



Thick-billed Murres in breeding pairs migrate and overwinter far apart but in similar photic environments

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Abstract

Scheduling between mates in species with long-term pair bonds can be essential for positive fitness. The annual cycle in photoperiod is the primary environmental cue used by many animals to synchronize behavior and physiology among members of a population, and animals that migrate must have similar annual schedules to ensure successful breeding. However, we know little about whether members of mated pairs in migratory species experience similar photic environments across the year, which could allow for synchronization in annual phenology. Here, we used light-based geolocation to estimate positions of mated pairs of Thick-billed Murres (*Uria lomvia*, a seabird a.k.a. Brünnich's Guillemot) which bred above the northern polar circle in Greenland. We tested the hypothesis that individuals in mated pairs occur in more similar locations and photic environments than randomly matched females and males. We found no difference in the amount of spatial separation or in the photic environment between mates and randomized heterosexual pairings. In general, the distance between females and males ranged from 1,198.5 km during August to 737.4 km during January. The sexes remained in photic environments with highly correlated photoperiods and moderately correlated times of solar noon in UTC. The spatial separation of, but similar photic environments experienced by, female and male murres regardless of pair status is probably adaptive by facilitating the synchronization of annual schedules between sexes, while allowing individuals in mated pairs the freedom to pursue the best foraging opportunities during migration and overwintering independent of their mate.

Keywords Greenland · Pair migration · Photoperiod · Seabird · Thick-billed Murre · *Uria lomvia*

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Zusammenfassung

Brutpartner der Dickschnabellumme ziehen und überwintern fern voneinander unter ähnlichen Lichtbedingungen

Zeitliche Abstimmung zwischen Brutpartnern kann bei Arten mit langer Paarbindung wesentlich zu positiver Fitness beitragen. Der Jahreslauf der Photoperiode ist bei vielen Tieren das primäre Signal für die Synchronisation von Verhalten und Physiologie innerhalb von Populationen, und bei ziehenden Arten sind ähnliche Jahreszyklen notwendig für erfolgreiche Reproduktion. Jedoch ist kaum bekannt, ob Brutpartner ziehender Arten über den Jahreslauf ähnliche Lichtbedingungen erfahren, die sie dann zur Synchronisation ihrer Jahreszyklen nutzen könnten. Die vorliegende Studie verwendete Licht-basierte Geolokatoren zur Abschätzung der Aufenthaltsorte von Paaren der Dickschnabellumme (*Uria lomvia*), die nördlich des Polarkreises in Grönland brüten. Wir überprüften die Hypothese, dass Brutpartner eines Paares an

ähnlicheren Orten und unter ähnlicheren Lichtbedingungen überwintern als zufällig ausgewählte andere weibliche und männliche Individuen derselben Population. Wir fanden keine Unterschiede in der räumlichen Trennung oder in den Lichtbedingungen zwischen Brutpartnern und gegengeschlechtlich zufällig ausgewählten Vergleichsvögeln. Allgemein lag die Entfernung zwischen Weibchen und Männchen zwischen 1198,5 km im August und 737,4 km im Januar. Weibchen und Männchen überwinterten in Lebensräumen, in denen Photoperioden eng und Zeiten der Mittagshöhe (in koordinierter Weltzeit UTC) moderat miteinander korreliert waren. Die räumliche Trennung unter ähnlichen Photoperioden von weiblichen und männlichen Dickschnabellummen, unabhängig von Paarzugehörigkeit, ist vermutlich adaptiv. Sie trägt bei zur Synchronisierung von Jahreszyklen der Geschlechter, stellt Individuen jedoch frei, unabhängig von ihren Brutpartnern ausserhalb der Brutzeit die besten Nahrungsbedingungen aufzusuchen.

Introduction

Many animals use the annual transition in photoperiod to schedule behavior and physiology (Farner 1964; Gwinner 1996; Coppack and Pulido 2004; Åkesson and Helm 2020). Photoperiod can initiate the seasonal development of gonads or initiate migration (Farner 1964; Åkesson and Helm 2020). This may be especially vital for migratory birds that travel 100s to 1,000s of kilometers before arriving to mate in areas with restricted breeding seasons. Thus, photoperiod may act to align the physiology required for the exchange of gametes among mates (Rowan 1925; Farner 1964; Dawson et al. 2001). In addition, birds with established long-term pair-bonds are generally expected to benefit from similar annual schedules, coordination, and synchronized behavior (Hatch 1990; González-Solis et al. 1999; Bebbington and Groothuis 2023), and remaining in similar photoperiods across the annual cycle as a long-term mate could synchronize their breeding phenotype. Yet, many birds with long-term pair-bonds are migratory, and whether migratory birds in mated

pairs reside in an environment with similar photic cues is rarely evaluated.

Generally, birds in long-term pairs can migrate separately (Davis et al. 2016; Fayet et al. 2017; Kubo et al. 2018; Byholm et al. 2022), migrate together (Elder and Elder 1949; Spendelov and Lugo 2017; Gupte et al. 2019; Kölzsch et al. 2020), or reunite after initiating migration separately (Smith et al. 2000). For example, the Black-tailed Godwit (*Limosa limosa*) schedules arrival to breeding sites within days of each other after spending the winter apart (Gunnarsson et al. 2004), while some birds, such as Rockhopper Penguins (*Eudyptes chrysocome*) and Scopoli's Shearwaters (*Calonectris diomedea*), remain in similar habitat, but are spatially separated from their long-term mate (Müller et al. 2015; Thiebot et al. 2015). Other birds, such as geese, may migrate within close proximity to their mate (Elder and Elder 1949; Gupte et al. 2019; Kölzsch et al. 2020) or, in the case of the Harlequin Duck (*Histrionicus histrionicus*), may reunite with their mate during winter after being separated for up to 90 days (Smith et al. 2000). However, for pair members not migrating or overwintering together, individuals could be separated temporally, latitudinally, longitudinally, or a combination thereof, despite occupying habitat that may have similar characteristics. This could result in mates experiencing different photic environments during migration and overwintering.

To understand better whether migratory birds within established breeding pairs remain in similar photic environments across the annual cycle, we studied a migratory seabird breeding in northwest Greenland, the Thick-billed Murre (a.k.a. Brünnich's Guillemot, *Uria lomvia*). Thick-billed Murres generally have long-term pair-bonds for their reproductive-lifespan (up to about 25 years; Gaston and Jones 1998; Gaston and Hipfner 2000). At the breeding site, Thick-billed Murres generally have coordinated rhythms of egg-incubation and chick-brooding that aligns with the 24-h light cycle, where each male and female spends approximately 12 h incubating or brooding and 12 h foraging (Elliott et al. 2010; Huffeldt and Merkel 2016; Huffeldt et al. 2021). At the annual scale, the father begins fall

migration by swimming with their small flightless chick for at least 30 days (Elliott et al. 2017; Merkel and Strøm 2023), while the mother continues to visit the breeding site for up to approximately 15 days (Gaston and Jones 1998), before she and nonbreeding males begin fall migration by flying (Elliott and Gaston 2014; Frederiksen et al. 2016; Elliott et al. 2017). Both sexes overwinter mainly offshore in open ocean (Frederiksen et al. 2016). Little is, however, known about the migratory behavior of breeding pairs and whether synchronous breeding activity within pairs at the breeding colony corresponds with more similar annual strategies and photic environments among mates as compared to nonmates.

We hypothesized that members of established breeding pairs (mated pairs) of Thick-billed Murres inhabited more similar photic environments during their annual cycle than randomized heterosexual pairings (randomized pairings), because, by remaining in a similar photic environment, members of mated pairs could better synchronize the beginning of their breeding effort (Rowan 1925; Farner 1964; Gwinner 1996; Coppack and Pulido 2004). We predicted: (1) that individuals within mated pairs would be closer to each other than randomized heterosexual pairings and (2), that throughout the nonbreeding season, members of mated pairs would be located in photic environments with a similar photoperiod (*i.e.* at similar latitude) and time of solar noon in UTC (*i.e.* at similar longitude) than randomized pairings. We addressed our hypothesis and predictions using bird-borne geolocation sensors (GLSs) on known breeding pairs of Thick-billed Murres by measuring the distance between members of mated pairs and randomized pairings of females and males, the spatial overlap between the distribution of each sex in mated pairs, and the difference in photoperiod and time of solar noon among pair types throughout migration and overwintering.

Methods

Data collection and GLSs

Fieldwork occurred during multiple breeding seasons on Kippaku (73.72 °N, 56.62 °W) and Saunder's Island (76.57 °N, 70.04 °W), Greenland from 2007 through 2013. The locations of 10 breeding pairs of Thick-billed Murres were recorded daily for a minimum of one annual cycle using GLSs (mean error \pm standard deviation = 186 \pm 114 km; Phillips et al. 2004), with three pairs' behavior being recorded for multiple annual cycles. This resulted in 13 mated-pair annual-cycles from 20 individuals. These positions were included in a previous study on population-level migration of Thick-billed Murres breeding across the North Atlantic basin (Frederiksen et al. 2016), and a detailed account of our

capture, logger deployment, and data handling methods are described therein and in Linnebjerg et al. (2013).

Briefly, either LTD2400, LAT2500 (Lotek Marine Technology, Canada), or GLS-MK9 (British Antarctic Survey, U.K.) GLSs were attached to a standard metal leg-ring using cable ties and placed on a bird's tarsus. The total mass of each GLS model was < 6.5 g, which was < 1% of average mass of adult Thick-billed Murres during chick brooding (mean \pm standard error: 955 \pm 4.5 g; Frederiksen et al. 2014). Birds were captured using telescoping noose-poles. The sex of each individual was unknown when captured. Sex was identified molecularly for at least one member of each breeding pair using blood or feathers following standard methods (Griffiths et al. 1998; Huffeldt and Merkel 2016). GLSs were used to estimate two latitude and longitude positions daily as described in Frederiksen et al. (2016). Positions recorded within \pm 1.5 weeks of the equinoxes were excluded from further analyses, because of the near symmetrical photoperiod across latitudes during this time, which prohibits effectively estimating geolocation. Geolocation data from mid-May to mid-August when the sun was continuously above the horizon during polar summer were also excluded from analyses. In addition, due to the limitations of our GLSs during phases of continuous light, we are unable to estimate departure and arrival dates of individuals at the breeding colony using positional data. Four of the 13 mated-pair annual cycles had some GLS failure resulting in incomplete sampling.

Statistical analyses

All spatial and statistical analyses were performed using program R (R Core Team 2022). Within an annual cycle, the data from each individual was compared to their mated partner (mated pair, $N = 10$ pairs). Within an annual cycle, we also compared each individual within a mated pair to all other individuals of the opposite sex that originated from the same colony and were not the individual's mate (randomized pairing); this resulted in a total of 18 randomized pairings ($N = 18$ pairings).

We used linear mixed-effects models and the *lme4* (v. 1.1–35.1) R-package for all modelling (Bates et al. 2015). We tested significance of predictors by comparing the model representing our hypothesis or prediction to an intercept-only, or null, model that included the relevant random effects using a likelihood ratio test (Tredennick et al. 2021). We used the R-package *emmeans* (v. 1.8.9) to calculate estimated marginal means and 95% confidence intervals (CIs) of predictors used in linear mixed-effects models (Lenth 2023). When using day of year in models, we calculated days from the day of year 228 (DF228; day 0 = 16 or 17 August, depending on whether a leap-year), which allowed us to compare relationships that spanned different calendar years. We checked model assumptions visually using

histograms of residuals and the R-package *performance* (v. 0.10.8; Lüdecke and Ben-Shachar 2021).

We identified the correlation of each individual's photic environment within mated pairs and randomized pairings. For each combination of females and males within an annual cycle, we calculated the Pearson correlation coefficient of the photoperiod and the time of solar noon in UTC. We calculated photoperiod and time of solar noon using the R-package *mapproj* (v. 1.1–6; Bivand and Lewin-Koh 2022), and we use these parameters instead of latitude and longitude to provide an easily interpretable description of the photic environment experienced by the murre. To test whether mated pairs resided in more correlated photic environments than randomized pairings of females and males, we compared the resulting correlation coefficients using a linear mixed-effects model with pair type as a categorical predictor ("mated", "randomized") and pair ID as a random intercept.

Using linear mixed-effects models, we tested whether mated pairs would be in a more similar photic environment than randomized pairings. We calculated the difference in photoperiod and time of solar noon between females and males within mated pairs and randomized pairings as separate response variables. Each model included the random intercept of annual cycle nested within pair ID. We additionally identified that response variables had a quadratic relationship to day of year and included a quadratic function of day of year and its interaction with pair type as a predictor in each of the models. We used the same approach to test whether distance between members of mated pairs was shorter than distance between randomized pairings of females and males. Distance was square root transformed before modelling to improve model fit, and model predictions were reverse-transformed before plotting. For distance between individuals, we calculated the great-circle distance using the Haversine method and the *geosphere* (v. 1.5–18) R-package (Hijmans 2022).

All other spatial analysis were carried out using the R-package *adehabitatHR* (v. 0.4.21; Calenge 2006). Kernel utilization distributions (UDs) representing the birds' core distributions (50% UD) were estimated and plotted for different phases of the annual cycle when birds were away from the breeding colony: August and September, October and November, December and January, February, March and April, and May. We calculated the overlap of the 50% UD between females and males in mated pairs. We then tested whether females or males were more likely to overlap spatially with their mate during migration and overwintering using a linear mixed-effects model with the 50% UD overlap between an individual and their mate as the response variable and an interaction between the categorical predictors phase and sex. The random intercept was annual cycle nested within pair ID.

Results

Are mates found in the same location?

A similar distance separated members of mated pairs and randomized pairings throughout migration and overwintering (pairwise difference DF228*Pair-type: 0.005 ± 4.2 km, $Z = 0.03$, $P = 0.97$). The mean distance between females and males changed from a maximum of 1,198.5 km (95% CI = 1,054.1 to 1,352.2 km) around 17 August to a minimum of 737.4 km (95% CI = 631.8 to 851.1 km) in late January, before increasing again to 949.9 km (95% CI = 815.3 to 1,094.9 km) after the vernal equinox (Fig. 1; $\chi^2_4 = 225.8$, $P < 0.001$). The overlap of the 50% UD within mated pairs was less than 13% during migration and overwintering for males and females, supporting that members of pairs do not occur in the same location. The only exception was in the four mated pairs in which we had data in May; these pairs caused a significant interaction between phase and sex when predicting the spatial overlap within mated pairs (Fig. 2; $\chi^2_{11} = 20.84$, $P = 0.04$; Supplementary Materials). However, this was driven exclusively by an increased overlap by females with their mate in May because, when we reran the analysis excluding May, this significant interaction disappeared ($\chi^2_9 = 7.05$, $P = 0.63$; Supplementary Material). Most individuals migrated to and overwintered east of Newfoundland, Canada (Supplementary Material; Frederiksen et al. 2016). One male (K6) remained above the northern polar circle (66.56°N) for most of one nonbreeding season. During the following season this male remained mostly below the polar circle (Supplementary Material).

Do mates experience more similar photic environments than randomized heterosexual pairings?

Female and male Thick-billed Murres occupied locations with highly correlated photoperiods (Fig. 3), and mated pairs and randomized pairings did not differ significantly in this correlation ($\chi^2_1 = 0.093$, $P = 0.76$). The difference in photoperiod experienced within pairs of Thick-billed Murres differed across the year (Fig. 1; $\chi^2_4 = 905.2$, $P < 0.001$), but not between mated pairs and randomized pairings (pairwise difference DF228*Pair-type: -0.013 ± 0.31 h, $Z = -0.04$, $P = 0.97$). However, males remained farther north in longer photoperiods for more days in the beginning of the autumn as compared to females (Fig. 1). Females and males experienced more similar photoperiods from late autumn until the vernal equinox, after which males again moved farther north and experienced longer photoperiods than females (Fig. 1).

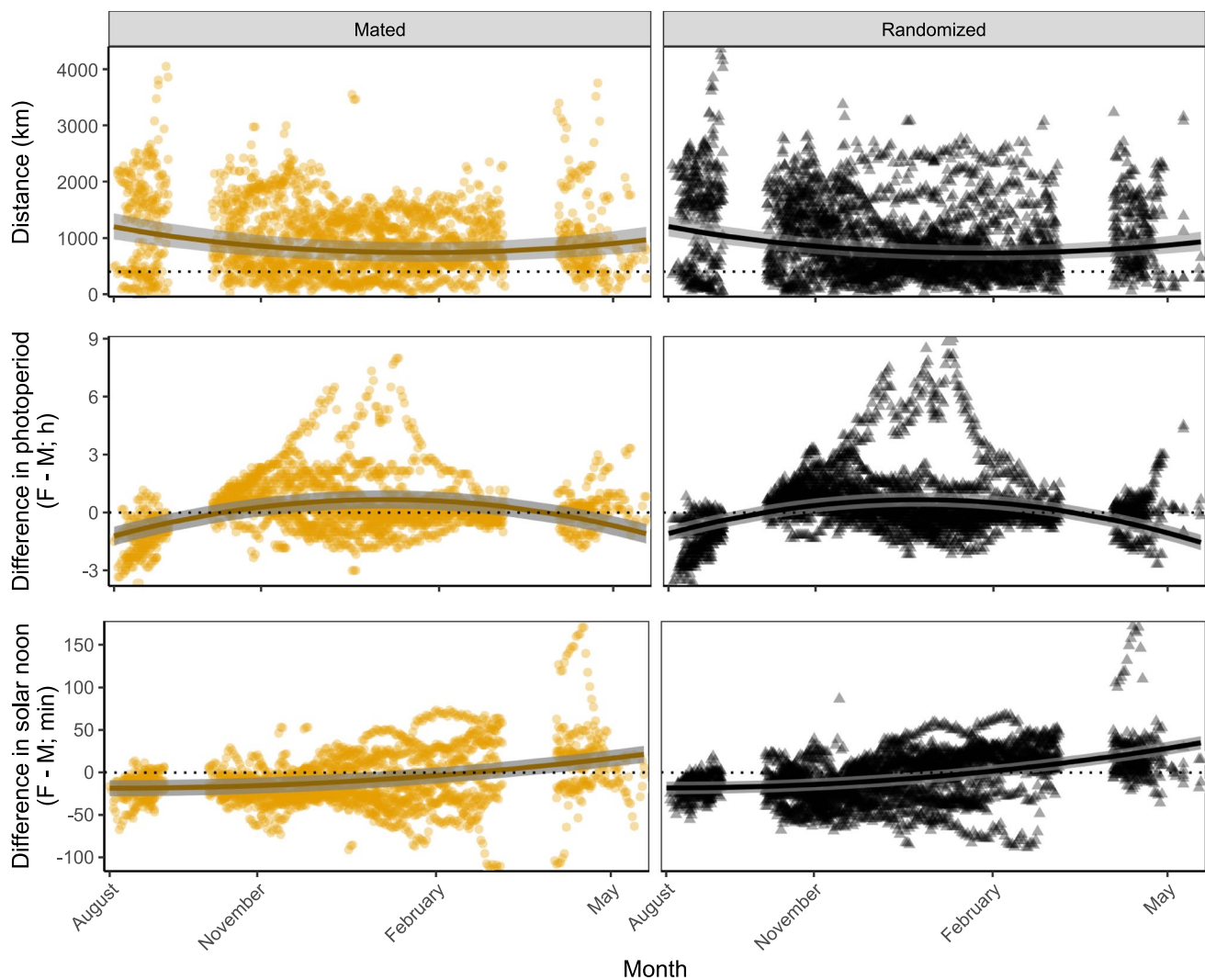


Fig. 1 Distance and difference in photic environment among mated pairs and randomized pairings of females and males. Solid lines are estimated marginal means and shaded areas are 95% CIs predicted from linear mixed-effects models. Points are the distance or difference between females (F) and males (M). The x -axis is day from

day of year 228 and annotated by month. The dotted line at 400 km in the top panel represents approximately twice the spatial error in GLSs. Positions recorded within ± 1.5 weeks of the equinoxes were excluded, because of inaccuracy of GLSs at this time

Female and male Thick-billed Murres occupied locations with a moderately correlated time of solar noon in UTC (Fig. 3), and mated pairs and randomized pairings did not differ significantly ($\chi^2_1 = 0.36$, $P = 0.55$). The difference in time of solar noon experienced within pairs of Thick-billed Murres differed across the year (Fig. 1; $\chi^2_4 = 1057.8$, $P < 0.001$), but not between mated pairs and randomized pairings (pairwise difference DF228*Pair: -2.98 ± 6.01 h, $Z = -0.50$, $P = 0.62$). However, males were farther west and experienced solar noon later in UTC than females in autumn, and females and males experienced increasingly similar times of solar noon until late winter (Fig. 1), after which males experienced solar noon earlier in UTC than females, indicating males were more east (Fig. 1).

Discussion

We had a robust sample of 10 mated pairs of Thick-billed Murres that contributed 13 mated-pair annual-cycles, and, counter to expectations, we found no difference between the photic environment experienced by mated pairs and randomized pairings of females and males. The sexes of Thick-billed Murres generally remained in similar photic environments despite being separated by more than 730 km while away from the breeding colony (Figs. 1, 3).

Despite females and males experiencing comparable photic environments, the sexes had time-dependent differences in migration and overwintering. The highly correlated photoperiods and moderately correlated times of solar noon

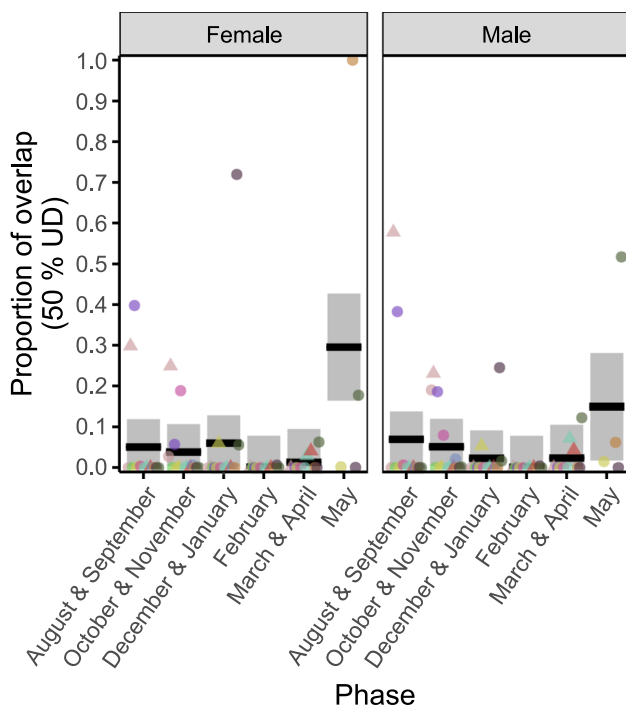


Fig. 2 Spatial overlap of females and males in mated pairs. Black bars are estimated marginal means and shaded areas are 95% CIs predicted from linear mixed-effects models. Circles and triangles are proportion of overlap of the 50% kernel utilization distribution (UD) of females or males within a mated pair. Circles are from the first and triangles are from the second annual cycle, respectively. Online only, each color illustrates a different mated pair

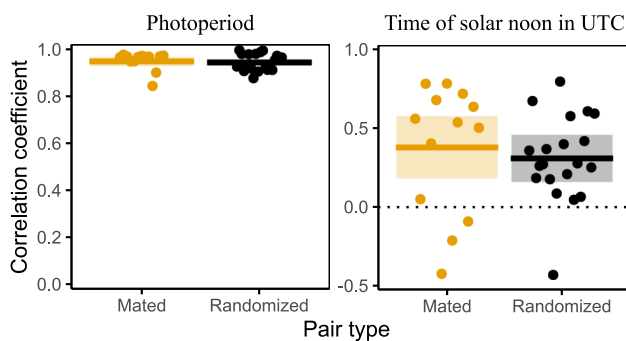


Fig. 3 Correlation of photic environment among mated pairs and randomized pairings of Thick-billed Murres. Left figure is the correlation of photoperiod. Right figure is the correlation of the time of solar noon in UTC. Solid bars are estimated marginal means and shaded areas are 95% CIs predicted from linear mixed-effects models. Points are correlation coefficients among members of pairs

(Fig. 3) suggest that females and males were more likely separated longitudinally than latitudinally and that photoperiod may be more important than the time of solar noon for the murres. In addition, males occurred in longer photoperiods at higher latitude than females before the autumnal

equinox (Fig. 1), probably due to the swimming migration undertaken by fathers and their offspring (Elliott and Gaston 2014; Elliott et al. 2017; Merkel and Strøm 2023). Indeed, females move more quickly south than males (Frederiksen et al. 2016), exposing them to shorter photoperiods sooner than males.

In the North Atlantic, the sexes of Thick-billed Murres generally begin to overlap substantially in the distance to the colony during spring migration (Frederiksen et al. 2016). However, our results based on a subset of these data indicate that males experienced longer and phase-shifted photoperiods as compared to females, suggesting males occurred farther north and east than females after the vernal equinox (Fig. 1). Although we were unable to track the full vernal migration, this result suggests that males may travel more quickly to the area of the colony than females. This aligns with more general evidence from seabirds and other animals that males often arrive earlier in the breeding area than females (Morbey and Ydenberg 2001; Thiebot et al. 2015). However, because of the limitations of our GLSs, more insight is needed to confirm this for Thick-billed Murres from the colonies studied.

Murres breeding in the same region will often overwinter in a similar region (Frederiksen et al. 2016). Our results clearly indicate that mates of Thick-billed Murres are spatially separated, but that male and female murres generally remain in similar photic environments when migrating and overwintering. Many seabirds occur in similar habit as their mate or others of the same sex (Müller et al. 2015; Thiebot et al. 2015), while spatial separation may allow individuals to prioritize their own condition or sex-specific energetic requirements independent of their mate (Sorensen et al. 2009; Fayet et al. 2017). Having the independence to pursue the best foraging opportunities could facilitate passing through the energetic bottleneck experienced by many seabirds during the nonbreeding season (Fort et al. 2009) and carry over to affect breeding positively (Sorensen et al. 2009; Fayet et al. 2017).

In addition, although the ultimate cause of the sexes remaining in comparable photic environments is not fully understood and may be caused by tracking similar resources (Orben et al. 2015), the comparable photic environments may ensure synchronized schedules between females and males. Indeed, individuals with a similar relationship to the photic environment are more likely to mate together (Hur et al. 1998; Randler and Kretz 2011; Steinmeyer et al. 2013), and puffin pairs return to their colony more synchronously than nonpaired individuals, while pairs with more similar migrations laid their egg earlier and had higher breeding success (Fayet et al. 2017). For thick-billed murres, the restricted Arctic breeding season probably selects for high synchronicity between females and males, but when and how this synchronicity originates requires further elucidation.

Conclusion

In conclusion, mated pairs of Thick-billed Murres migrate and overwinter in highly similar photic environments, but this similarity applies generally to female and male murres and changes across the annual cycle. The similar photic environment between sexes may facilitate synchronized schedules that benefit fitness. However, because of the spatial similarities between sexes, the synchronized annual schedules may originate from other mechanisms or environmental factors than the photic environment. In addition, the limitations of our GLSs hampered our ability to evaluate the full annual schedule and synchronicity between mates of Thick-billed Murres. More research is needed to resolve the synchronicity in annual schedules and habitats of Thick-billed Murre mates.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-024-02176-x>.

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Authors' contribution Authors are listed alphabetically by last name, except for N.P.H., M.B., and M.F. Conceptualization: Nicholas P. Huffeldt, Barbara Helm; Data curation: Morten Frederiksen, Jannie F. Linnebjerg; Formal analysis: Nicholas P. Huffeldt, Manuel Ballesteros; Funding acquisition: Morten Frederiksen, Flemming R. Merkel, Anders Mosbech; Investigation: Nicholas P. Huffeldt, Morten Frederiksen, Jannie F. Linnebjerg, Flemming R. Merkel, Anders Mosbech; Methodology: Nicholas P. Huffeldt, Manuel Ballesteros, Morten Frederiksen; Visualization: Nicholas P. Huffeldt, Manuel Ballesteros; Writing—original draft: Nicholas P. Huffeldt, Manuel Ballesteros, Morten Frederiksen; Writing—review and editing: Nicholas P. Huffeldt, Manuel Ballesteros, Morten Frederiksen, Barbara Helm, Jannie F. Linnebjerg, Flemming R. Merkel, Anders Mosbech.

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Data availability The dataset analysed during the current study is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflict of interests to declare that are relevant to the content of this article.

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