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Repeatability and Flexibility in the Migration Strategies of an Arctic Seabird

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Cover photo: Common eider (*Somateria mollissima*), by Tomas Taylor

Acknowledgements

Abstract

The strategy of migration has evolved independently in many animal groups, but it is most widely and well developed in birds. Migrating species are expected to be severely affected by human induces climate change, and the effects of climate change is already seen in the phenology of migrating birds, with trends for changes in spring arrival and breeding dates. The effects of climate change are particularly pronounced in the Arctic. Seabirds represent an essential component of the Arctic marine ecosystem, and are amongst the most threatened organisms on Earth. It has been suggested that spatial and temporal flexibility is advantageous in a rapidly changing climate. Little is known about the individual flexibility of migration and wintering strategies of seabirds breeding in Svalbard. In this study light-level geolocators have been used track the migration of females of an Arctic population of common eiders *Somateria mollissima* breeding in Kongsfjorden, Svalbard over several years (2-6). I looked at the consistency in winter area and the repeatability in the timing of migration in this population, and the individual flexibility in winter area and timing of migration. I also investigated which factors affect the timing of migration. The eiders in this breeding population winter in two distinct areas, Iceland and northern Norway, and only one of the individuals tracked switched between the two wintering areas. This consistency in the winter area may affect the eiders adversely if the conditions in their winter area are changing for the worse. There was a wide range of timing of migration and a relatively high repeatability in the timing of both spring and fall migration. There was some degree of individual temporal flexibility in migration, but I found no effect of year in the timing of migration. For flexibility to be beneficial it should respond to specific cues to allow behavioral changes to track the best timing. It therefore remains unclear whether or not the flexibility I observed will help this population buffer possible changes in the climate. Repeatability can be interpreted as an upper estimate for heritability, so the high repeatability and the wide range of timing of migration may indicate that if there is selection for individuals arriving earlier to the breeding ground, the eiders could perhaps adapt to earlier springs through natural selection.

Sammendrag

Migrasjon som strategi eksisterer i mange dyregrupper, men er mest utbredt og utviklet i fugler. Det er forventet at migrerende arter vil bli sterkt påvirket av menneskeskapte klimaendringer, og effekten av klimaendringer kan allerede bli observert i den endrede fenologien til migrerende fugler, der ankomst på hekkeområdet om våren og hekking har begynt å skje tidligere. Effekten av klimaendringer er spesielt tydelig i Arktis. Sjøfugl er en essensiell del av det marine økosystemet i Arktis, og er spesielt truet. Det har blitt foreslått at spatial og temporal fleksibilitet er fordelaktig i et klima i rask endring. Lite er visst om individuell fleksibilitet i migrasjons- og overvintringsstrategier for sjøfugl som hekker på Svalbard. I denne studien har "light-level geolocators" blitt brukt til å følge migrasjonen til ærfuglhunner *Somateria mollissima* fra en arktisk populasjon som hekker i Kongsfjorden på Svalbard over flere år (2-6). Jeg fant ut hvor konsekvente ærfuglhunnene var i bruken av vinterområde, om det var repeterbarhet i timing i vår- og høstmigrasjonen og om det er individuell fleksibilitet i tid for migrasjon og i overvintringsområde. Jeg undersøkte også hvilke faktorer som påvirker tidspunkt for migrasjon, både om våren og høsten. Ærfuglhunnene i denne hekkepopulasjonen overvintret i to distinkte områder, Island og Nord-Norge. Bare ett individ av de som ble fulgt byttet mellom disse to områdene mellom år. Siden ærfuglen antageligvis er nokså konsekvent i bruken av overvintringsområde, kan dette påvirke populasjonen negativt, om forholdene på overvintringsområdene endrer seg til det verre. Jeg fant en bred spredning i når de forskjellige individene migrerte, både om våren og høsten, og repeterbarheten for timing av migrasjon var relativt høy for begge migrasjonene. Det var en viss grad av individuell fleksibilitet i migrasjonstiming, men jeg fant ingen forskjell i timingen fra år til år. For at fleksibilitet skal være lønnsomt burde individet kunne reagere på konkrete signaler, sånn at individet, med endringer i sin adferd, kan benytte seg av den beste timingen for migrasjon. Det er derfor fortsatt uklart hvorvidt den observerte fleksibiliteten faktisk kan hjelpe denne populasjonen med å tilpasse seg mulige endringer i klimaet. Repeterbarhet kan også bli tolket som en øvre grense for arvbarhet, så den relativt høye repeterbarheten, sammen med det brede spekteret av migrasjonstiming, kan kanskje gjøre at hvis det er seleksjon for individer som ankommer tidligere om våren, vil denne populasjonen kanskje kunne tilpasse seg en tidligere vår i Arktis.

Content

Introduction

Migration is an adaptive response to seasonal or geographic variation in resources (Alerstam and Lindström, 1990, Dawson, 2008). The strategy of migration has evolved independently in many animal groups, including fish, mammals, reptiles, insects and marine invertebrates (Alerstam et al., 2003), but it is most widely and well developed in birds (Newton, 2008). The most common form of migration for birds is movement between wintering and breeding areas in spring and fall (Newton, 2008). In some bird species only part of the populations migrate, while the other populations are sedentary (Herrera, 1978, Lack, 1968, Newton and Dale, 1996) and even within populations individuals may differ both in route and timing of their migration (Phillips et al., 2007, Egevang et al., 2010, Magnusdottir et al., 2012). In seasonal environments, where food availability varies, there is a limited time period where reproduction is possible, so the timing of breeding is a key factor for reproductive success in birds (Dunn, 2004, Reed et al., 2009), and the timing of migration, especially the arrival to the breeding area in spring is crucial (McNamara et al., 1998). Individuals that arrive too early in the spring can be penalized for it, because the food in the breeding area can be poor, and individuals that arrive late may either arrive too late for successful breeding, or if they mange to breed, both they and their offspring may struggle to attain the state they need to be in to migrate to their winter area (McNamara et al., 1998, Pulido, 2007).

Migrating species are expected to be severely affected by human induced climate change (Both et al., 2006, Sanderson et al., 2006, Gordo, 2007), and effects of climate change are already seen in the phenology of migrating birds, with long-term trends for changes in spring arrival and breeding dates (Parmesan and Yohe, 2003, Root et al., 2003). The effects of climate change are visible worldwide, and they are particularly pronounced in the Arctic, which has a two-fold higher increase in temperature compared to the global increase (Kattsov et al., 2005). The onset of spring in the Arctic is already occurring earlier, with the timing of snow melt becoming 15 days earlier in Greenland over the last decade (Høye et al., 2007), and the sea ice extent in the Arctic ocean has decreased linearly by 3 % to 9 % per decade during the last three decades (Serreze et al., 2007). The combined effects of climate change and anthropogenic activities cause rapid changes to the marine ecosystems in the North Atlantic and Arctic oceans, with important impacts on marine biodiversity (Gilg et al., 2012, Beaugrand et al., 2010). By exerting predation pressure on lower trophic levels, seabirds represent an essential component of marine ecosystems, including in the North Atlantic and

the Arctic. Yet, seabirds are among the most threatened organisms on Earth, with 40 % of all seabird species affected by climate change (Croxall et al., 2012, Gremillet and Boulinier, 2009). With such rapid ongoing changes, seabird populations will likely have to adapt to the new climatic conditions on both a spatial and temporal scale (Fredriksen et al., 2012, Dias et al., 2011). Such adaptations can be achieved either with adaptive evolution, i.e. genetic changes in the population following selection, with plasticity, or a combination of the two (Pulido, 2007).

Species vary in their capacity to respond and adapt to a rapidly changing environment (Wilcove and Wikelski, 2008, Bradley et al., 1999, Sutherland, 1998, Hamer, 2010). How individual species will handle global climate change, and the role flexibility will play in it, is still debated. However, it has been suggested that behavioral plasticity and flexibility is advantageous in a changing climate (Bradley et al., 1999, Dias et al., 2011). Consistent strategies in terms of a fixed wintering area and fixed timing of migration will likely render species more vulnerable to climate changes, and species that have variability and plasticity in their migratory traits will most likely have an advantage in a rapidly changing environment (Pulido, 2007). For long-lived species adaptation is a slow process that may not be able keep up with rapid changes, so behavioral plasticity may be the only way to rapidly respond to these changes (Tufto, 2015). Little information exists on individual flexibility or consistency in migration and wintering strategies of seabirds breeding in Svalbard.

In this study light-level geolocators, which represent a revolutionary technological development in seabird tracking, have been deployed on females of an arctic population of common eiders (*Somateria mollissima*) breeding in Kongsfjorden, Svalbard. Hanssen et al. (2016) presented migration data for the first year tracked for female eiders. This thesis extends on the data from Hanssen et al (2016), by including tracking data from a longer time period (2009-2015). Most important, my thesis includes data on females that have been tracked for more than one year (2-6 years).

The aim of my thesis to quantify the degree of flexibility of a migrating bird breeding in the high arctic, and test which factors affect the timing of migration. I will investigate the consistency in winter area and the repeatability in timing for this population. I will look at the individual spatial and temporal flexibility, and at a possible correlation between the two, and test whether there is a difference in the degree of flexibility in the spring and fall migrations.

Methods

Study species

Common eiders are large, long-lived, iteroparous sea ducks with a circumpolar distribution that extends from the Netherlands in the south to Svalbard and Franz Josef Land in the high Arctic. Some eider populations are sedentary, while others, including the populations in the high Arctic migrate south in the winter (Del Hoyo and Sargatal, 1992). The females are strongly philopatric, always returning to breed in or close to their birth colony (Swennen, 1990, Tiedemann et al., 1999). Eiders are benthic feeders; their diet consists mainly of mussels and other invertebrates. They typically dive to depths of 1-6 meters, and therefore winter in coastal areas (Guillemette et al., 1993, Bustnes and Lønne, 1997). The eider population is the largest population of waterfowl breeding in Svalbard (Gabrielsen et al., 1991). The eider population in Svalbard consists of between 15,000 and 30, 000 pairs, with about 3000 of them breeding in Kongsfjorden (Hanssen et al., 2013). To avoid terrestrial egg predators, eiders in Svalbard mainly breed on islands and islets along the coast (Mehlum, 1991, Bustnes and Lønne, 1997, Gabrielsen et al., 1991).

Eiders are capital breeders that rely extensively on body reserves during incubation. Indeed, female eiders do not eat during the average 25 days of incubation, and can lose up to 40% of their mass (Gabrielsen et al., 1991, Parker and Holm, 1990). Consequently, female eiders need to build up reserves before breeding. They mainly gain this mass after arrival to the breeding area (Sénéchal et al., 2011, Kilen, unpublished master's thesis). Females in better body condition during incubation show higher nest attendance and are less vulnerable to nest predation (Hanssen et al., 2002). The eiders that breed in Kongsfjorden migrate to northern Norway and Iceland. They usually migrate directly, using the shortest routes to the wintering areas. They spend on average 4 days on the fall migration, and 3 days on the spring migration (Hanssen et al., 2016).

Field procedures

The fieldwork took place in Kongsfjorden in Svalbard (79°N, 12°E) during six consecutive breeding seasons (2009-2015), and I took part in the fieldwork in 2014 and 2015. We used a long fishing rod with a nylon noose attached to the end to capture the female eiders on their nests. The eiders were equipped with geolocators (Mk9 or Mk15, weight 2.5g; British Antarctic Survey, Cambridge, UK, Mk3006, weight 2.5g: Biotrack, Cambridge, UK or c250, weight 2.5g Migrate Technology). The geolocators were mounted on a plastic ring on the

birds' tarsus, using cable ties and cyanoacrylate glue (Loctite super glue, Henkel Corporation, Rocky Hill, USA). Altogether the logger and the ring weighed about 5 grams, that is, less than 0.3% of average bird weight. We also weighed and measured the eiders and followed the individual nests in order to obtain data on clutch size, egg size and hatching success. During the six years' study period, geolocators were deployed on 124 female common eiders, and 63 of the birds were recaptured one or more times. Data were successfully collected for 60 female eiders.

Light-level Geolocators

Geolocators are archival light-level sensors. They measure light intensity every minute and record the maximum value every 5 or 10 minutes allowing the estimation of the time of sunrise and sunset. These data can be translated into latitudinal and longitudinal position. Latitude is estimated from the length of the day or night, and longitude from the timing of midday or midnight. For approximately 15 days on each side of the vernal and autumnal equinoxes only the longitude is reliable. Raw position estimates obtained from geolocators have an error of about 200 km (Phillips et al., 2004). From the geolocator data it is also possible to infer the periods of nest incubation (Conklin et al., 2010, Eichhorn et al., 2006). On Svalbard, where there is continuous daylight during the breeding season, the geolocators will register no light when the female is incubating the eggs and light when she is standing to turn the eggs or having a short recess off the nest to drink. I used this light pattern to determine date of egg-laying (Hanssen et al 2016).

Twilight events, calibration and calculation

To determine the timing of apparent sunrise or sunset, we manually investigated the daily light curves with the softwares BASTrack and Intiproc for geolocators from British Antarctic Survey/Biotrack and Migrate Technology, respectively. Threshold values of 9, 10 and 11 were used for Mk9/15, Mk3006 and c250, respectively. The threshold values in Bastrack are arbitrary units, while those in IntiProc are lux units. Since the loggers recorded maximum light value every 5 or 10 minutes, the dusks were advanced by 4 and 9 min, respectively (Fox, 2010, Fox, 2015). For further details, see Hanssen et al. (2016).

The Geolight package in R (Lisovski and Hahn, 2012, R Core Development Team 2014) was used for further processing and calculations. Twilight events were filtered out using the loessFilter function (k=1.5), and positions were calculated using the coord function. The sun elevation angle was determined individually for each geolocator, averaged at -3.2° (range -1.6° to -4.5°). Two methods were combined to determine the sun elevation angle for each

geolocator. In-habitat calibration was performed during a winter period. We calculated the average longitude for the period between January 5th and February 15th. This period was chosen since all the eiders were in their wintering areas and relatively stationary. Since the eiders are benthic feeders, they stay close to the coast, and this allowed us to obtain candidate coastal locations and their latitudes. For the candidate locations we used the getElevation function to calculate appropriate sun elevation angles. With north-south-oriented coastlines there is a large range of possible latitudes, so this is not possible. In these scenarios we produced plots of latitude as a function of date for each sun elevation angle from -1° to -6°. This allowed us to assess the fit of the sun elevation angle over the entire year, focusing specifically on how the latitudes matched before and after equinox periods.

The raw positions were smoothed using a procedure of double smoothing adapted from Phillips et al. (2004) and Fox (2015). This reduced the influence of any inaccurate positions and compensated for movements. Around the vernal and autumnal equinoxes, the locations were removed between February 20th and April 5th in spring and September 10th and October 18th in fall. In some individual cases additional locations were removed, when the latitudes were clearly not reliable. For further details, see Hanssen et al. (2016).

Consistency in winter area

To look at the consistency in winter area we calculated the winter centroids for all the birds that had been tracked for more than one year, using orthometric (great-circle) distances. The geolocators give two locations every day, apart from when the birds are in areas with continual sunlight or continual darkness, or in the equinox periods. We averaged the two positions per day, and the three day running mean of the daily averages was used to estimate the average positions for the period we selected (Gilg et al., 2013), which was January 5th to February 15th. In this period all the eiders were in their winter area.

Statistical analysis

In this study my aim is to quantify the degree of consistency in the migration strategies of this population of common eiders, both on a temporal and spatial scale, and test which factors affect the timing of migration. I will investigate the degree of individual flexibility and find out if there is a difference in the flexibility of the timing of the spring and fall migration, and see if there is a correlation between temporal and spatial flexibility.

Timing

To test which factors affected the timing of migration, I used linear mixed-effect models, with individual as a random factor. The Julian date of migration was used as the response variable in the models. Since there is often continual daylight in Svalbard when the birds arrive in the spring and continual darkness when they migrate south in the fall, the timing of these events could not be recorded. I therefore used the departure date from the wintering area for estimating spring migration timing, and arrival date in the winter area for the fall migration timing. For both the timing of spring and the fall migration, I tested the effect of the year and the winter area (Norway or Iceland). For the timing of fall migration, I also included the breeding success of the preceding breeding season as a predictor variable. For the years when a female were not recaptured, but were tracked with a geolocator, I estimated the incubating pattern from the geolocator's data. If the hen had incubated the eggs for the 25 days, I considered that the breeding was successful. I ran the models both with and without the individual switching between the two winter areas.

For the fall migration our sampling was unbalanced, so I were unable to include an interaction between year and breeding success. Furthermore, using generalized mixed effect models I found that the breeding success significantly varied across years. Therefore, breeding success and year were partly confounded, rendering the distinction between the two effects difficult.

I did the same procedure for the timing of first egg lay, where the timing of the spring migration was included as a fixed effect. Model selection was performed using Akaike's information criterion corrected for small sample size (Burnham and Anderson, 2002).

Repeatability

To quantify the degree of individual consistency in the wintering areas and timing of migration, I used repeatability or the intra-class correlation coefficient, *r*, as an index:

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2} \qquad (1)$$

where σ_α^2 is the among group variance, and σ_ε^2 is the within group variance. Repeatability is an index for quantifying the constancy of phenotypes (Lessells and Boag, 1987, Nakagawa and Schielzeth, 2010). It represents the proportion of the total phenotypic variation that exists between subjects or groups. The non-repeatable part of the variation is the sum of phenotypic flexibility and measurement error (Nakagawa and Schielzeth, 2010). Repeatability is measure of the consistency in a population. It doesn't tell us about the absolute consistency of the

individuals, because *r* combines the value for the individual and the population, so the variation is on two different scales. When there is a there is a number of viable alternative strategies in a population r will be larger, regardless of the consistency within individuals (Conklin et al., 2013).

The repeatability in the timing of migration was estimated using the variance components obtained from linear mixed-effect models (Nakagawa & Schielzeth, 2010). In these models I only included individuals tracked for more than one year in the analysis. Separate models were made for the spring and fall migrations and for birds migrating to Iceland and Norway. I used the rptR package in R (Nakagawa & Schielzeth, 2010) to calculate the confidence intervals for the repeatabilties.

Individual flexibility

While repeatability is measure of the consistency of the population, I also wanted to look at the flexibility within individuals.

Individual flexibility in winter area.

Spatial flexibility, or intra-individual variation in the wintering area was estimated as the mean absolute distance between all winter centroids for each individual (Veness, 2016).

Individual flexibility in timing

To estimate individual flexibility in timing of migration, I used the absolute difference in Julian dates between years for the timing of the two migrations. I calculated the differences between all the years, and calculated the mean per individual. This makes it comparable to our variable for individual spatial flexibility. To test if there was a difference in the flexibility in the spring and fall migrations I used a paired t-test. In order to see whether birds that display high variability in their spring migration also display high variability in their autumn migration I performed Spearman correlation tests to see if the intra-individual variance in timing for the spring and fall migrations were correlated. I also used Spearman correlation to test if individuals that are more flexible in timing of migrations are also more flexible in winter area.

All statistical analyses were performed using R 3.2.3 (R Core Team, 2013).

Results

Winter area

Locations for the winter period were obtained for 60 female common eiders (Table 1), of which 38 individuals were tracked for 2 to 6 years. Table 2 shows which years the individuals were tracked. The eiders wintered in two distinct areas, Iceland and northern Norway. Of the individuals tracked, 48 (80%) wintered in Iceland and 11 (18%) wintered in Norway. Only one individual switched between the two wintering areas and spent two of the winters in Norway, and one in Iceland. The winter centroids for the eiders ranged from northwest to southeast in Iceland, and from central to North Norway, see Figure 1.

Although all birds but one stayed in the same wintering area every year, some of the birds varied their migration route between years. One individual, which was tracked for five years (2010-2015), spent about two months at Jan Mayen during the fall migrations to Iceland in 2012 and 2013, spent some time at sea during the migration in 2010, and flew directly to Iceland in 2011 and 2014. Another individual tracked from 2010 to 2015, wintered in Iceland and spent 5 days at Jan Mayen during her spring migration in 2013 but flew directly to Svalbard the other years. A third individual wintering in Iceland, also tracked for 5 years (2010-2015), spent 3 days in east Greenland during one spring migration (2012).

Timing

The range of timing was quite large in both the spring and fall migrations, between February 6th and May 25th in the spring and August 18th to December 31st in the fall. For the timing of the spring migration, the best model (Table 1, Appendix) showed that birds migrating from Norway arrived to the breeding area 11.17±4.63 days (t=2.41; p=0.018; N=60) later than the birds arriving from Iceland. The effect of year was not statistically significant. Removing the individual that switched also decreased the effect of winter area on the spring migration. The individual that switched wintering area was very late to migrate from Norway both years (May 25th in 2010 and May 23rd in 2012), and strongly affected the estimate. When this individual was removed from the analysis, there was still a tendency for the individuals from Norway to leave the winter area later (5.70 ± 4.94 days; t= 1.15; p= 0.25; N=59), but it was not statistically significant.

For the timing of the fall migration the best model (Table 3 Appendix) showed that birds that migrated to Norway arrived in the winter area 23.21±8.38 (t=2.78; p=0.007; N=57) days later than the birds migrating to Iceland. Furthermore, successful breeders migrated

11.74±4.72 (t=2.49; p=0.02; N=57) days later than non-successful ones. The results from the generalized linear mixed model I ran to test which factors affected the breeding success showed that there was no difference in success between the birds wintering in the two wintering areas. The year effect was not statistically significant for the timing of the fall migration, although as mentioned, the effect of year is difficult to disentangle from the effect of breeding success, since the success varies significantly between years. The breeding success did have a significant effect on the timing of the fall migration. Removing the individual that switched between the wintering areas from the analysis did not qualitatively change the outcome of model selection (Table 4, Appendix).

Egg laying happened between May 21st and June 29th. For the timing of egg laying, two models were equally good (ΔAICc=1.36), see Table 5 in the Appendix. In both models, year had a significant effect on the timing of egg laying, see Table 3. The timing of spring migration had a significant effect on the timing of first egg laying in both models (0.18± 0.03 days; t=5.71; p<0.01 and 0.19±0.039 days; t=5.77; p<0.01; N=58). The winter area did not have a significant effect on laying date in either models. Removing the individual that switched winter areas did not affect the results.

Repeatability in timing

The repeatability for timing of the spring migration was 0.535 (CI$_{95\%}$ =[0.289, 0.69]; p<0.01), see Table 4. Among individuals wintering in Iceland the repeatability was 0.524 (CI$_{95\%}$ = [0.269, 0.706]; p<0.01), and for birds wintering in Norway the repeatability was 0.54 (CI$_{95\%}$ = [0, 0.882]; p<0.01).

For the timing of the fall migration, the repeatability was 0.644 (CI$_{95\%}$ = [0.431, 0.771]; p<0.01) for the whole population, 0.539 (CI$_{95\%}$ = [0.282, 0.71]; p<0.01) for individuals wintering in Iceland and 0.774 (CI$_{95\%}$ = [0.126, 0.947]; p<0.01) for individuals wintering in Norway.

Individual flexibility

Individual flexibility of the wintering area

The mean absolute distances between winter centroids for the individuals ranged from 14 km to 365 km, with most of the individuals having mean distances of under 200 km (median 83.68 km), see Figure 2. While the smoothing of the raw data and the calculation of winter centroids remove some of the measurement error of the geolocators, any mean absolute distance less than 200 kilometers can also be caused by the measurement error of the

geolocator. Notice that the individual that switched winter areas between Iceland and Norway was excluded from this analysis (she had a mean distance of 940 km between winter areas).

Individual flexibility in timing

The individual absolute mean differences in day for spring migration ranged from 1 to 42 days, with most individuals having a difference of under 20 (median= 8.67), see Figure 3. The absolute mean individual difference in day for the autumn migration ranged from 2 to 71 days, with a median of 10 days (Figure 4). The results of the paired t-test showed that flexibility in the timing of the fall migrations was 5.9 days ($CI_{95\%}$ =[0.11, 11.69]; t=2.084; p=0.04; N=30) larger than the flexibility in the spring migration.

Correlations in individual flexibility

Flexibility in timing of spring and fall migration were not correlated with each other (Spearman correlation test, ρ=0.16, p=0.12) indicating that individuals that were more flexible in the timing of the spring migration were not necessarily more flexible in the timing of the fall migration. Neither the flexibility in spring nor fall migration was correlated with the flexibility in winter area, indicating that individuals that are more flexible in the timing of either spring or fall migration are not more flexible in the winter area.

Discussion

In this study, I have shown that female eiders breeding in Kongsfjorden have two distinct winter areas, Iceland and northern Norway, and elaborating on the findings of Hanssen et al. (2016) I showed that and the birds generally do not switch between the two areas. Some of the individuals wintering in Iceland used stopovers in Greenland and Jan Mayen and stayed there for different amounts of time each year. This could suggest that there is some flexibility in the migration routes of the eiders. Since the eiders prefer to feed at shallow waters (Guillemette et al., 1993, Bustnes and Lønne, 1997), and the sea between Svalbard and both the wintering areas is deep, they are limited in where they can feed on the migration route. However, Jan Mayen on the route to Iceland and Bjørnøya on the route to Norway are possible stopover sites. My data did not, however, show individuals wintering in Norway staying at Bjørnøya for any length of time. This could indicate that the birds migrating to Iceland are more flexible in their route than the individuals wintering in Norway, although, since fewer of the individuals tracked wintered in Norway, this could also be an artifact of the sample size, although this is difficult to say for sure. The birds migrating to Iceland also has a longer

distance to fly, the median distance from the colony in Svalbard to the winter area being 1724 km for the birds wintering in Iceland and median 1303 km for the birds wintering in Norway, so the birds migrating to Iceland may have a larger need for stopovers.

There are several studies that show breeding populations to have several distinct wintering areas, like the eider population in this study. For instance a study on great skuas *Stercorarius skua* breeding in Foula, Shatland found that about half the population wintered over the continental shelf off West Africa, while the other half wintered over the continental shelf of Iberia (Furness et al., 2006). A study of sooty shearwaters breeding in New Zealand found that they migrated to three discrete regions off Japan, Alaska or California (Shaffer et al., 2006) and a study of northern gannets *Morus bassanus* breeding in Bass Rock, United Kingdom found that they used four distinct wintering areas (Kubetzki et al., 2009).

Several other studies have found flexibility in migration routes and wintering areas for different seabird species. Some species, for instance Cory's shearwaters *Calonectris diomeda*, have shown great individual flexibility in routes and wintering areas (Dias et al., 2011, Dias et al., 2013), while others, such as the black-browed albatrosses *Thalassarche melanophrys* (Phillips et al., 2005) and gray-headed albatrosses *T. chrystostoma* (Croxall et al., 2005), have a smaller degree of spatial flexibility within individuals. Quillfeldt et al. (2010) found high individual flexibility in winter area and migratory direction in thin-billed prions breeding in the Falkland Islands. European shags have been found to have high among-individual variation and high individual site fidelity in winter locations for adults breeding in the same colony (Grist et al., 2014), much like the eiders in this study.

The sedentary population of common eiders in Norway is declining (Fauchald et al., 2015). This suggests less ideal circumstances in Norway, which may also impact the migrant populations from Svalbard wintering there. Indeed, our recapture data could indicate that the proportion of Svalbard eiders wintering in Norway has declined over the study period, suggesting lower survival in Norway, or that the birds that have wintered in Norway are not in a condition to breed. Since individuals only very rarely switch winter area, the birds wintering in Norway might have a disadvantage. There are several examples of bird species showing high site fidelity even when the habitat is deteriorating, for example the populations of harlequin ducks *Histrionicus histrionicus* that were affected by the Exxon Valdez Oil spill in Alaska took a long time to recover due to their strong site fidelity (Esler et al., 2000).

For the timing of migration, I found that in the fall birds leaving for Norway and birds breeding successfully migrate later. The reason birds with breeding success leave Svalbard later is most likely that they have to stay in Svalbard until the ducklings are ready to migrate.

For the female eiders with no ducklings, it might not be advantageous to stay in Svalbard as long, perhaps because the conditions in their winter area are better than the conditions in Svalbard late in the fall. As suggested by Hanssen et al. (2016), the eiders migrating to Norway staying longer in Svalbard in the fall, could be because they are regulating their decision to migrate based on the food availability in their wintering area. Late departure from Svalbard might be costly, seeing as there is continual darkness, which could affect the foraging efficiency of the eiders, and the cold temperatures and high winds in the winter months may cause a high thermoregulatory cost. However, in the fall there are virtually no predators left in Svalbard, apart from glaucous gulls *Larus hyperboreus*, which kleptoparasitize from the eiders, so overall it may be advantageous for the birds migrating to Norway to stay in Svalbard as long as possible. As I mentioned, the conditions in Norway may not be ideal for the eiders wintering there. If the eiders migrating to Norway are modulating their decision to leave based on the conditions in the winter area, that could indicate that these eiders may have the ability to adapt to different conditions on a temporal scale.

There was no difference between years in the timing of either spring or fall migration. There was, however, an effect of year on the timing of egg laying which was also affected by the timing of spring migration. Studies of an eider population in the Canadian Arctic have found seasonal decline in clutch size, and that the probability that an egg surviving from laying to hatching decreased with later laying date (Descamps et al., 2011). Ducklings that were hatched later generally had a lower survival than those hatched earlier (Love et al., 2010). Love et al. (2010) found that the temperature was a good predictor of the laying date, hatching date, and also the first day of ice-free conditions in the bay. The chicks that hatched just before there was ice-free conditions on the water had the highest probability of return. Eider ducklings forage independently of their mother, and need open water to maximize the amount of time spent foraging (Love et al., 2010), and their future reproductive returns (Christensen, 1999). These results point to timing of breeding being very important for the eiders' fitness, and since timing of egg laying is affected by arrival date in the spring, the timing of migration also seems to be quite crucial for the eiders. As mentioned the eiders are capital breeders, and need to gain mass before breeding (Sénéchal et al., 2011, Gabrielsen et al., 1991). The earlier onset of spring in the Arctic will therefore most likely affect the fitness of the eiders arriving later to the breeding area severely.

The repeatability in timing in both the spring and fall migrations was relatively high, and slightly higher in the fall than in the spring. In this population there is a large range in the

timing of migration, and a large among individual variance, so while the repeatability is relatively high, there is still variance within individuals. The repeatability in timing of fall migration was slightly higher for the eiders migrating to Norway, but again, there were also fewer birds migrating to Norway, so this could be an effect of the sample size. The repeatability of the spring migration being slightly lower than in the fall is caused by the overall variance, both between and within individuals, being smaller in the spring. This points to the timing of spring migration being more constrained than the timing of the fall migration.

Other studies have found different degrees of repeatability in timing for fall and spring migrations for different bird species with a large variation in repeatability for the different species, and in a meta-analysis of repeatability, migratory behavior was found to be one of the least repeatable behaviors (Bell et al., 2009). For instance, for Bewick's swans *Cygnus columbianus* the repeatability for arrival in the winter area was found to be 0.03 (Rees, 1989), while for Bar-tailed godwits *Limosa lapponica* it was found to be 0.66 (Conklin et al., 2013). For the spring arrival the repeatability for female Greater snow geese *Chen caerulescens* was 0.42 (Bety et al., 2004), and for Black-tailed godwits *Limosa limosa* it was 0.18 (Gunnarsson et al., 2006), and Lourenco et al. (2011) found that it was 0.18 for female Black-tailed godwits. Conklin et al. (2013) found that the repeatability for the spring arrival for the Bar-tailed godwits was 0.91. In a study on passerine species Thorup et al. (2013) found that there generally was significant repeatability in the range of 0.2-0.5 in the migratory timing of both the spring and fall migrations of both short and long distance migratory passerines.

I found some individual spatial flexibility for the eiders, but as mentioned the mean absolute distances between winter centroids under 200 km could also just stem from the measurement error of the geoloctors, so overall it could be that most of the individuals are quite consistent in where they winter, even on a smaller scale, within the two distinct winter areas.

There was some individual flexibility in timing. Some individuals were more flexible that others, however the median difference in days between years for the individuals was still more than a week for the timing of both the spring and fall migration, this shows that there is some flexibility in the timing of the migrations in this population. The flexibility in the timing of spring migration was significantly smaller than for the timing of the fall migration.

While the eiders showed individual flexibility in the timing of migration, I found no effect of year in the timing of either spring or fall migrations. Flexibility may help populations to buffer the effects of climate change more rapidly than adaptation because it should allow individual to track the best time for migration (Conklin et al., 2013), and flexibility is favored

for environmental changes that occur during the life time of an individual (Pulido, 2007). However, for flexibility to be beneficial it should respond to specific cues to allow behavioral changes to track the best timing of migration. Although there is flexibility in the timing of migration in this population, the flexibility does not seem to respond to yearly variation in climate, since there is no effect of year in the timing of migration. It therefore remains unclear whether or not the flexibility observed in this study will help this eider population buffer possible changes in the climate.

The range of the timing of migrations in this eider population is quite large, both for the spring and fall migrations, and the repeatability is relatively high. Eiders are a long-lived species, so natural selection will work more slowly for the eiders than for species with shorter life spans (Tufto, 2015). However, since there is phenotypic variation in the population in the timing of migration, natural selection may lead to adaptation if the variation is heritable (Endler, 1986). The timing of spring migration seems to be correlated with fitness differences, since it affects the timing of egg laying, which has been found to affect the fitness of common eiders (Descamps et al., 2011, Love et al., 2010). Repeatability can be interpreted as an upper estimate for heritability (Nakagawa and Schielzeth, 2010), and since the repeatability in the timing of spring migration in this population is quite high, this further suggests that, if selection strongly favors the female eiders arriving earlier to the breeding ground, adaptation may occur. Further research could focus on the causes of the consistency and flexibility in the migration strategies of common eiders, and the fitness consequences of these strategies.

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Tables

Table 1. Which years the individuals were tracked

Year tracked	Wintering in Iceland	Wintering in Norway
2009-2010	18	7
2010-2011	17	5
2011-2012	27	6
2012-2013	17	2
2013-2014	15	1
2014-2015	12	1

Table 2. The number of eiders from the two winter areas, and how many years they were tracked.

| Number of years tracked	All individuals	Wintering in Iceland	Wintering in Norway
1	22	17	5
2	15	11	4
3	9	8	1
4	6	5	1
5	6	6	
6	1	1	

Table 3. The two best models for day of first egg laying with AICc values, estimates ± s.e and t-values.

|	year tracked+day of spring migration	year tracked +day of spring migration + winter area
AICc	756.52	757.88
AICc weights	0.60	0.30
Intercept	139.08±3.66	138.59±3.69
Year tracked 2010-2011	0.08±1.68 t=0.05	0.04±1.68 t=0.03
Year tracked 2011-2012	-4.83±1.52 t=-3.17	-4.94±1.53 t=-3.24
Year tracked 2012-2013	-2.44±1.75 t=-1.39	-2.65±1.77 t=-1.50
Year tracked 2013-2014	5.97±2.05 t=2.91	5.73±2.07 t=2.78
Year tracked 2014-2015	-1.24 ±1.99 t=-0.62	-1.53±2.01 t=-0.76
Day of spring migration	0.18±0.03 t= 5.71	0.19±0.03 t=5.77
Wintering in Norway		-1.38±1.41 t=-0.98

Table 3. The variance components and repeatability values for the spring and fall migration. Total is the values for the whole population, Iceland is for the individuals wintering in Iceland and Norway is for the individuals wintering in Norway. Sample sizes are in parentheses.

|		Among individual variance	Within individual variance	Repeatability
Spring migration	Total	141.6	123.0	0.54 (N=30)
	Iceland	152.4	138.2	0.52 (N=24)
	Norway	29.97	25.57	0.54 (N=6)
Fall migration	Total	561.8	311.2	0.64 (N=30)
	Iceland	358.8	306.8	0.54 (N=24)
	Norway	1148.2	335.9	0.77 (N=6)

Figures
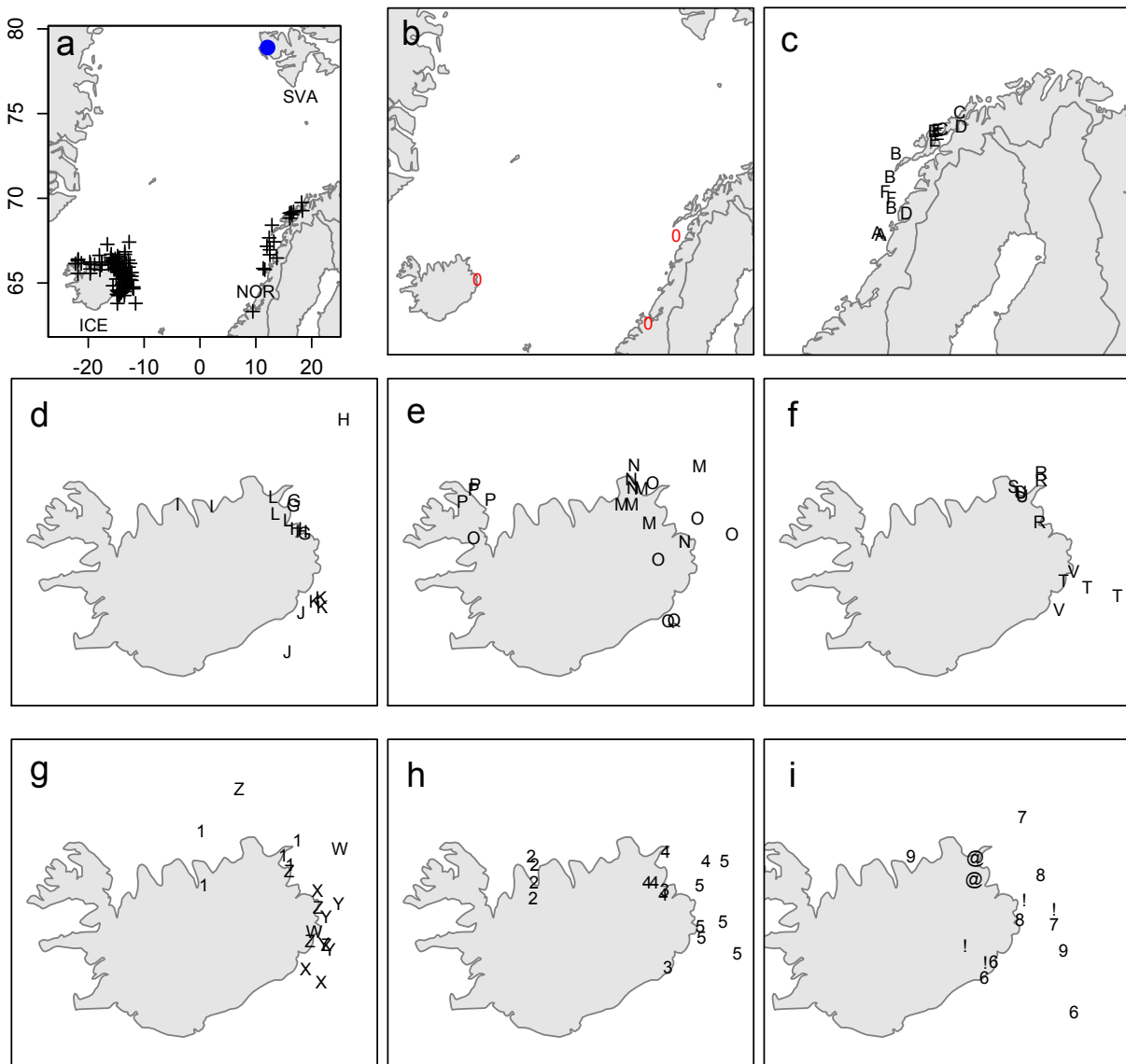
Figure 1. Winter centroids for all the female eiders tracked for more than one year. Each letter, number, or symbol represents one female eider, and each time that letter, number, or symbol shows is a different year. On **a** where the breeding colony is marked with a blue dot, is all the winter centroids for all individuals. **b** shows the one individual that switched winter areas between Norway and Iceland, the individual also moved a long distance within Norway. On **c** are all the birds wintering in Norway. The winter centroids for the birds wintering in Iceland are split into several maps (**d-i**), so that it is possible to distinguish the different individuals. They are divided so that the symbols mostly do not overlap. This figure illustrates that most of the individuals are quite consistent in where they winter, also within the different winter areas. Centroids that are over land or offshore represent the error of the geolocators, since the eiders are always located at the coast .
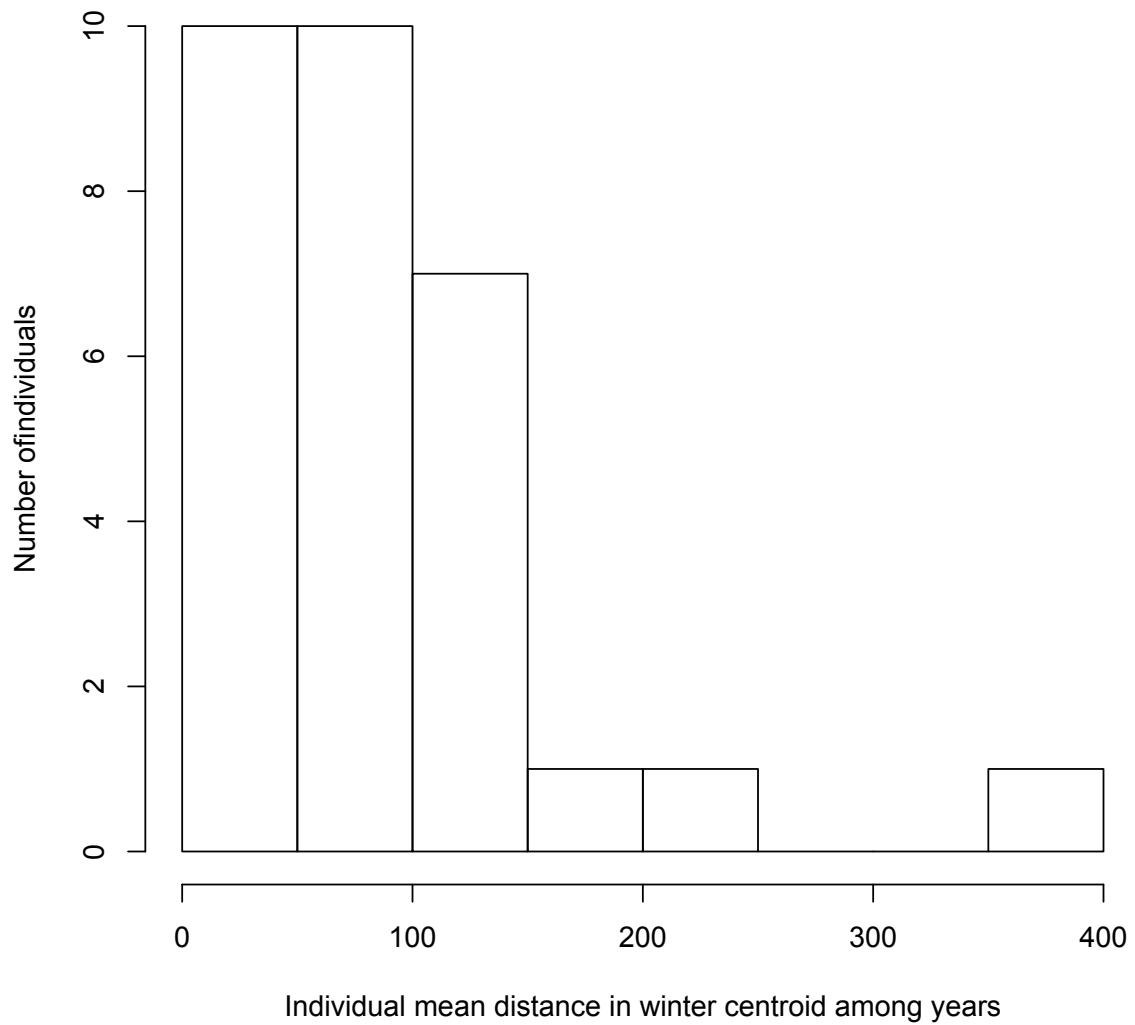
Figure 2. Individual flexibility in winter area, represented by mean absolute distances between winter centroids among years for each individual, in kilometers. Median mean absolute distance for the population is 83.68 km.
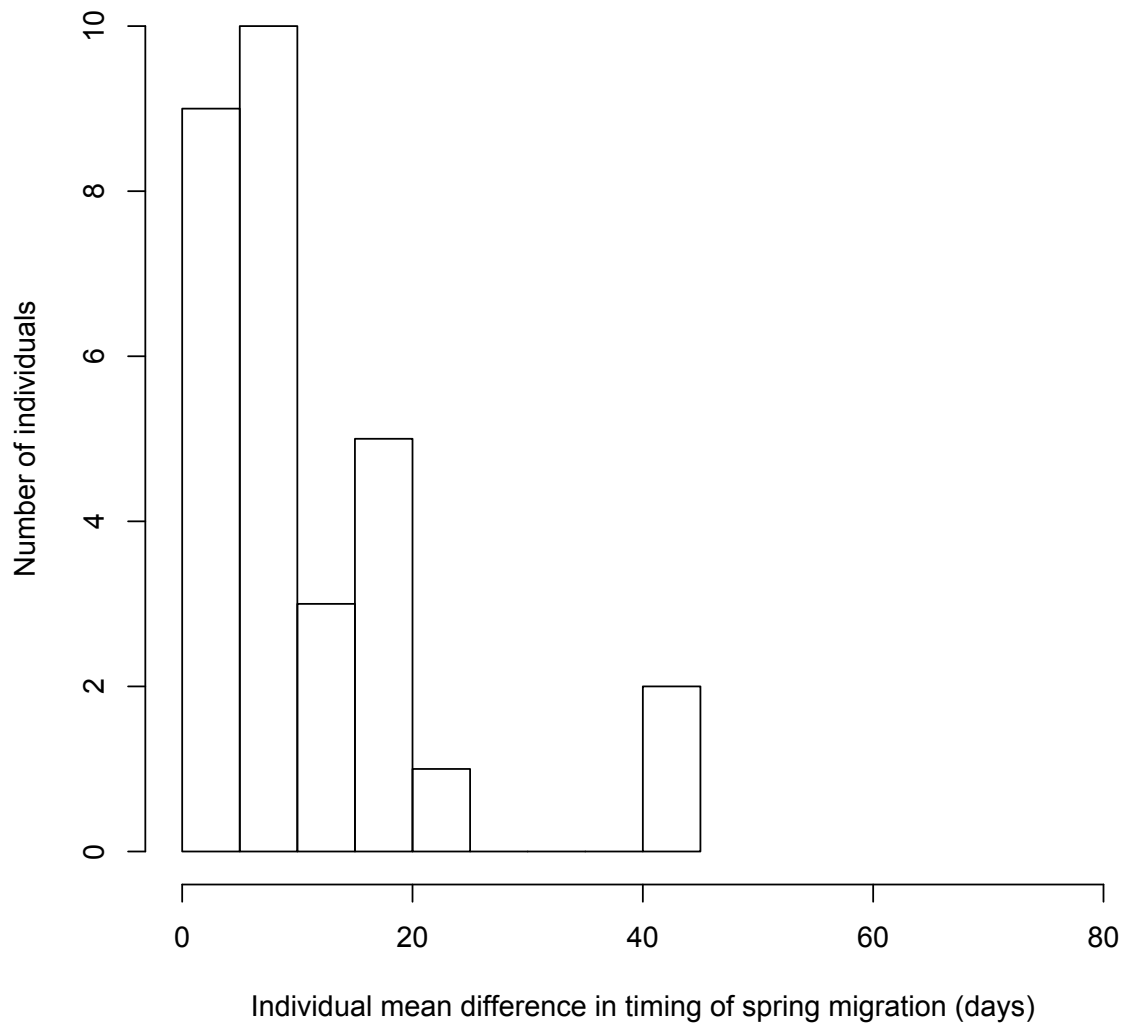
Figure 3. Individual flexibility in the timing of the spring migration, represented by mean absolute differences between timing of spring migration among years for each individual, in days. Median mean absolute difference for the population is 8.67 days.
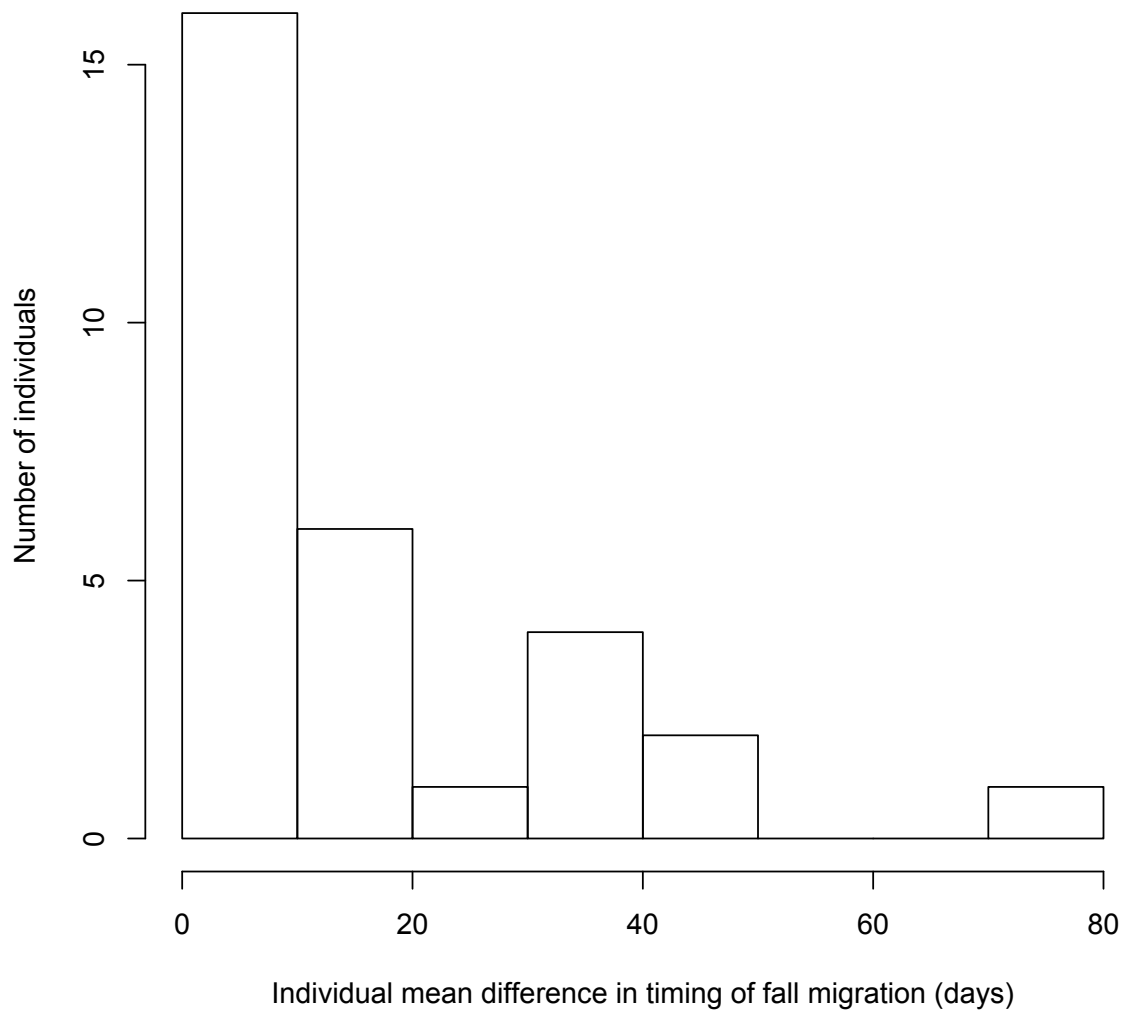
Figure 4. Individual flexibility in the timing of the fall migration, represented by mean absolute differences between timing of fall migration among years for each individual, in days. Median mean absolute difference for the population is 10 days.

Appendix

Table 1 Model selection for the effects of year and winter area (Iceland and Norway) on the timing of spring migration in female common eiders. K is the number of parameters estimated, AICc is the Aikake information criterion corrected for small sample size, and ΔAICc is the difference in AICc compared to the model with lowest AICc.

Effect of year and winter area on timing of spring migration.

Predictors	K	AICc	ΔAICc	AICc weight
Winter area	4	1060.33	0.00	0.85
1	3	1063.97	3.63	0.14
Year + Winter area	9	1069.36	9.03	0.01
Year	8	1072.41	12.08	0.00
Year × Winter area	14	1079.96	19.63	0.00

Table 2 Model selection for the effects of year and winter area (Iceland and Norway) on the timing of spring migration in female common eiders. In this analysis the individual that switched between Norway and Iceland was excluded.

Effect of year and winter area on timing of spring migration.

Predictors	K	AICc	ΔAICc	AICc weight
1	3	1028.75	0.00	0.59
Year + Winter area	4	1029.52	0.77	0.40
Year	8	1037.28	8.53	0.01
Year + Winter area	9	1038.52	9.77	0.00
Year × Winter area	14	1048.55	19.81	0.00

Table 3 Model selection for the effects of year, winter area (Iceland and Norway), and breeding success on the timing of fall migration in female common eiders.

Effect of year, winter area and breeding success on timing of fall migration.

Predictors	K	AICc	ΔAICc	AICc weight
Winter area + Breeding success	5	1172.91	0.00	0.56
Breeding success × Winter area	6	1174.91	2.01	0.20
Year + Winter area + Breeding success	10	1175.77	2.86	0.13
Year + Winter area + Breeding success × Winter area	11	1177.90	4.99	0.05
Breeding success	4	1177.99	5.08	0.04
Year + Breeding success	9	1180.14	7.23	0.02
Year × Winter area + Breeding success	15	1184.86	11.95	0.00

	K	AICc	ΔAICc	AICc weight
Year × Winter area + Breeding success × Winter area	16	1186.55	13.64	0.00
Winter area	4	1315.27	142.36	0.00
Year + Winter area	9	1315.60	142.68	0.00
Year	8	1321.68	148.77	0.00
1	3	1322.83	149.92	0.00
Year × Winter area	14	1324.28	151.37	0.00

Table 4 Model selection for the effects of year, winter area (Iceland and Norway), and breeding success on the timing of fall migration in female common eiders. In this analysis the individual that switched between Norway and Iceland was excluded.

Effect of year, winter area and breeding success on timing of fall migration.

Predictors	K	AICc	ΔAICc	AICc weight
Winter area + Breeding success	5	1145.25	0.00	0.47
Year + Winter area + Breeding success	10	1146.60	1.35	0.24
Breeding success × Winter area	6	1147.22	1.97	0.17
Year + Winter area + Breeding success × Winter area	11	1148.74	3.50	0.08
Breeding success	4	1151.09	5.85	0.03
Year + Breeding success	9	1153.09	7.84	0.01
Year × Winter area + Breeding success	15	1155.02	9.78	0.00
Year × Winter area + Breeding success × Winter area	16	1157.49	12.24	0.00
Year + Winter area	9	1287.87	142.63	0.00
Winter area	4	1288.82	143.57	0.00
Year	8	1295.46	150.21	0.00
1	3	1296.09	150.84	0.00
Year × Winter area	14	1296.73	151.49	0.00

Table 5 Model selection for the effects of year, winter area (Iceland and Norway), and the start of spring migration on the timing of egg laying in female common eiders.

Effect of year, winter area and the start of spring migration on the timing of fall migration.

Predictors	K	AICc	ΔAICc	AICc weight
Year + Spring migration	9	756.52	0.00	0.59
Year + Winter area + Spring migration	10	757.88	1.36	0.30
Year + Winter area + Spring migration × Winter area	11	760.31	3.79	0.09
Spring migration × Year	14	765.44	8.91	0.01
Year + Winter area + Spring migration × Year	15	766.28	9.76	0.00
Year + Winter area + Spring migration × Winter area + Spring migration	16	768.71	12.18	0.00

× Year

Year × Winter area + Spring migration	15	769.05	12.52	0.00
Year × Winter area + Spring migration × Winter area	16	771.64	15.12	0.00
Spring migration	4	776.29	19.77	0.00
Winter area + Spring migration	5	777.57	21.04	0.00
Year × Winter area + Spring migration × Winter area + Spring migration × Year	21	779.59	23.07	0.00
Spring migration × Winter area	6	779.77	23.24	0.00
Year	8	784.46	27.94	0.00
Year + Winter area	9	786.61	30.09	0.00
Year × Winter area	14	796.63	40.11	0.00
1	3	797.78	41.26	0.00
Winter area	4	799.83	41.26	0.00