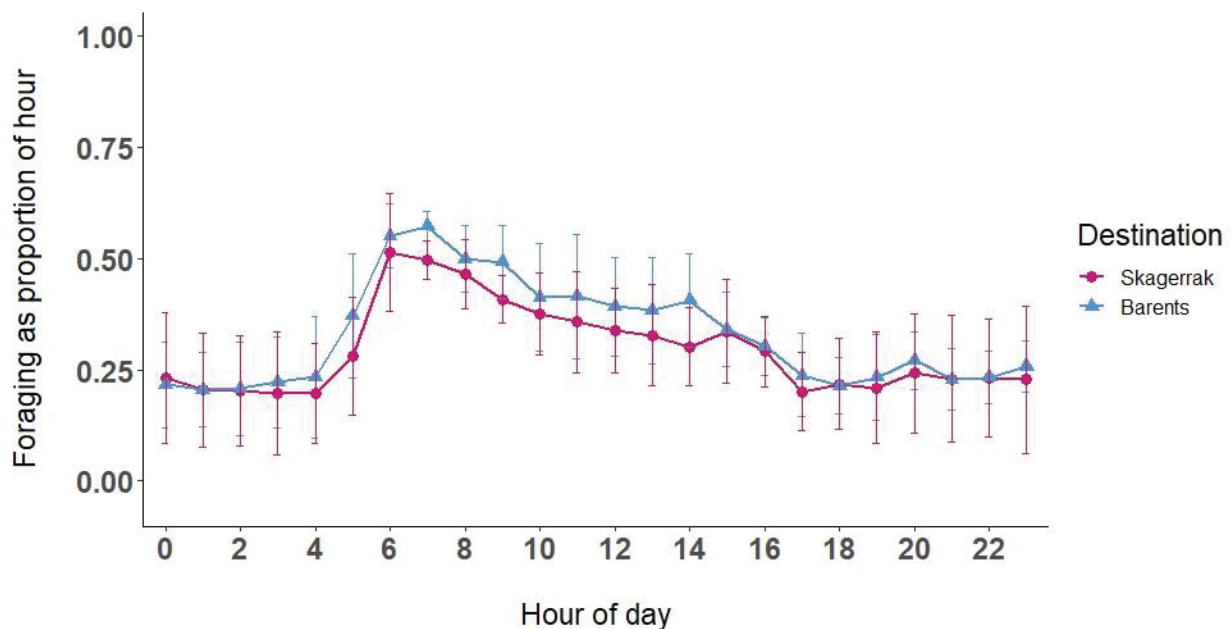


Figure B5: Daily pattern of razorbill foraging in February depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.

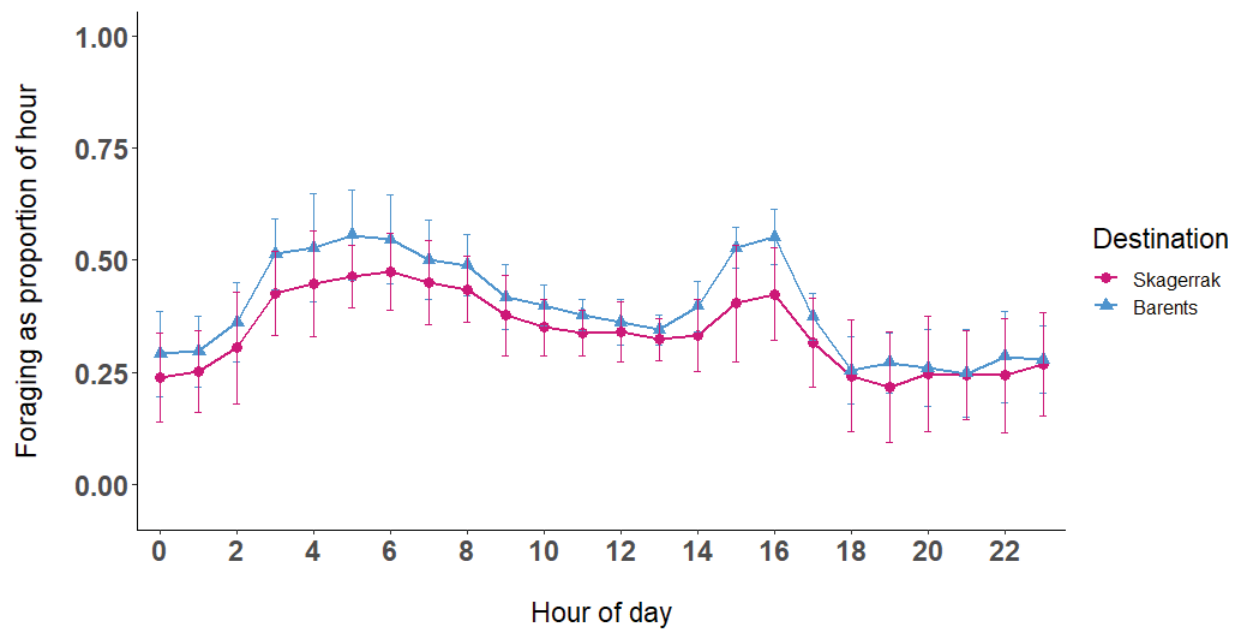


Figure B6: Daily pattern of razorbill foraging in March depending on their wintering destination. Values are given as mean proportion of hour of day \pm SD. Hour of day is given in GMT-times. Foraging time was defined as the sum of all 10-minute intervals registered by the geolocators as being between 1 and 99% wet.



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

Postboks 5003
NO-1432 Ås
Norway