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How Does Spring Migration and Day Length Affect the Diving Ecology of a Capital Breeder Wintering at High Latitudes?

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ABSTRACT

Foraging strategies in animals are influenced by conflicting constraints such as migration, reproduction and seasonal changes in the environment. Sea ducks are capital breeders and rely on endogenous reserves for reproduction. Further, they are mainly diurnal feeders that feed on low-energy prey. There is little information on the diving behaviour of sea ducks around the time of spring migration, and on how they cope with decreasing day lengths in winter. I have studied the diving movements of common eiders (*Somateria mollissima*) breeding in Kongsfjorden, Svalbard and on Grindøya in northern Norway. The aim of this thesis is to investigate whether spring migration and day length affect the diving ecology of common eiders wintering in high latitude areas. To do this, I deployed time-depth recorders (TDRs) on 64 adult female common eiders during the breeding season in 2012-2014, and retrieved and successfully downloaded data from 20 TDRs. Data from these TDRs provided me with information on individual diving frequency, dive duration and dive depth, as well as light intensity and location. Two females from the Kongsfjorden population wintered in northern Norway, and the rest wintered in Iceland. The last two females were from the sedentary population at Grindøya. Comparisons of daily diving frequency before and after spring migration, revealed an effect of year, where eiders migrating in 2013 (n=5) showed no difference in diving frequency before and after migration. In 2014 (n=9) and 2015 (n=6) daily diving frequency was significantly higher after arrival on Svalbard, and the pooled average was also higher after spring migration. This suggests that female eiders prefer gaining weight after arriving on the breeding ground. Average dive depth did not differ before and after spring migration, which may indicate similarities in feeding habitat and prey choice. Averages on both hourly diving frequency and dive depth showed idiosyncratic variation throughout the non-breeding season, and dive depth was not affected by light intensity. This may further suggest a consistency in choice of feeding habitat. However, diving frequency increased significantly during daylight and twilight hours in the darkest period in winter. Nocturnal foraging also occurred in this period. This shows that female common eiders wintering at high latitudes are able to compensate for decreasing day lengths by increasing diving intensity in daylight and twilight, as well as extending their feeding period into the night.

SAMMENDRAG

Fôringsstrategier hos dyr påvirkes av motstridende begrensninger som migrasjon, reproduksjon av endringer i miljøet. Sjøender er avhengige av endogene fettlagre under egglegging og inkubasjon. Videre er de også hovedsakelig dagaktive og spiser byttedyr med lavt energiinnhold. Det er lite informasjon om dykkeatferden hos sjøfugler rundt migrasjon, og om hvordan de håndterer redusert daglengde om vinteren. Jeg har studert dykkebevegelsene hos ærfugl (*Somateria mollissima*) som hekker i Kongsfjorden, Svalbard og på Grindøya i Nord-Norge. Målet med denne avhandlingen er å undersøke om vårmigrasjon og daglengde påvirker dykkeøkologien hos ærfugl som overvintrer ved nordlige breddegrader. For å gjøre dette utplasserte jeg tid-dybde loggere (TDR-loggere) på 64 voksne ærfuglhunner under hekkesesongen i 2012-2014. Jeg innhentet og lastet ned data fra 20 loggere. Data fra disse loggerne ga meg informasjon om individuell dykkefrekvens, varighet og dybde, samt lysintensitet og lokalisasjon. To hunner fra Kongsfjordpopulasjonen overvintret i Nord-Norge, og resten overvintret på Island. De to siste hunnene var fra den stedfaste populasjonen på Grindøya. Sammenligninger av daglig dykkefrekvens før og etter vårmigrasjon avslørte en årseffekt, hvor hunner som migrerte i 2013 (n=5) viste ingen forskjell i dykkefrekvens før og etter migrasjon. I 2014 (n=9) og 2015 (n=6) var daglig dykkefrekvens signifikant høyere etter ankomst på Svalbard, og samlet gjennomsnitt var også høyere etter vårmigrasjon. Dette antyder at ærfuglhunner foretrekker å legge på seg etter å ha ankommet på hekkeområdet. Gjennomsnittlig dykkedybde var ikke forskjellig før og etter vårmigrasjon, noe som kan indikere likheter i fôringshabitat og valg av byttedyr. Gjennomsnitt i både dykkefrekvens og dybde per time viste idiosynkratisk variasjon gjennom hele vinterperioden, og dykkedybde var ikke påvirket av lysintensitet. Dette kan videre antyde at de er konsekvente i valg av fôringshabitat. Det var derimot en signifikant økning i dykkefrekvens i dagslys og skumringstimer i den mørkeste perioden om vinteren. Også dykking i mørket ble observert i denne perioden. Dette viser at ærfuglhunner som overvintrer ved nordlige breddegrader er i stand til å kompensere for redusert daglengde ved å øke dykkefrekvensen når det er dagslys og skumring, samtidig som de kan forlenge fôringsperioden inn i nattetimene.

CONTENT

INTRODUCTION

The time and energy animals spend on foraging vary according to seasonal food availability and energetic requirements. Foraging may be influenced by conflicting constraints such as migration, reproduction and seasonal changes in the environment. Energetic needs vary between different life stages and activities, such as annual migration and reproduction (Guillemette et al., 2007). Many species accumulate extra energy reserves before migration to use as fuel during long journeys over unsuitable habitats (Biebach et al., 1986). Similarly, many animals increase the amount of energy resources available to compensate for the demands of reproduction (Jönsson, 1997). To achieve this, animals may apply different tactics of resource use and acquisition that also include foraging decisions (Jönsson, 1997). Foraging decisions will have direct influence on fitness.

Sea ducks (tribe Mergini) are capital breeders. They build up large fat deposits as energy storage prior to reproduction, and allocate this capital into egg laying and incubation. Female common eiders, *Somateria mollissima* (L., 1758), can increase their body mass by 20-37 % above winter level (Korschgen, 1977, Parker and Holm, 1990). They rely almost exclusively on endogenous reserves for egg-laying and incubation (Korschgen, 1977), during which these females can lose up to 37-46 % of their pre-laying body mass (Parker and Holm, 1990, Gabrielsen et al., 1991, Meijer and Drent, 1999, Criscuolo et al., 2002). This functions as an anti-predator mechanism since the females stay on the nest the entire incubation period, but the strategy can also be beneficial under unpredictable food conditions and time limitations (Jönsson, 1997). The most important feature is perhaps that it allows feeding and reproduction to be decoupled both spatially and temporally. However, increased body mass also increases the energetic costs of locomotion, and can influence flight performance (Hedenstrøm, 1992) and diving behaviour (Lovvorn and Jones, 1991). For diving sea ducks the energetic costs are linked to two factors, diving frequency and time spent diving (Guillemette et al., 2004, Heath and Gilchrist, 2010).

Common eiders have long been considered the archetype of capital breeders, accumulating the body reserves necessary for reproduction before migrating to the breeding grounds (Parker and Holm, 1990, Hario and Öst, 2002, Lovvorn et al., 2003, Mosbech et al., 2006). However, capital breeders can exhibit different tactics when it comes to foraging around migration and reproduction. Barnacle geese (*Branta leucopsis*) breeding in the Arctic have been found to rely

on resources acquired both at the wintering area and stopover sites, as well as on local food resources for reproduction (Hahn et al., 2011). Findings by Hario and Öst (2002) suggest that common eiders breeding in the Baltic sea rely on resources accumulated on the wintering ground, while common eiders in Canada have been found to accumulate most of their energy stores on the breeding ground (Guillemette et al., 1992, Guillemette, 2001). Thus, to what degree eider reproductive effort depend local or distant food resources is poorly understood. One of the main aims in my thesis is to investigate which of these foraging strategies are used by common eiders breeding in Svalbard. Currently, it is not known whether the Svalbard eiders gain their breeding condition in the wintering areas or after arrival at the breeding ground in spring. I will analyse diving strategy in female eiders around the time of spring migration in order to determine if diving intensity, an indication of resource accumulation, differs between the wintering and breeding area.

Sea ducks are believed to be mainly diurnal feeders relying on visual cues to locate prey (Goudie and Ankney, 1986, McNeil et al., 1992), although knowledge about their foraging technique is limited. They are benthic feeders that feed on invertebrates such as molluscs, echinoderms and crustaceans. Most of these prey species have relatively low energy content compared to size, and large amounts of food are required to balance the energy budget, which necessitates a high level of feeding activity (Bustnes and Erikstad, 1990, Guillemette et al., 1992, Guillemette, 1998). Energetic requirements increase with the harsh conditions associated with winter, such as low temperature and strong wind that increase the costs of thermoregulation and diving (Gabrielsen et al., 1991, Weathers and Sullivan, 1993, deLeeuw, 1996). In addition, day length decreases dramatically in winter, reducing the amount of time available for foraging for diurnal feeders. The extent of which diurnal feeders are able cope with such environmental constraints can vary between species and populations. The harlequin duck (*Histrionicus histrionicus*) wintering in Alaska was found to forage exclusively during the day, despite high energetic requirements, harsh weather conditions and short days (Rizzolo et al., 2005). Similarly, Svalbard barnacle geese (*Branta leucopsis*) increased their foraging effort when days were short, but were not found to feed at night (Cope, 2003). Some eider species have been found to increase the proportion of the day spent feeding (Guillemette, 1998, Systad et al., 2000), as well as extending the foraging period into lower light intensities as a response to short day lengths in winter (Systad et al., 2000). Diurnal feeders are sensitive to factors that increase foraging requirements or decrease foraging efficiency. Thus, the energy budget of diurnal sea ducks is expected to be adversely affected by the combination of short days and

high food requirements in winter, but still little is known about the foraging strategies of sea ducks in coping with environmental constraints. Accordingly, the second goal of my thesis is to test whether female eiders wintering at high latitudes (>65°N) maintain their energy intake during the winter by diving during low light conditions and night, or by increasing the diving frequency during daylight hours.

I will report on the foraging activity of common eiders breeding in Kongsfjorden, Svalbard (78°55′N, 12°17′E), and at Grindøya, Norway (69°38'N, 18°51'E). There are about 2-3000 breeding pairs in Kongsfjorden (Hanssen et al., 2013), and they migrate south before winter (Hanssen et al., 2016). The eider population at Grindøya is sedentary and consists of ca. 150 breeding pairs (pers. comm. SA Hanssen). The Kongsfjorden population has been subjected to monitoring and studies since 1981, and a recent study by Hanssen et al. (2016) revealed that this eider population winter at the coasts of Iceland and northern Norway, a distance of approximately 1700 km and 1300 km from the breeding ground, respectively. Further, day lengths in Iceland are reduced to less than three hours of daylight in the darkest period in winter, whilst in northern Norway the sun is below the horizon from November to January. Knowledge on how sea ducks are affected by the energetic demands of migration and seasonal changes in the environment is valuable for the purposes of conservation and management of the species and its feeding habitat. Seabirds are among the most threatened bird species worldwide (Gremillet and Boulinier, 2009, Croxall et al., 2012), and the common eider is considered a keystone predator in the benthic community (Guillemette et al., 1996, Hamilton, 2000). Few studies have looked at the diving behaviour of sea ducks around spring migration (Guillemette, 2001), and the effect of decreasing day length (Systad et al., 2000). It is important to have more data to be able to draw comparisons and increase our understanding on how seabirds cope with constraints on foraging. The main objective of my thesis is to describe how spring migration and seasonal conditions on the wintering grounds affect the diving and foraging ecology of the common eider, focusing on how they cope with the constraints of being a capital breeder migrating to the Arctic, and being a diurnal feeder wintering in areas where day lengths are greatly reduced in winter. I will investigate 1) if diving intensity increase prior to or after spring migration, and if there is a difference in dive duration and depth before and after arrival on the breeding ground, and 2) how differences in day length at the wintering areas affect the diving frequency, duration and depth at different times of the non-breeding season. To do this, female common eiders were fitted with time-depth recorders (Lotek, LAT 2800L, called TDR hereafter) during the breeding season in 2012-2014, and loggers retrieved in the following

summers (2013-2015). These TDR-loggers record all dives throughout the deployment period. Long-term detailed monitoring on diving movements at this scale has not been done on sea ducks before, and should offer valuable insight in the foraging ecology of diving seabirds. This should help us to understand the energetic constraints and consequences of being a capital breeder in high Arctic and high latitude areas.

METHODS

Adult female eiders were caught on their nest using a noose pole in Kongsfjorden and on Grindøya during June-July, 2012-2015. A TDR-logger was attached to a plastic ring on the tarsus of 64 female eiders (52 in Kongsfjorden, 12 on Grindøya) using super glue and cable ties (fig. 1). Each TDR-logger is 36x13x10 mm and weighs 9 grams (0.45 % of a bird of 2000 g). They have a pressure resolution of 0.05 %, 128 Mb memory, record depths down to 50 meters, and a minimum life time of two years. Loggers were set to record pressure (dBars) every 5 seconds when the pressure was more than 1 dBar (equivalent to a depth of 1.02 meters). They also recorded light intensity and temperature every 10 minutes. From this information the dive frequency, depth and duration, as well as location can be extracted. N=29, 20 and 15 TDR-loggers were deployed in 2012, 2013 and 2014, respectively. A total of 26 (40.6 %) female eiders were recaptured, and data were successfully downloaded from n=20 loggers (18 from Kongsfjorden, and two from Grindøya). Three loggers contained two years of data, 15 loggers had one year of data, and two loggers stopped recording after eight months of deployment.

Data handling and statistical analysis
All calculations and statistics were carried out in R 3.2.1 (R Development Core Team 2014). I extracted diving frequency, dive depth and dive duration from the TDR-loggers using the 'diveMove' package v2.8.0 (Luque, 2007). The Lotek TDR-loggers has a built-in algorithm that automatically assigns timing of apparent sunrise and sunset along with estimates of positions (latitude and longitude). However, this automatic procedure is associated with a lot of error. For better assignment of sunrise and sunset events, I manually inspected the light-data using TransEdit in the BASTrack software package (British Antarctic Survey, Cambridge, UK) and assigned the events using a light threshold of 100-150 (arbitrary units). The threshold was set individually for all loggers to get above the baseline level of noise and below the minimum daylight level. The saved sunrise and sunset events were then used in Locator (also part of the BASTrack package) to estimate positions (latitude and longitude) using individually assigned

Figure 1: A female common eider (*Somateria mollissima*) with a time-depth recorder (TDR) attached to a plastic ring on her left tarsus. Photo: Børge Moe.

sun elevation angles (mean -7.6°; range -6.3° to -9°). See Hanssen et al. (2016) for details about the principles used for assigning appropriate sun elevation angles. From the estimated positions I determined migration dates and wintering grounds for each individual. To determine day length throughout the year at Svalbard, Iceland and northern Norway, I applied the 'maptools' package to extract solar elevation based on the location coordinates. All values of solar elevation $>0°$ were defined as daylight, values between $0°$ and $-6°$ were defined as twilight, and values $<-6°$ were defined as darkness.

The two dive variables depth and duration were highly intercorrelated (r=0.92 with Pearson's correlation test). Visualisation of the data confirmed that they produce the same results, and will I therefore present only dive depth, since vertical movements in the water column may give a better indication of the feeding habitat. Because the loggers record each dive throughout the logging period, the data set consisted of a large amount of data that needed to be summarized. To test whether diving behaviour in female eiders is affected by spring migration, I summarized the average daily diving frequency and depth for the 30 days before departure from the wintering areas, and the 30 days after arrival on the breeding ground in the n=17 eiders migrating to Svalbard, using the time of migration as index. Further, to test whether female eiders compensate for reduced day lengths in winter, I summarized the average hourly diving frequency and dive depth in 10 weekly periods throughout the non-breeding season when females were at the wintering grounds. Analyses were done with the linear mixed-effects models (LME) procedure with individual as random factor. For the analysis on daily dive data, location was also added as a random factor. The assumptions of LME models were satisfied without transforming the data. Values are reported as means ± SE, unless specified otherwise. P-values <0.05 are considered statistically significant.

RESULTS

Of the 20 collected TDR-loggers, 18 were from female eiders breeding in Svalbard, of which 16 wintered in Iceland and two in northern Norway. The two other loggers were from the sedentary population at Grindøya. Visual inspection of the data revealed large individual variation in diving behaviour (see Appendix 1 for data on individual averages of the diving parameters). Individual maximum dive depth ranged from 23.57-44.95 meters, with a dive duration of 75 s and 90 s, respectively. Start of spring migration ranged from March 14th to June 4th (n=17) Start of autumn migration ranged from August 17th to November 27th (N=18), the last bird leaving Svalbard after spending one month in darkness. The yearly variation in diving frequency show a large increase during ca. 30 days prior to the time of breeding (ca. 300 dives day^{-1}, fig. 2). Females begin incubating from the start of June to the start of July in Kongsfjorden, although some lose their eggs to predation or refrain from breeding all together (pers. observation). This increase in diving activity corresponds to the eiders strategy of accumulating extra endogenous reserves for reproduction. The diving peak was directly followed by a dramatic decrease in diving frequency for approximately the same amount of time (ca. 50 dives day^{-1}, fig. 2). This drop reflects that female eiders rely on accumulated capital, and thus don't feed, during incubation. The fact that there still were some diving activity in the breeding period can reflect a lack of synchrony in the timing of egg laying and incubation in female eiders, as well as some females failing to reproduce (both confirmed in the field).

The effect of spring migration on diving behaviour
In order to have a better understanding of the diving frequency before and after spring migration, I centred the data of daily diving frequency around the time of spring migration, specifically in the 30 days prior to and after the migration period. The mean daily diving frequency was 233.89 ± 7.26 and 297.96 ± 7.14 dives day^{-1} before and after spring migration, respectively (table 1). However, the maximum recorded daily diving frequency was higher in the period before migration than after (table 1), reflecting large variation among individuals. Daily average diving frequency increased with 3.35 ± 0.72 dives day^{-1} (p<0.001; t=4.65; n=17) in the period before departure from the wintering grounds, reaching a maximum of
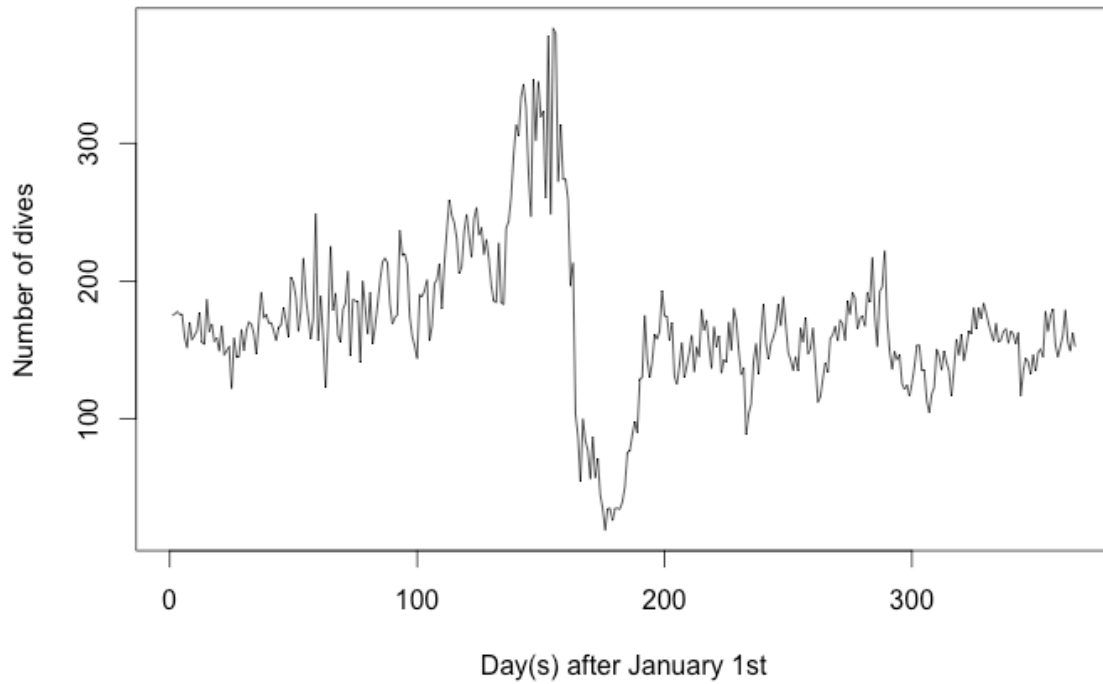
Figure 2: Yearly variation in daily average diving frequency for 20 females common eiders (*Somateria mollissima*) for years 2012-2015 pooled.
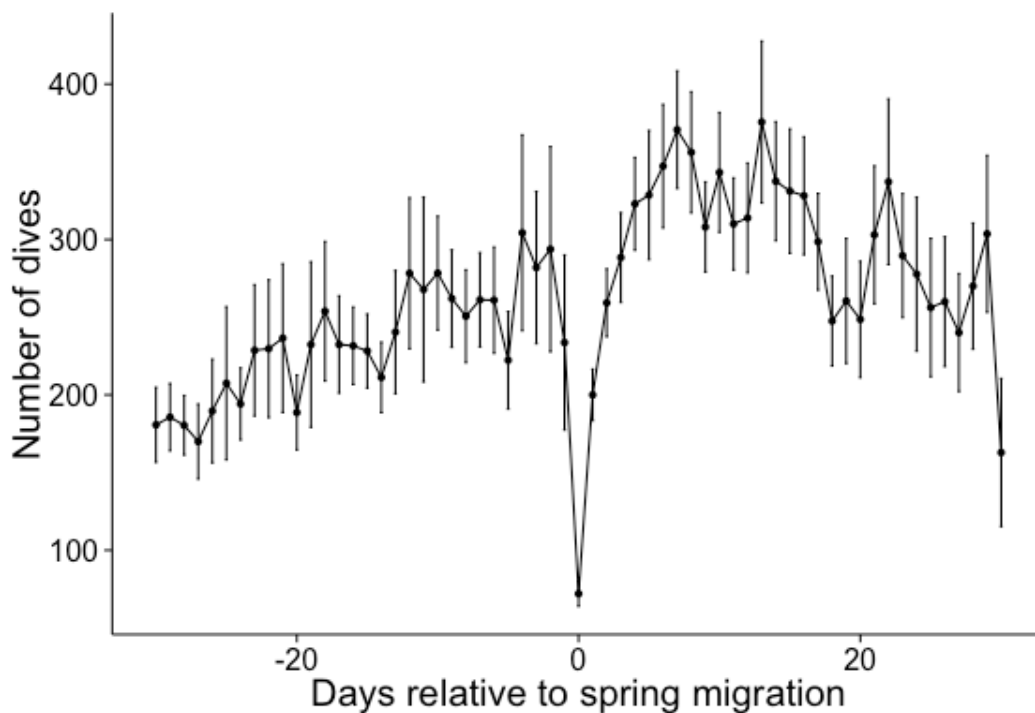

Figure 3: Mean ± SE daily diving frequency in the 30 days before departing on spring migration and the 30 days after arrival with time of migration for 17 females common eiders breeding in Kongsfjorden, Svalbard. The value 0 on the x axis represents the time of migration.

371.37 ± 37.59 dives day^{-1} after arrival on Svalbard (fig. 3). This increase before departure indicate that female eiders start gaining energy stores prior to migration, perhaps as fuel for the journey and/or as extra reserves for reproduction, but that they forage most intensely on the breeding ground. Even though daily diving frequency reaches a plateau after spring migration, diving started to decrease with days after arrival on the breeding ground (fig. 3). However, there was a significant interaction effect with year. In 2013 (n=5), daily average diving frequency did not differ before and after spring migration, and was significantly higher in both periods compared to in 2014 (n=9) and 2015 (n=6) (fig. 4; table 2). Females migrating in 2014 and 2015 had a significant increase in daily diving frequency after arrival on Svalbard (fig. 4; table 2). Three of the recorded females that migrated in 2013 were also tracked in 2014. Thus, the year effect suggests that environmental factors influence foraging behaviour. The increased diving intensity on the breeding ground suggest that female eiders prefer gaining weight after migration. Daily average dive depth did not differ significantly before and after spring migration (fig. 4; table 3). This indicates that female eiders forage on prey that are found at similar depths on the wintering and breeding grounds.

Table 1: Daily averages and maximum recorded daily diving frequency, dive depth and duration in the periods 30 days before departure from the wintering ground and 30 days after arrival on the breeding ground in 18 female common eiders breeding in Kongsfjorden, Svalbard.

	Diving frequency		Dive depth (m)		Dive duration (s)	
	Mean ± SE	Maximum	Mean ± SE	Maximum	Mean ± SE	Maximum
Before spring migration	233.89 ± 7.26	1377	5.84 ± 0.17	22.24	33.13 ± 0.58	76.75
After spring migration	297.96 ± 7.14	919	4.99 ± 0.15	23.50	29.62 ± 0.47	79.06

Table 2: Effects of spring migration and year on daily diving frequency for N=17 Common Eiders breeding in Svalbard. Estimates are based on the model with the lowest AICc score (table 1 in Appendix 2). Linear mixed effects model with individual and location as random factors. The factors "before spring migration" and "after spring migration" are the mean number of dives per day for the 30 days before departure from Iceland and Norway, and the 30 days after arrival at Svalbard, using the time of migration as index.

Predictors	Estimates ± SE	t-value	p-value
Intercept (After spring migration in 2013)	362.79 ± 30.01	12.09	<0.01
Before spring migration	-3.79 ± 18.10	-0.21	0.83
Year (2014)	-81.81 ± 19.64	-4.17	<0.01
Year (2015)	-88.22 ± 47.49	-1.86	0.08
Before spring migration x Year (2014)	-81.70 ± 22.62	-3.61	<0.01
Before spring migration x Year (2015)	-80.93 ± 24.35	-3.32	<0.01

Table 3: Effects of spring migration and year on daily dive depth for n=17 common eiders breeding in Svalbard. Estimates are based on the model with the lowest AICc score (table 2 in Appendix 2). Linear mixed effects model with individual and location as random factors. The factors "before spring migration" and "after spring migration" are the mean number of dives per day for the 30 days before departure from Iceland and Norway, and the 30 days after arrival at Svalbard, using the time of migration as index.

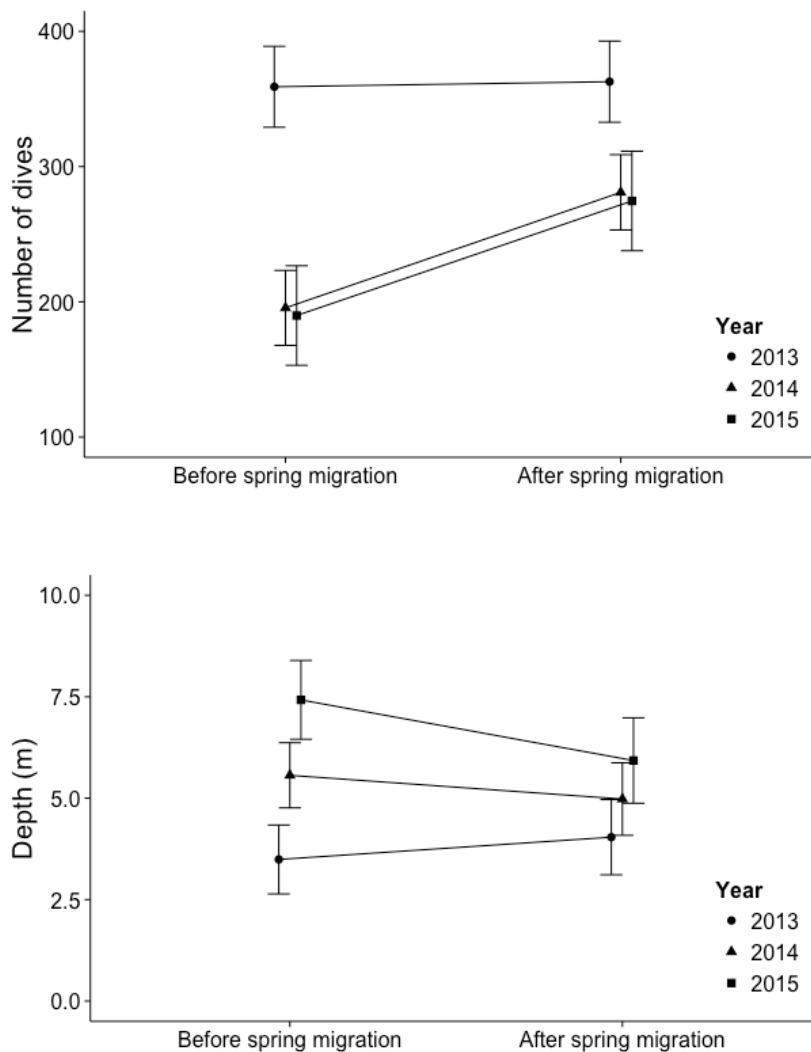| Predictors	Estimates ± SE	t-value	p-value
Intercept (After spring migration in 2013)	4.04 ± 0.93	4.36	0.05
Before spring migration	-0.55 ± 0.90	-0.61	0.68
Year (2014)	0.94 ± 0.43	2.18	0.03
Year (2015)	1.89 ± 1.09	1.73	0.10
Before spring migration x Year (2014)	1.13 ± 0.50	2.27	0.02
Before spring migration x Year (2015)	2.04 ± 0.54	3.77	<0.01

Figure 4: Difference in daily diving frequency (above) and dive depth (below) in the 30 days before and after spring migration for 17 female common eiders breeding in Kongsfjorden, Svalbard in 2013-2015 (n=5, n=9 and n=6 in 2013, 2014 and 2015, respectively). Mean ± SE are obtained from the parameter estimates from tables 2 and 3 for diving frequency and dive depth, respectively.

The effect of day length on diving behaviour

To determine if day length affects diving behaviour, I summarised diving activity at different periods when the eiders were on the wintering area. Both hourly average diving frequency and dive depth shows idiosyncratic variation throughout the non-breeding season (fig. 5). This suggests that female eiders forage in relatively similar feeding habitats the entire time they are on the wintering ground. However, it may look like increasing diving frequency during daylight hours is necessary in order to maintain the hourly average diving frequency on the wintering area (fig. 5 and 6). Figure 6 shows that diving frequency in daylight and especially twilight hours is higher when day lengths are shorter in winter (see table 3 and 4 in Appendix 2 for model selection and parameter estimates from the best model). This implies that female eiders compensate for reduced day length by increasing foraging effort during the daylight and twilight. Nocturnal foraging also occurred in this period, implying that when the time for foraging under optimal light conditions is limited, the eiders need to extend their feeding period into the night. There was no continuous difference in hourly average dive depth in daylight, twilight and darkness (fig. 6; see table 5 and 6 in Appendix 2 for model selection and parameter estimates from the best model), showing that female eiders do not forage at different depths as a response to changing light conditions on the wintering area.
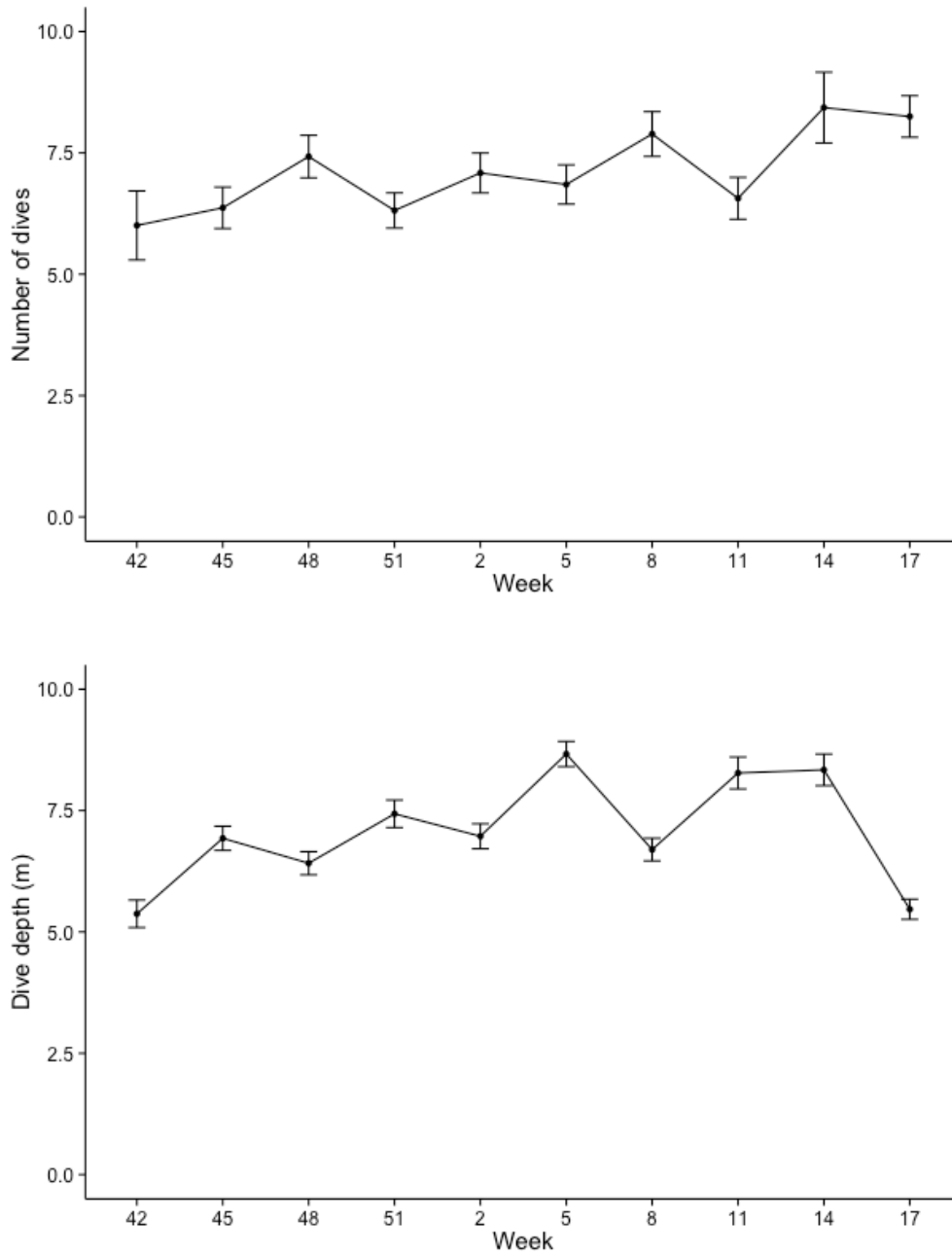
Figure 5: Mean ± SE number of dives (above) and dive depth (below) per hour at different periods in the non-breeding season in 20 female common eiders wintering in Iceland and northern Norway.
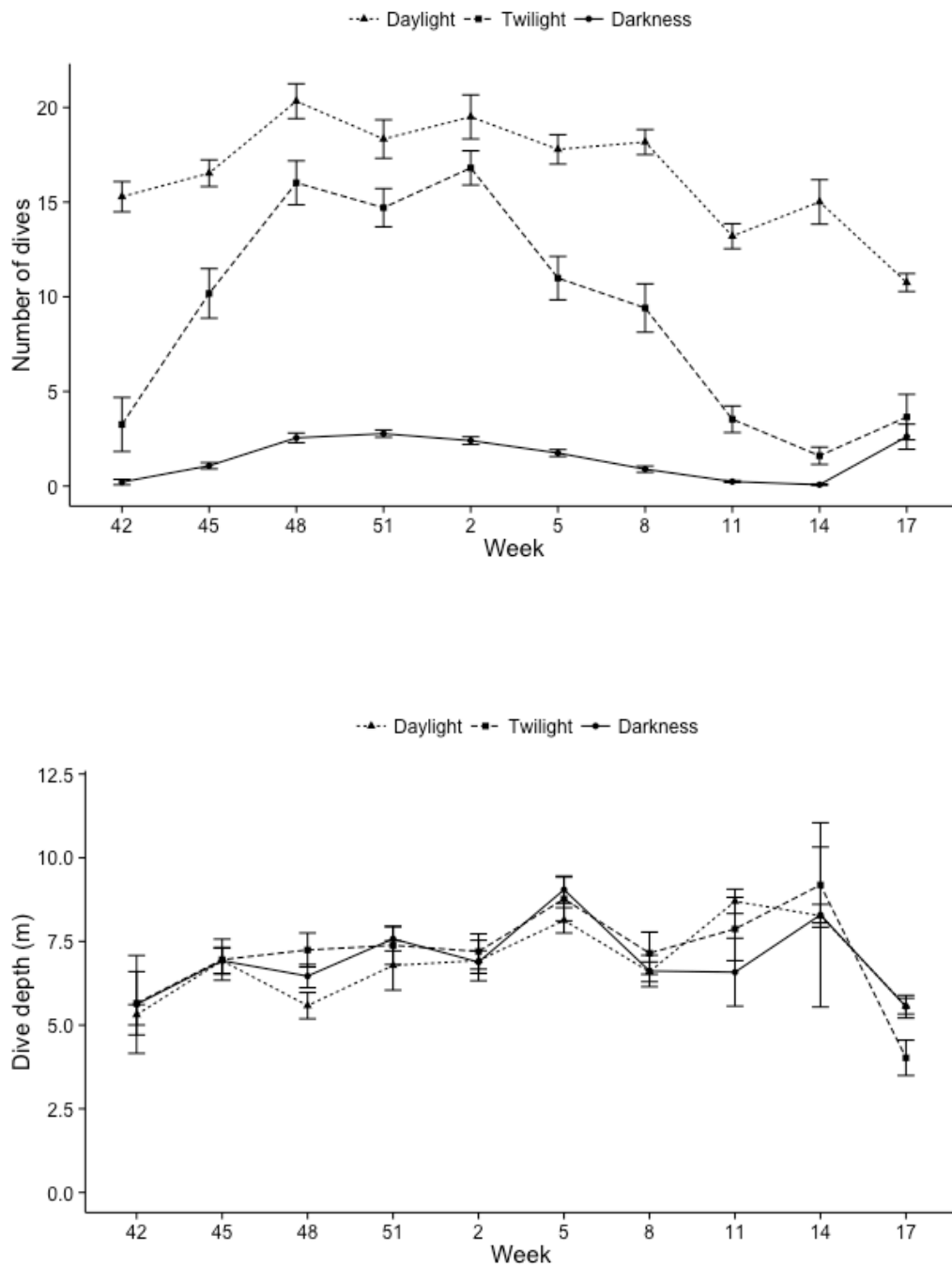
Figure 6: Mean ± SE number of dives (above) and dive depth (below) per hour in three different light intensities (daylight, twilight and darkness) at different periods in the non-breeding season in 20 female common eiders wintering in Iceland and northern Norway.

DISCUSSION

This is the first study to track the diving movements of common eiders from Svalbard and Norway, and to my knowledge, the first large-scale monitoring on diving movements of any seabird at such a detailed level. Knowledge on how seabirds cope with constraints on foraging, such as migration and time available for feeding, is important for improving our understanding on different foraging strategies, and for conservation and management purposes.

Diving strategy around spring migration
The results show that, on average, female eiders forage most frequently after arriving on the breeding ground than before departing on spring migration (table 1; fig. 3). However, there was a difference among years, where the eiders migrating in 2013 did not differ in diving frequency before vs after spring migration. Since three eiders were recorded in both 2013 and 2014, the year effect most likely reflect that foraging behaviour is influenced by environmental and climatic factors. Perhaps feeding conditions on the wintering ground were better in spring 2013 compared to the other years. One might expect that the timing of spring migration would influence foraging decisions, but the large individual variation in both timing of migration and egg-laying (own data and pers. observation) makes it difficult to determine how much time they need to prepare for reproduction, and thus what resources they rely upon. The higher daily average diving frequency on Svalbard implies that female eiders prefer gaining weight after spring migration. This was also seen in common eiders in the Gulf of St. Lawrence, which were found to accumulate most of their body reserves on the breeding ground, and increasing in body mass only slightly prior to spring migration (Guillemette et al., 1992, Guillemette, 2001). It may also indicate that the breeding ground on Svalbard is an important feeding site for accumulating sufficient endogenous reserves for reproduction for the eiders breeding here. Still, daily average diving frequency increased towards the timing of migration (fig. 3). If this increase is related to gaining energy for migration or for breeding, or a combination of the two, requires additional information on energy acquisition and allocation. Thus, whether Svalbard eiders gain their breeding condition on the wintering area or the breeding area, cannot be determined from these results alone. There can be large differences in the reliance on local versus distant capital for reproduction even among different populations of the same species (Korschgen, 1977, Parker and Holm, 1990, Christensen, 2000, Guillemette, 2001, Hario and Öst, 2002). For example, barnacle geese breeding on Svalbard employ a mixed strategy of using capital gained at wintering area, along the migration route and on the breeding area for

reproduction (Hahn et al 2011). Relying on distant capital can increase the potential for early onset of egg laying on the breeding ground independent of the local feeding conditions. Since eiders are benthic feeders, they rely on ice free shallow waters. Global climate change has led to warmer sea surface temperatures and reduced the extent of sea ice in the Arctic (Rayner et al., 2003, Comiso et al., 2008, Moe et al., 2009, Rodrigues, 2009). In addition, warm ocean currents have enabled blue mussels, the preferred prey of common eiders, to reappear in Svalbard after a 1000 year absence (Berge et al., 2005). The lower extent of sea ice in the Arctic make benthic prey accessible earlier in the spring, leading to more secure foraging possibilities for benthic feeders such as the common eider. Some Svalbard eiders also spend some time foraging along the coast of Svalbard where sea ice disappears earlier, before retreating to breeding sites in the fjords.

Gaining extra weight before migration can incur additional time, energy and predation costs (Witter and Cuthill, 1993), and the benefits of carrying extra weight declines with travelling distance (Kvist et al., 2001). Common eiders have one of the highest wing loadings among birds (Guillemette, 1994), making flight a costly activity. The Kongsfjorden population fly long distances over deep seas unsuitable for foraging. The only potential stopover sites *en route* are Jan Mayen for the Icelandic birds, and Bjørnøya for the Norwegian birds, but recent findings revealed that most eiders in the Kongsfjorden population migrate directly to the breeding ground (Hanssen et al., 2016). The long migration distance, along with the foraging potential on Svalbard, might explain why they dive more frequently on Svalbard rather than on the wintering area. However, after reaching a plateau the daily diving frequency decreased with days after arrival on Svalbard. The reason for this decline is uncertain.

Further, there was no significant difference in daily average dive depth before departure from the wintering ground compared to after arrival on the breeding ground (fig. 4). This suggests that female eiders prefer diving at a certain depth, which has been observed in several eider populations (Guillemette et al., 1993, Bustnes and Lønne, 1997). It may also be related to similarities in the feeding habitats and prey selection at the wintering and breeding area. Common eiders prefer feeding on blue mussels (*Mytilus edulis*) and different sea urchins (Goudie and Ankney, 1986, Bustnes and Erikstad, 1990, Guillemette et al., 1992), which can be found in shallow waters <10 m, and this corresponds well to the average dive depth seen in these eiders.

Diving behaviour on the wintering area

The data show that female eiders essentially dive during daylight, although some diving at night were recorder during the darkest periods in winter (fig. 6). Consequently, female eiders wintering at high latitudes compensate for reduced feeding time due to shorter days, by foraging more often during daylight and twilight hours. Especially diving in twilight increased when day lengths shortened, indicating that they fully exploit the opportunity of foraging before it gets dark. Occurrence of diving at night suggests time available for feeding in winter is too short, and it may be necessary for the females to forage outside of optimal conditions to maintain a positive energy budget. Switching foraging strategies in response to environmental changes has been reported in other species as well. For instance, a population of dark-bellied brent geese (*Branta bernicla bernicla*) fed more at night when temperature during the day increased (Lane and Hassall, 1996). Feeding in lower light intensities and nocturnal feeding in sea ducks has been suggested as a coping mechanism for short days (Systad et al., 2000, Systad and Bustnes, 2001) and high levels of disturbance from predators and humans during the day (Merkel and Mosbech, 2008).

It appears that female eiders need to uphold a certain level of foraging effort in order to maintain the average diving frequency throughout the non-breeding season. Even though diving frequency increased in daylight and twilight hours in winter, the average hourly diving frequency throughout the non-breeding season remained relatively stable (fig. 5). One might expect that eiders would increase foraging effort in winter to balance the demands of thermoregulation (Gabrielsen et al., 1991). However, Guillemette and Butler (2012) found that neither the daily energy expenditure nor resting heart rate varied negatively with water temperature in common eiders. Eiders may hold a strategy of minimizing energy expenditure to reduce the energy gain required for energy balance. The results suggest that female eiders are able to adjust to seasonal changes in day length by increasing diving frequency in daylight and twilight, and even diving in darkness in the darkest period of the year.

There was no predictable variation in hourly dive depth in the non-breeding season (fig. 5), and depth did not differ at different light intensities (fig. 6). The relatively stable diving pattern in both frequency and depth, might indicate that female eiders forage in the same type of feeding habitat the entire period they are on the wintering ground. Prey species differ in density, size and distribution. Accordingly, diving frequency, duration and depth will vary with prey selection and feeding habitats. The composition of prey species can vary considerably even

between feeding sites located short distances apart (Bustnes and Erikstad, 1988, Merkel et al., 2007). Common eiders in the Gulf of St. Lawrence were found to change diving tactics in relation to feeding habitat (Guillemette et al., 1996). Hence, changes in depth or frequency would suggest that eiders switch to different types of prey, but this was not apparent from my findings.

The loggers used in this study recorded only dive depths below 1 m. However, eiders also use dabbling and upending as foraging techniques, so it is likely that not all foraging effort is reflected in this data. Systad and Bustnes (2001) found that steller's eiders (*Polysticta stelleri*) fed more at low tide and by using non-diving techniques such as up-ending and surface feeding in the coldest periods of the winter. This was suggested as a strategy to increase feeding effort while simultaneously reducing feeding costs. Thus, if common eiders inhabit a similar foraging strategy as that seen in steller's eiders, the foraging movements may look different than what is presented here.

In conclusion, the findings in this study reveal that female common eiders prefer gaining body mass after arriving on the breeding ground in spring, and that they compensate for reduced day lengths in winter by increasing diving frequency during daylight and twilight. Information from such tracking devices inhabit great potential for further studies on diving and foraging in seabirds. It would be interesting to combine data on diving activity with information on ambient temperature, prey selection and individual fitness measures in order to achieve a greater understanding of the diversity of factors that influence foraging decisions in seabirds.

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APPENDIX 1

Individual average (±SE) and maximum recorded number of dives, dive duration and dive depth per day in 20 female common eiders (*Somateria mollissima*) breeding in Kongsfjorden, Svalbard and Grindøya, Norway tracked in different periods from 2012 – 2015.

ID number	Wintering area	Diving frequency			Dive duration (s)			Dive depth (m)		
		Mean ± SE	Variation	Range	Mean ± SE	Variation	Maximum	Mean ± SE	Variation	Maximum
119	Iceland	172.36 ± 3.99	4099.87	0 to 341	32.65 ± 1.12	324.99	76.75	6.21 ± 0.31	24.17	19.79
127	Iceland	253.11 ± 5.02	7697.63	0 to 492	28.86 ± 0.30	26.46	45.65	4.37 ± 0.08	1.87	9.50
131	Iceland	202.20 ± 12.73	52668.22	10 to 1377	38.32 ± 0.50	82.71	61.67	5.53 ± 0.13	5.42	20.21
134	Grindøya	112.46 ± 3.60	2110.93	12 to 315	49.15 ± 1.01	166.61	69.88	10.48 ± 0.28	13.06	18.84
140	Iceland	123.84 ± 3.71	3546.15	11 to 389	38.05 ± 0.70	125.82	66.97	7.43 ± 0.25	16.73	20.73
142	Iceland	175.12 ± 5.38	10084.44	1 to 1237	34.56 ± 0.54	102.10	67.20	5.82 ± 0.17	10.47	20.93
146	Grindøya	90.61 ± 5.14	6967.50	1 to 476	28.07 ± 0.53	75.49	47.88	5.68 ± 0.14	5.29	10.90
227	Iceland	198.47 ± 5.83	6902.81	19 to 388	29.58 ± 0.51	53.24	60.07	4.80 ± 0.17	5.83	15.36
230	Iceland	223.10 ± 6.04	7765.01	47 to 444	24.44 ± 0.58	72.87	60.32	2.99 ± 0.11	2.66	10.26
234	Iceland	192.83 ± 5.82	3114.80	32 to 400	40.12 ± 1.43	188.26	72.18	6.50 ± 0.40	14.66	17.05
241	Norway	158.45 ± 5.78	5513.88	0 to 352	29.16 ± 0.87	122.43	62.31	4.88 ± 0.21	7.39	16.51
244	Iceland	232.90 ± 5.20	6883.77	19 to 488	36.62 ± 0.91	212.91	67.45	6.93 ± 0.26	16.78	17.92
246	Iceland	177.01 ± 6.08	7319.35	1 to 500	23.70 ± 0.97	185.65	86.10	4.37 ± 0.41	33.09	30.07
248	Iceland	93.76 ± 4.02	2534.12	26 to 392	51.39 ± 0.83	107.01	69.58	13.25 ± 0.42	28.12	21.33
322	Norway	200.66 ± 6.31	4731.34	91 to 526	43.01 ± 0.96	109.66	59.63	8.21 ± 0.25	7.31	12.21
323	Iceland	110.02 ± 4.52	3700.19	4 to 381	57.39 ± 1.02	187.99	86.07	14.13 ± 0.40	29.44	25.39
324	Iceland	211.65 ± 6.92	7665.13	17 to 528	29.34 ± 0.80	103.24	63.39	5.42 ± 0.30	14.79	22.24
326	Iceland	87.62 ± 2.01	730.59	23 to 209	52.00 ± 0.40	28.64	61.47	11.67 ± 0.15	4.15	15.04
341	Iceland	148.44 ± 8.45	13343.41	0 to 583	18.08 ± 0.92	153.17	55.08	2.71 ± 0.18	6.08	11.95
343	Iceland	161.97 ± 4.48	3640.00	1 to 356	47.60 ± 1.00	181.25	62.61	9.99 ± 0.27	13.63	15.27

APPENDIX 2

Table 1: Model selection for the effects of spring migration and year on daily average diving frequency in 18 female common eiders breeding in Kongsfjorden, Svalbard. Before spring migration represents the period 30 days before departure from the wintering ground, and after spring migration represents the period 30 days after arrival on the breeding ground. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, ΔAICc is the difference in AICc compared to the model with lowest AICc, and wAICc is the AICc weights.

Predictors	K	AICc	ΔAICc	wAICc
Spring migration × Year	9	15216.97	0	1
Spring migration + Year	7	15228.02	11.05	0
Spring migration	5	15280.11	63.14	0
Intercept only	4	81349.64	66132.67	0
Year	6	81234.9	66017.93	0

Table 2: Model selection for the effects of spring migration and year on daily average dive depth (m) in 18 female common eiders breeding in Kongsfjorden, Svalbard. Before spring migration represents the period 30 days before departure from the wintering ground, and after spring migration represents the period 30 days after arrival on the breeding ground. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, ΔAICc is the difference in AICc compared to the model with lowest AICc, and wAICc is the AICc weights.

Predictors	K	AICc	ΔAICc	AICcWt
Spring migration x Year	9	6225.63	0	0.99
Spring migration + Year	7	6234.48	8.86	0.01
Spring migration	5	6251.92	26.29	0
Intercept only	4	35155.03	28929.4	0
Year	6	35064.7	28839.08	0

Table 3: Model selection for the effects of period of the year and light intensity level (daylight, twilight and darkness) on hourly average diving frequency of 20 female common eiders wintering in Iceland (n=16) and Norway (n=4). The factor period represents 10 weekly periods in the non-breeding season. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, ΔAICc is the difference in AICc compared to the model with lowest AICc, and wAICc is the AICc weights.

Predictors	K	AICc	ΔAICc	AICcWt
Period x Light intensity	32	28531.12	0	1
Period + Light intensity	14	28734.24	203.12	0
Light intensity	5	29019.31	488.19	0
Intercept only	3	31438.33	2907.21	0
Period	12	31427.3	2896.17	0

Table 4: Effects of period of the year and light intensity level (daylight, twilight and darkness) on hourly average diving frequency in 20 female common eiders wintering in Iceland and Norway.

Predictors	Estimates ± SE	t-value	p-value
Intercept (Week 11 in darkness)	0.25 ± 0.75	0.34	0.74
Week 14	-0.05 ± 0.74	-0.06	0.95
Week 17	3.01 ± 0.99	3.04	<0.01
Week 2	2.17 ± 0.61	3.56	<0.01
Week 42	0.95 ± 0.98	0.96	0.34
Week 45	1.05 ± 0.65	1.62	0.10
Week 48	2.31 ± 0.61	3.78	<0.01
Week 5	1.50 ± 0.62	2.44	0.01
Week 51	2.54 ± 0.61	4.19	<0.01
Week 8	0.56 ± 0.64	0.87	0.38
Daylight	12.93 ± 0.68	19.10	<0.01
Twilight	3.24 ± 1.16	2.80	<0.01
Week 14 x Daylight	2.05 ± 0.98	2.10	0.04
Week 17 x Daylight	-4.74 ± 1.18	-4.00	<0.01
Week 2 x Daylight	3.97 ± 1.15	3.45	<0.01
Week 42 x Daylight	2.03 ± 1.47	1.38	0.17
Week 45 x Daylight	2.44 ± 1.02	2.39	0.02
Week 48 x Daylight	4.60 ± 1.08	4.27	<0.01
Week 5 x Daylight	3.01 ± 0.98	3.06	<0.01
Week 51 x Daylight	2.42 ± 1.25	1.94	0.05
Week 8 x Daylight	4.37 ± 0.95	4.58	<0.01
Week 14 x Twilight	-1.67 ± 1.58	-1.05	0.29
Week 17 x Twilight	-1.94 ± 1.77	-1.10	0.27
Week 2 x Twilight	11.24 ± 1.42	7.92	<0.01
Week 42 x Twilight	0.20 ± 2.31	0.08	0.93
Week 45 x Twilight	5.84 ± 1.58	3.70	<0.01
Week 48 x Twilight	10.35 ± 1.46	7.11	<0.01
Week 5 x Twilight	6.04 ± 1.49	4.06	<0.01
Week 51 x Twilight	8.67 ± 1.43	6.05	<0.01
Week 8 x Twilight	5.34 ± 1.53	3.48	<0.01

Table 5: Model selection for the effects of period of the year and light intensity level (daylight, twilight and darkness) on hourly average dive depth (m) of 20 female common eiders wintering in Iceland (n=16) and Norway (n=4). The factor period represents 10 weekly periods in the non-breeding season. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, ΔAICc is the difference in AICc compared to the model with lowest AICc, and wAICc is the AICc weights.

Predictors	K	AICc	ΔAICc	AICcWt
Period	12	14989.41	0	0.57
Period + Light intensity	14	14990.57	1.16	0.32
Period x Light intensity	32	14992.77	3.36	0.11
Intercept only	3	15179.94	190.53	0
Light intensity	5	15181.22	191.81	0

Table 6: Effects of period of the year on hourly average dive depth (m) in 20 female common eiders wintering in Iceland and Norway. The factor period represents 10 weekly periods in the non-breeding season.

Predictors	Estimate ± SE	t-value	p-value
Intercept (Week 11)	8.42 ± 0.72	11.65	<0.01
Week 14	0.03 ± 0.31	0.08	0.93
Week 17	-3.05 ± 0.31	-9.74	<0.01
Week 2	-1.20 ± 0.29	-4.19	<0.01
Week 42	-3.69 ± 0.53	-6.94	<0.01
Week 45	-1.34 ± 0.31	-4.36	<0.01
Week 48	-1.81 ± 0.29	-6.26	<0.01
Week 5	0.15 ± 0.29	0.54	0.59
Week 51	-0.94 ± 0.28	-3.33	<0.01
Week 8	-1.52 ± 0.30	-5.13	<0.01