



HAL
open science

Testing the abundant centre hypothesis in a seabird: higher energy expenditure at the wintering range centre does not reduce reproductive success

Don-jean Léandri-Breton, Kyle Elliott, Arnaud Tarroux, Pierre Legagneux,
William Jouanneau, Françoise Amélineau, Frédéric Angelier, Pierre Blévin,
Vegard Bråthen, Per Fauchald, et al.

► To cite this version:

Don-jean Léandri-Breton, Kyle Elliott, Arnaud Tarroux, Pierre Legagneux, William Jouanneau, et al.. Testing the abundant centre hypothesis in a seabird: higher energy expenditure at the wintering range centre does not reduce reproductive success. *Ecography*, 2025, pp.e07498. 10.1111/ecog.07498 . hal-04921152

HAL Id: hal-04921152

<https://hal.science/hal-04921152v1>

Submitted on 30 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

ECOLOGY

Research article

Testing the abundant centre hypothesis in a seabird: higher energy expenditure at the wintering range centre does not reduce reproductive success

Don-Jean Léandri-Breton^{1,2}, Kyle H. Elliott¹, Arnaud Tarroux³, Pierre Legagneux^{2,4}, William Jouanneau^{2,5}, Françoise Amélineau⁶, Frédéric Angelier^{1,2}, Pierre Blévin⁷, Vegard Sandøy Bråthen⁸, Per Fauchald³, Geir W. Gabrielsen⁵, Aurélie Goutte⁹, Sabrina Tartu^{1,2}, Børge Moe⁸ and Olivier Chastel²

¹Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, QC, Canada

²Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 – CNRS and Université de La Rochelle, Villiers-en-Bois, France

³Norwegian Institute for Nature Research, Tromsø, Norway

⁴Département de Biologie, Université Laval, Québec, QC, Canada

⁵Norwegian Polar Institute, Tromsø, Norway

⁶Univ Rennes, CNRS, ECOBIO (Ecosystèmes, biodiversité, évolution), Rennes, France

⁷Akvaplan-niva AS, Fram Centre, Tromsø, Norway

⁸Norwegian Institute for Nature Research, Trondheim, Norway

⁹École Pratique des Hautes Études (EPHE), PSL Research University, UMR 7619 METIS, Sorbonne University, Paris, France

Correspondence: Don-Jean Léandri-Breton (don-jean.leandri-breton@mail.mcgill.ca)

Ecography

2025: e07498

doi: [10.1111/ecog.07498](https://doi.org/10.1111/ecog.07498)

Subject Editor: Miguel Araújo

Editor-in-Chief: Miguel Araújo

Accepted 4 December 2024



www.ecography.org

Understanding variation in animal distributions is a central and challenging question in ecology that has become particularly critical in the context of global environmental changes. While distributions are often studied for resident or breeding species, species range limits are equally important for migratory species in winter when population regulation may occur due to limited resources in the non-breeding season. A central hypothesis in several theories is that the density, fitness and performance of individuals decrease towards the edge of the range as organisms become maladapted when approaching the limit of their environmental tolerance ('abundant centre hypothesis'). Energy is a critical resource, especially in winter when environmental conditions deteriorate, and this hypothesis predicts that high energy expenditure (low performance) at the range limit would lead to rapidly dwindling body mass and reduced fitness. We investigated this hypothesis in an Arctic-breeding seabird wintering in the North Atlantic, the black-legged kittiwake *Rissa tridactyla*. From 2008 to 2019, we tracked 117 adult kittiwakes ($n = 176$ tracks) with geolocation devices and saltwater immersion sensors to estimate the migratory strategies, time–activity budget and energy expenditure of individuals during winter, and estimated their reproductive success after their return to the colony during summer. Population density was indeed higher towards the centre of the range. However, contrary to the predictions, the energy expenditure of individuals was higher at the centre of the range and decreased towards the edge. In contrast, there were no spatial differences in the reproductive success of individuals wintering at the centre versus at the edge of their range. We conclude that performance and fitness did not increase towards the centre of the wintering range, implying that

© 2025 The Author(s). Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

although resource acquisition was likely higher at the abundant centre, energy expenditure was also higher, so that individual fitness was constant across the winter range.

Keywords: animal movement, migratory species, non-breeding distribution, range limits, reproductive success, *Rissa tridactyla*

Introduction

The geographic distribution of all species is constrained by abiotic and biotic factors creating boundaries beyond which individuals are not found. Understanding how species ranges are shaped, and how they can shift, is a central and challenging question in ecology that has become particularly critical in the context of global changes (Parmesan 2006, Sexton et al. 2009, Alexander et al. 2022). That question is particularly challenging for migratory species where population regulation may occur at different times of the year, and so range limits may reflect processes occurring thousands of kilometres from the breeding range. Because a species' geographic range is the expression of the ecological niche at large scales, investigating the drivers of range limits requires defining the set of environments throughout the annual cycle where populations can maintain a positive growth to persist over time (Holt 2009, Sexton et al. 2009, Hargreaves et al. 2014). Indeed, the environment plays a key role in determining metabolic demands and health, which themselves influence individual fitness. Quantifying spatial variations in fitness across the annual range is essential to assess the fit between phenotypes and environments across their range (Sexton et al. 2009). Although most studies of range limits focus on the breeding season because of its impact on reproductive success, understanding links between performance and distribution in winter may be equally important, as over-winter survival and carryover effects can be important components of fitness (Norris et al. 2004, Woodworth et al. 2017).

Models of range limits largely imply that fitness and performance of individuals decrease towards the edge of the range distribution, as phenotypes become maladapted when approaching the limit of their environmental tolerance (Sexton et al. 2009, Hargreaves et al. 2014). This can be expressed as an overall niche where fitness and performance are broadly positive and similar across a wide range, and the range limit occurs where that niche ends (Gaston and Sheffield 2009). An alternative is that there is a gradient of performance and fitness from the range limit to the core. This latter idea is known as the 'abundant centre hypothesis', which states that a species is more abundant where environmental conditions are most suitable and that environmental conditions are most suitable towards the centre of the distribution (Hengeveld and Haeck 1982, Guo et al. 2005). Although intuitive, this hypothesis is still debated and has found mixed support so far. Empirical studies are needed to explore how abundance and fitness vary towards range limits (Sagarin et al. 2006, Dallas et al. 2017, Pironon et al. 2017, Santini et al. 2019).

For migratory species, key demographic components (i.e. birth and death) can occur in very disjunct and sometimes distant seasonal distributions, as a significant part of the annual cycle is often spent outside the breeding range (Newton 2008). Environmental conditions experienced within the non-breeding range can lead to mass mortality events in migratory taxa such as insects (Brower et al. 2004), mammals (Kock et al. 2018, Anderson and Alexander 2020) and birds (Camphuysen et al. 2002, Newman et al. 2007, Fort et al. 2009). Moreover, a growing body of evidence shows that conditions experienced over the non-breeding range can also have non-lethal effects, carrying over consequences into the reproductive output of the following breeding stage (Harrison et al. 2011, O'Connor et al. 2014). This highlights the need to assess whether fitness of migratory species varies predictably across the non-breeding range as a result of adaptations to optimal non-breeding conditions. This is especially difficult for marine organisms, for which direct observations are challenging in offshore areas.

For species wintering at high latitudes, winter represents an energetically demanding period with deterioration in weather conditions, reduced daylight, temperature and/or food quality creating a potential 'energetic bottleneck' in their annual cycle (Fort et al. 2009, Kautz et al. 2020, Dunn et al. 2022). Winter conditions are strongly linked to survival through their impact on energy budget (Mysterud et al. 2001, Grosbois and Thompson 2005, Woodworth et al. 2017). The ability of wintering individuals to maintain their energy balance has profound consequences on life history traits, which ultimately shape population dynamics (Schneider 2004). Maintaining the energy balance is thus under strong evolutionary pressure, potentially driving the migratory behaviour itself, as migratory animals respond to seasonality by engaging in costly long-distance movements to avoid more energetically challenging environments and maximize their net energy intake across their annual cycle (Greenberg and Marra 2005, Dingle and Drake 2007). The migratory strategies adopted by individuals are thus pivotal in maintaining energetic balance, as movement decisions determine exposure to environmental conditions and locomotion costs when individuals traverse heterogeneous environments, notably when facing varying wind conditions (Shepard et al. 2013). Energy is a key currency linking behaviour to fitness for non-breeding animals, as a negative energy balance will lead to starvation, a reduced reproductive success and ultimately death. Estimating energy expenditure of individuals across their range is thus an excellent indicator of individual performance, especially for marine animals where direct observations of mortality are rare. Measuring energy expenditure

throughout the year is challenging, but can now be achieved using miniaturized biologgers. Animal tracking gives new insights into the movement, behaviour and internal state of individuals, especially during life stages where they are out of reach (Wilmers et al. 2015, Davidson et al. 2020).

We tested the abundant centre hypothesis by investigating whether population density, fitness and performance of individuals are higher at the range centre, and decreased towards the edge. We used energy expenditure as a proxy for variation in foraging performance across the winter distribution range, and linked it to subsequent reproductive success. We hypothesized that individuals wintering towards the edge of the winter distribution would encounter higher energy expenditure compared to the majority of individuals wintering closer to the centre. If this is the case, we further hypothesized that this difference in winter energy expenditure would lead to a decrease in fitness of individuals wintering towards the edge of the wintering range, due to carry-over effects on subsequent reproductive attempts. Additionally, we examined spatial variations in wind intensity and temperature (specifically, sea surface temperature), given their potential influence on the energy expenditure of flying animals. Finally, we tested whether the winter energy expenditure was further predicted by the movement strategies of individuals, reflected in their wintering home range and movement rate.

We tested these hypotheses in a migratory seabird, the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake') wintering in the North Atlantic Ocean. This species' migration is one of the best studied of any seabird, as the species is one of the most abundant North Atlantic seabirds, and individuals breeding across the ocean basin show high inter-population overlap in their winter distribution, with an estimated 4.5 million individuals congregating in the western part of the ocean near the Great Banks of Newfoundland (Frederiksen et al. 2012). This high degree of overlap in a densely occupied but restricted core area (Frederiksen et al. 2012), with a decreasing abundance of individuals towards the edges of the distribution range, makes the Atlantic kittiwake an apparent example of the abundant centre hypothesis, yet it is unclear what performance might drive this relationship. The kittiwake populations breeding around the North Atlantic are panmictic in winter (Frederiksen et al. 2012) and the winter distribution of the studied population is likely representative of the Atlantic subspecies (Léandri-Breton et al. 2021).

We used 11 years of geolocation tracking (fall 2008–spring 2019) from 117 individuals to estimate the energy expenditure through activity patterns of individuals (i.e. flying, resting and active foraging). This method therefore incorporates the behavioural response of individuals to abiotic and biotic factors they experienced and, to the best of our knowledge, is used for the first time to estimate the performance of individuals across their population range in the context of range limits. We combined this with reproductive monitoring data during the breeding period to estimate reproductive success as a proxy for individual annual fitness.

Material and methods

Study population and logger deployment

The studied population is a long-term monitored colony located in Kongsfjorden, Svalbard (78°54'N, 12°12'E) (details in the Supporting information). During the study period (2008–2019), nest content monitoring was conducted at the colony every two to six days. We used the success of rearing at least one chick for 10 days after hatching (hereafter 'reproductive success') as a proxy of individual fitness. Three-quarters of kittiwake chick mortality occurs within 10 days after hatching (Coulson and Porter 1985) and, in some years, monitoring of nests had to stop before chicks fledged, so we considered this measurement to be representative of reproductive success. The sex of individuals was determined by molecular sexing of blood following Fridolfsson and Ellegren (1999).

We used solar geolocators (global location sensors, GLS) to track the non-breeding movements of kittiwakes. From 2008 to 2019, adults were captured on their nests, using a noose attached to a fishing rod, and equipped with geolocators. We used mk18 and mk13 (British Antarctic Survey), mk4083 and mk4093 (Biotrack) and Intigeo F100 and C65 (Migrate Technology) mounted on a Darvic leg band. Devices measured light intensity every 1 min and recorded the maximum light intensity every 5 or 10 min. They also measured saltwater immersion (used as a proxy for bird activity) every 3 or 30 s and stored the number of wet measurements within every 10 min period.

Over the study period, we recaptured 83% of the individuals at their return to the colony the following year and recovered the geolocators. The estimated adult survival rate at the study site is 85%, suggesting that the geocator recovery rate closely reflected the expected adult return rate (Goutte et al. 2015). Only complete annual tracks were used in the analyses after filtering out tracks without saltwater immersion data and partial tracks caused by device failure or battery discharge. Overall, we acquired 176 complete tracks from 117 different individuals (Fig. 1, 55 females and 62 males), covering 11 non-breeding seasons, continuously (fall 2008–spring 2019).

Our study does not include data on mortality because the tracking devices we used require the recapture of individuals to recover the data, meaning that particularly poor strategies (e.g. energetically costly strategies) may have been excluded from the dataset via early-life mortality. In particular, juveniles may use an exploration and route refinement approach to migration (Guilford et al. 2011), so that breeding adults have a good enough strategy that it does not impact breeding success. However, adult mortality mostly occurs in winter and the link between energy expenditure and survival is clear and well studied (Myserud et al. 2001, Grosbois and Thompson 2005, Woodworth et al. 2017). We could thus expect that a potential spatial trend in mortality across the winter range would parallel trends in individual energy expenditure and reproductive success.

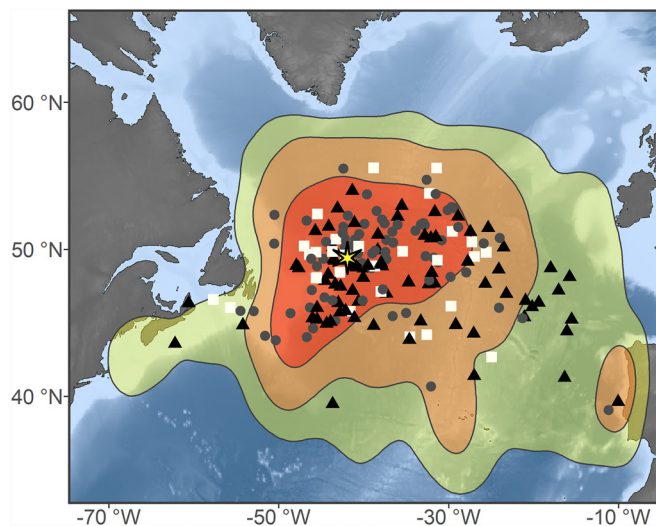


Figure 1. Winter distribution of black-legged kittiwakes with 95% (in yellow), 80% (in orange) and 50% (in red) utilization distribution kernels. The yellow star (*) indicates the centroid of the population's range centre ($n = 21\ 510$ positions) and the symbols show the centroid of each individual's distribution ($n = 176$ tracks), with the colour and shape coding indicating the reproductive status in the following breeding season (black triangles (▲) for 'reproductive success', white squares (■) for 'reproductive failure' and grey dots (●) for 'unknown status'). The Atlantic populations of kittiwakes are panmictic in winter and the winter distribution of the studied population is thus representative of most colonies (Frederiksen et al. 2012).

Winter range and migratory strategies

To infer geographic positions, geolocator data were processed according to the procedure based on the threshold method and developed for the SEATRACK initiative, a collaborative project focused on tracking North Atlantic seabird wintering movements, of which this study is part (Bråthen et al. 2021; all details are provided in the Supporting information). Individuals from the study population engage in long-distance migration characterized by directional north-east–southwest movements in fall and spring between their breeding site in Svalbard and their wintering area south of 60°N in the North Atlantic (Léandri-Breton et al. 2021). We examined the tracks to identify these directional migratory movements before 30 November and after 1 February and determined the wintering period as the last date (wintering area arrival in fall) and first date (wintering area departure in spring) of these movements. The first and last 10 days of the resulting wintering tracks were excluded to ensure that any migratory movements were omitted, as they are associated with high energy expenditure from extended periods of flight.

We calculated the 95, 80 and 50% utilization distribution kernels (UDs) over the population's winter positions (from all tracks, $n = 21\ 510$ positions) projected using a Lambert Azimuthal Equal Area coordinate system and the package 'adehabitatHR' (Calenge 2006) with a smoothing factor (h)

of 200 km and grid cells of 50×50 km (Fig. 1). The centre of the population's winter range was defined as the centroid of the 95% UD.

To characterize the migratory strategies of individuals we extracted for each wintering track 1) the winter home range area (i.e. 95% UD); 2) the movement rate (i.e. averaged daily distance) and 3) the distance from the population centre, defined as the distance between the population's winter centroid and the centroid of each individual's home range.

Time–activity budget and daily energy expenditure (DEE)

Saltwater immersion data were used to build a time–activity budget based on the identification of three behaviours (similar Material and methods in McKnight et al. 2011, Fayet et al. 2016, Dunn et al. 2020, Léandri-Breton et al. 2024a): sustained flying (T_{fly}), resting on water (T_{res}) and active foraging (T_{for}). The saltwater immersion data were standardized to be comparable among individuals and logger models, such as $x_{\text{st}} = x/x_{\text{max}}$, where x_{max} is the maximum value over the 10-min summing period. The standardized saltwater immersion data (thereafter SSI) were then used to estimate 10-min periods of sustained flying (SSI value of 0%), resting on water (SSI value $\geq 98\%$) and active foraging ($0\% < \text{SSI} < 98\%$) which is characterized by a succession of short flights and short swimming or shallow diving bouts (Jodice et al. 2003). The saltwater immersion thresholds were defined to consider only continuous flight bouts, and avoid overestimation of foraging behaviour at night as the nighttime activity data were largely biased towards very low activity levels ($98\% < \text{SSI} < 100\%$, Supporting information).

To calculate the DEE, we combined the time–activity budget with the population-specific resting metabolic rate (i.e. $1.64 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; Gabrielsen et al. 1988, Blévin et al. 2017) and the activity-specific field metabolic rates (Léandri-Breton et al. 2024a). We used the field metabolic rates (expressed as multiple of the resting metabolic rate) estimated with doubly labelled water technique by Jodice et al. (2003) for the kittiwake's flying and foraging behaviours (combining surface feeding and searching flight). To include thermoregulation costs relative to the environment, field metabolic costs for the resting behaviour on water were estimated using the thermal conductance of kittiwakes in water ($0.1 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) and the sea surface temperature (SST). To account for the non-linear relation between thermoregulatory costs and temperature in endotherms (Scholander's curve; Gabrielsen et al. 1988), we used Eq. (1) when the SST was below the species' thermoneutral zone ($< 4.5^\circ\text{C}$) and Eq. (2) when above it:

$$\text{DEE} = 7.3 \text{ RMR} \times T_{\text{fly}} + 4.05 \text{ RMR} \times T_{\text{for}} + (\beta - \text{TC} \times \text{SST}) T_{\text{rest}} \quad (1)$$

$$\text{DEE} = 7.3 \text{ RMR} \times T_{\text{fly}} + 4.05 \text{ RMR} \times T_{\text{for}} + \text{RMR} \times T_{\text{rest}} \quad (2)$$

where RMR is the resting metabolic rate (in ml O₂ g⁻¹ h⁻¹), β is the intercept of the RMR at 0°C, TC is the thermal conductance in water (O₂ g⁻¹ h⁻¹ C^{o-1}), SST is the sea surface temperature (C°) and T_{fly}, T_{for} and T_{res} correspond to the time (h) spent daily flying, foraging actively and resting on water, respectively. The DEE in ml O₂ g⁻¹ was then converted to kJ by multiplying by the averaged body mass for the study population (365 g, Gabrielsen et al. 1988) and using the caloric conversion factor of 20.1 J per ml O₂ (Schmidt-Nielsen 1997). With the objective of strictly comparing the winter energy expenditure among individuals, our method assumes that 1) the saltwater immersion data have been converted correctly into activity budgets; 2) energy expenditure is primarily associated with activity and thermoregulation; 3) heat produced during foraging and flight substitutes for thermoregulation and is not additive to thermoregulatory costs (Lovvorn 2007); 4) the Scholander curve of thermoregulation costs against temperature developed by Gabrielsen et al. (1988) for breeding kittiwakes in air applies to the non-breeding season with a revised thermal conductance in water; and 5) that the thermal conductivity in water is 2.14 times that in air, as found in murre (Croll and McLaren 1993).

Environmental data

Sea surface temperature (SST, daily temporal resolution, product: global-reanalysis-phy-001-031-grepv2-daily, doi.org/10.48670/moi-00024) and sea surface wind intensity (i.e. wind speed expressed in m s⁻¹, 6 h temporal resolution, product: cmems-obs-wind-glo-phy-my-l4-0.125deg-PT1H, doi.org/10.48670/moi-00185) grids were downloaded from the EU Copernicus Marine Service (<https://resources.marine.copernicus.eu/products>) at a 0.25° spatial resolution. SST and wind intensity were extracted over the geolocation positions using package 'seabiRds' (Patterson 2022), at a daily resolution. For graphical representation only, grid cells with fewer than 10 observations were discarded.

Statistical analyses

The results from the daily time–activity budget were bootstrapped 10 000 times to calculate the averaged winter DEE, and the averaged time of flying, foraging and resting behaviours for each individual track during the winter period. The orthodromic distances between the population's distribution centroid and the individuals' distribution centroids were calculated using the ellipsoid method (*distVincentyEllipsoid* function from the package 'Geosphere'; Hijmans 2021).

We fitted a negative binomial regression (NBR; function *glm.nb*; package 'MASS'; Venables and Ripley 2002) to test whether the density of individuals' wintering centroids decreased with distance from the centre of the population's wintering distribution. To do so, individual counts were calculated per 200 km distance bin and the midpoint of each bin was used. We fitted linear mixed-effects models ('lmer', package 'lme4'; Bates et al. 2015) to determine whether the averaged winter DEE and its components (averaged time

flying, foraging and resting during winter) varied with the distance from the centroid of the population's winter range. Sex was included as fixed factor to account for potential male–female differences in behavioural activity and DEE that may be related, for instance, to sexual size dimorphism. The averaged scaled day length experienced by individuals during winter to account for variations in activity duration related to day length (Supporting information). Although the behavioural activity responses (averaged daily time flying, foraging and resting) are bounded by the 24-h duration, we assumed a normal distribution and used a linear mixed-effects model to facilitate the interpretation of the coefficient effects. However, we also fitted beta regression models using package 'glmmTMB' (function *glmmTMB*, Brooks et al. 2017), which generated very similar results (Supporting information).

To further explore consequences of migration strategies on DEE, we fitted two LME models testing for the effect of winter home range area (km², scaled) and movement rate (km day⁻¹). Additional LME models were fitted to assess if the averaged wind intensity and SST experienced by individuals during the winter period varied non-randomly over the averaged wintering latitude and longitudes of individuals.

Finally, we tested if the reproductive success of individuals varied according to the distance from the centre of the winter range using a generalized linear mixed-effects (GLME) model. To do so, the explanatory variable was scaled. In all models, individual identity and year were included as random factors. The resulting residuals met the homoscedasticity and normality assumptions. The revised R-squared (R² marginal) were estimated using the *r.squaredGLMM* function (package 'MuMIn'; Nakagawa and Schielzeth 2013, Bartoń 2022). When specified, scaling of variables was performed using z-score normalization. All analyses were carried out in R ver. 4.2.0 (www.r-project.org).

Results

Population density

The population's winter distribution was spread across the North Atlantic Ocean with the centre of the population's distribution situated at the eastern edge of the Grand Banks of Newfoundland (n=21 510 positions, Fig. 1). The centroids of the 176 tracks were dispersed over distances to the centre of the population's distribution ranging from 40 to 3871 km (Fig. 1). The individuals' wintering centroids were clustered around the centre of the population's range, with a decreasing density of individuals towards the edge (NBR, coef = -0.0008, SE = 0.0001, 95% CI [-0.0011; 0.0006], p < 0.0001, Fig. 2).

Energy expenditure and activity budget

Over the entire winter period, the daily time–activity budget of individuals averaged 4.85 ± 0.69 h of flying time (range 3.3–6.8 h day⁻¹), 6.44 ± 0.79 h of foraging time (range

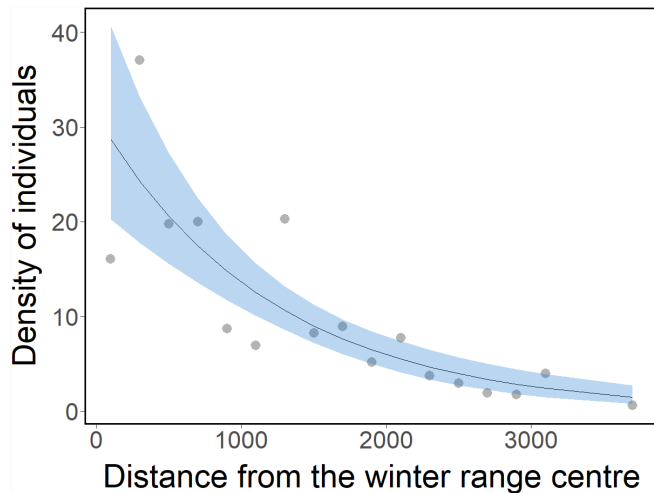


Figure 2. Model predictions of a negative binomial regression showing the density of wintering individuals (wintering centroids) over the distance from the centre of the population's wintering distribution (by 200 km distance class), with 95% confidence intervals. Population's wintering centre estimated over a utilization distribution kernel.

4.9–8.8 h day⁻¹) and 12.66 ± 0.89 h of resting time on the water (range 9.4–14.7 h day⁻¹). The winter DEE within the population averaged 846 ± 60 kJ daily, and was reflected in individuals' migratory destination (Fig. 3). The winter DEE decreased by 14.1% (-124.6 kJ day⁻¹) from the centre to the edge of the population winter distribution (3872 km; Table 1, Fig. 5). This variation in DEE was driven by the averaged flying activity of individuals, which decreased by 26.7% (-1.4 h day⁻¹) from the centre to the edge of the population winter distribution (Table 1, Fig. 5). In contrast, there was a significant increase of 18.27% (1.4 h day⁻¹) in the averaged foraging activity towards the edge of the winter distribution, while no significant variation was detected for the averaged resting activity (Table 1, Fig. 5). Sex had a significant but very marginal effect on the DEE, as well as foraging and resting activities, with males spending on average 2.4% (-21.0 kJ day⁻¹) less energy, 3.6% (0.3 h/day) less time foraging and 2.4% (0.3 h day⁻¹) more time resting on water than females (Table 1).

Wind and SST conditions

The average wind intensity experienced by individuals also varied greatly over the population's winter range with individuals being exposed to wind speed up to 32.6 m s⁻¹ (mean = 11.3 ± 4.4 m s⁻¹, $n = 21\,510$ observations). The wind intensity was higher near the centre of the population's winter range (LME, coef = -0.0007 m s⁻¹, SE = 0.0001 , 95% CI [-0.0009 ; -0.0005], $df = 165$, R^2 marginal = 0.58 , $p < 0.0001$) and decreased by 23% (-2.8 m s⁻¹) towards the edge of the range (Supporting information). Wind intensity also increased with latitude (LME, coef = 0.18 m s⁻¹, SE = 0.01 , 95% CI [0.15 ; 0.21], $df = 171$, $p < 0.0001$) and longitude (LME, coef = 0.16 m s⁻¹, SE = 0.01 , 95% CI [0.001 ; 0.032], $df = 164$, $p < 0.05$) of the average wintering position of

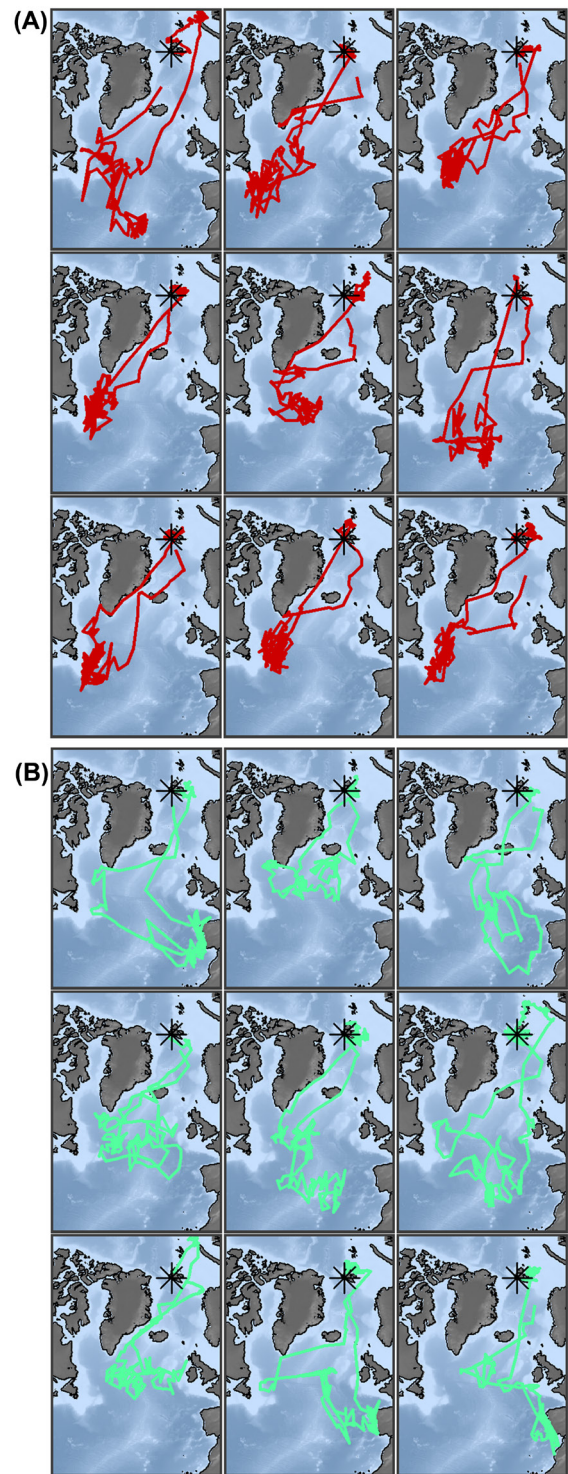


Figure 3. Non-breeding tracks (migratory and wintering movements) showing migratory strategy differences between (A) individuals with the highest daily energy expenditure migrating mainly to the western North Atlantic near the population's core wintering range; and (B) individuals with the lowest daily energy expenditure distributed widely across the wintering range, including the European coast (out of 176 tracks). The black star (*) indicates the colony location in Svalbard, Norway. Plotted using a Lambert Azimuthal Equal Area projection.

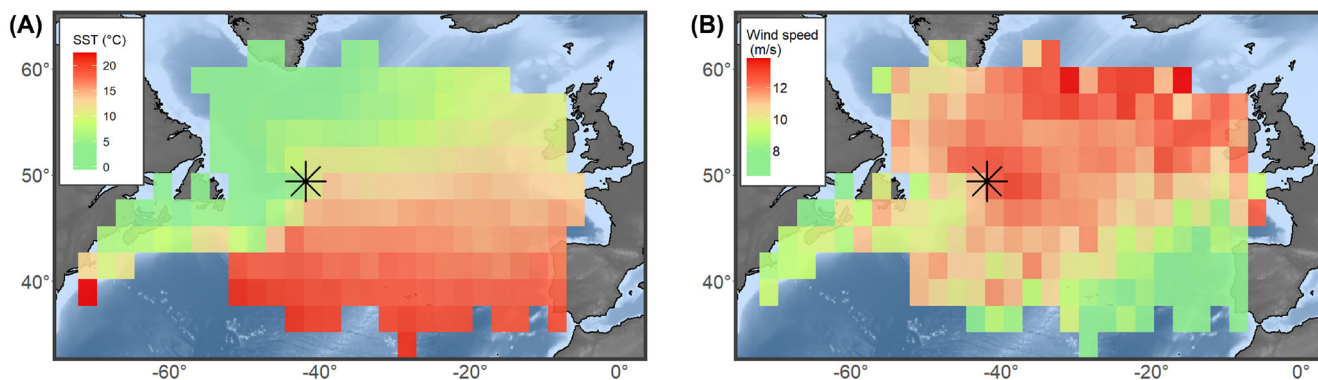


Figure 4. Heat maps illustrating spatial heterogeneity in (A) sea surface temperature and (B) wind intensity (m s^{-1}) experienced by individuals during winter. Values for each variable extracted over the individuals' wintering positions. Darker grid cells (2.5° latitude \times 2.5° longitude) indicate areas of higher values for each variable. The black star (*) shows the centroid of the population's winter range ($n=21\ 510$ positions).

individuals (Fig. 4, Supporting information). SST also increased towards the edge of the population's wintering range (LME, $\text{coef}=0.0006^\circ\text{C}$, $\text{SE}=0.0001$, 95% CI [0.0003; 0.0009], $\text{df}=134$, R^2 marginal=0.42, $p < 0.0001$), although the population's range centre was located at the confluent of two water body masses with contrasting SST (Fig. 4, Supporting information). SST also decreased with latitude (LME, $\text{coef}=-0.28^\circ\text{C}$, $\text{SE}=0.04$, 95% CI [-0.4; -0.2], $\text{df}=132$, $p < 0.0001$) and increased with longitude (LME, $\text{coef}=0.13^\circ\text{C}$, $\text{SE}=0.02$, 95% CI [0.1; 0.2], $\text{df}=139$, $p < 0.0001$).

Migratory strategies and reproductive success

Although migratory strategies varied greatly among individuals in terms of wintering area and distance covered (Fig. 3), the winter home range area ($\text{coef}=-0.65$ scaled km^2 , $\text{SE}=4.16$, 95% CI [-8.9; 7.5], $\text{df}=167$, $p=0.9$) and movement rate ($\text{coef}=0.13$, $\text{SE}=0.16$, 95% CI [-0.19; 0.44], $\text{df}=165$, $p=0.4$) of individuals did not predict the DEE. The daily movement rate was not related to the time spent flying (LME, $\text{coef}=0.380 \text{ h day}^{-1}$, $\text{SE}=2.895$, 95% CI [-5.4; 6.0], $\text{df}=164$, $p=0.9$), suggesting that individuals did not increase their flying time to cover greater distances but

instead relied on more directional movement or favourable wind conditions to travel rapidly (Amélineau et al. 2023).

The reproductive success of individuals did not vary over the distance from the population's winter range centre ($n=105$, GLME, $\text{coef}=0.33$, $\text{SE}=0.32$, 95% CI [-0.74; 2.63], R^2 marginal=0.002, $p=0.3$; Fig. 1).

Discussion

Using a well-studied model species for avian migration, we tested the predictions of the abundant centre hypothesis that population density, performance and fitness are higher at the centre of the population range. To do that we estimated energy expenditure derived from a proxy of activity as an indicator of individual performance and analyzed an extensive tracking dataset spanning over 11 years. To the best of our knowledge, this is the first time an empirical study based on tracking of individual energy expenditure, a key currency in nature, is used to investigate drivers of range limits. Although density did increase towards the range centre, the energy expenditure of individuals was higher at the centre of the range and decreased towards the edge, thus challenging

Table 1. Results of linear mixed models estimating daily energy expenditure (DEE) and its components (flying, foraging and resting activities) as a function of distance from the centre to the edge of the population's winter range ('Distance'), while accounting for the average day length ('Day.length') and 'Sex'. The sampling year and the individual were included as random factors in all models.

| Response variable | Fixed factors | <i>b</i> | SE | df | 95% CI | <i>p</i> | R^2 |
|-------------------------------|----------------|-----------|----------|-----|--------------------|----------|-------|
| DEE (kJ) | Distance (km) | -0.026 | 0.005 | 160 | [-0.036; -0.016] | <0.0001 | 0.18 |
| | Day.length (h) | 7.04 | 3.85 | 164 | [-0.81; 14.67] | 0.07 | |
| | Sex | -20.97 | 9.44 | 112 | [-39.48; -2.59] | 0.02 | |
| Flying activity (h) | Distance (km) | -0.0004 | 0.0001 | 143 | [-0.0005; -0.0002] | <0.0001 | 0.21 |
| | Day.length (h) | -0.11 | 0.05 | 172 | [0.02; 0.20] | 0.02 | |
| | Sex | -0.02 | 0.10 | 156 | [-0.22; 0.18] | 0.8 | |
| | | | | | | | |
| Foraging activity (h) | Distance (km) | 0.0004 | 0.0001 | 147 | [0.0002; 0.0005] | <0.0001 | 0.21 |
| | Day.length (h) | 0.18 | 0.05 | 168 | [0.08; 0.29] | <0.001 | |
| | Sex | -0.28 | 0.12 | 109 | [-0.52; -0.04] | 0.03 | |
| | | | | | | | |
| Resting on water activity (h) | Distance (km) | -0.000004 | 0.000001 | 142 | [-0.0002; 0.0002] | 0.9 | 0.14 |
| | Day.length (h) | -0.30 | 0.06 | 169 | [-0.42; -0.17] | <0.0001 | |
| | Sex | 0.30 | 0.14 | 109 | [0.03; 0.57] | 0.003 | |
| | | | | | | | |

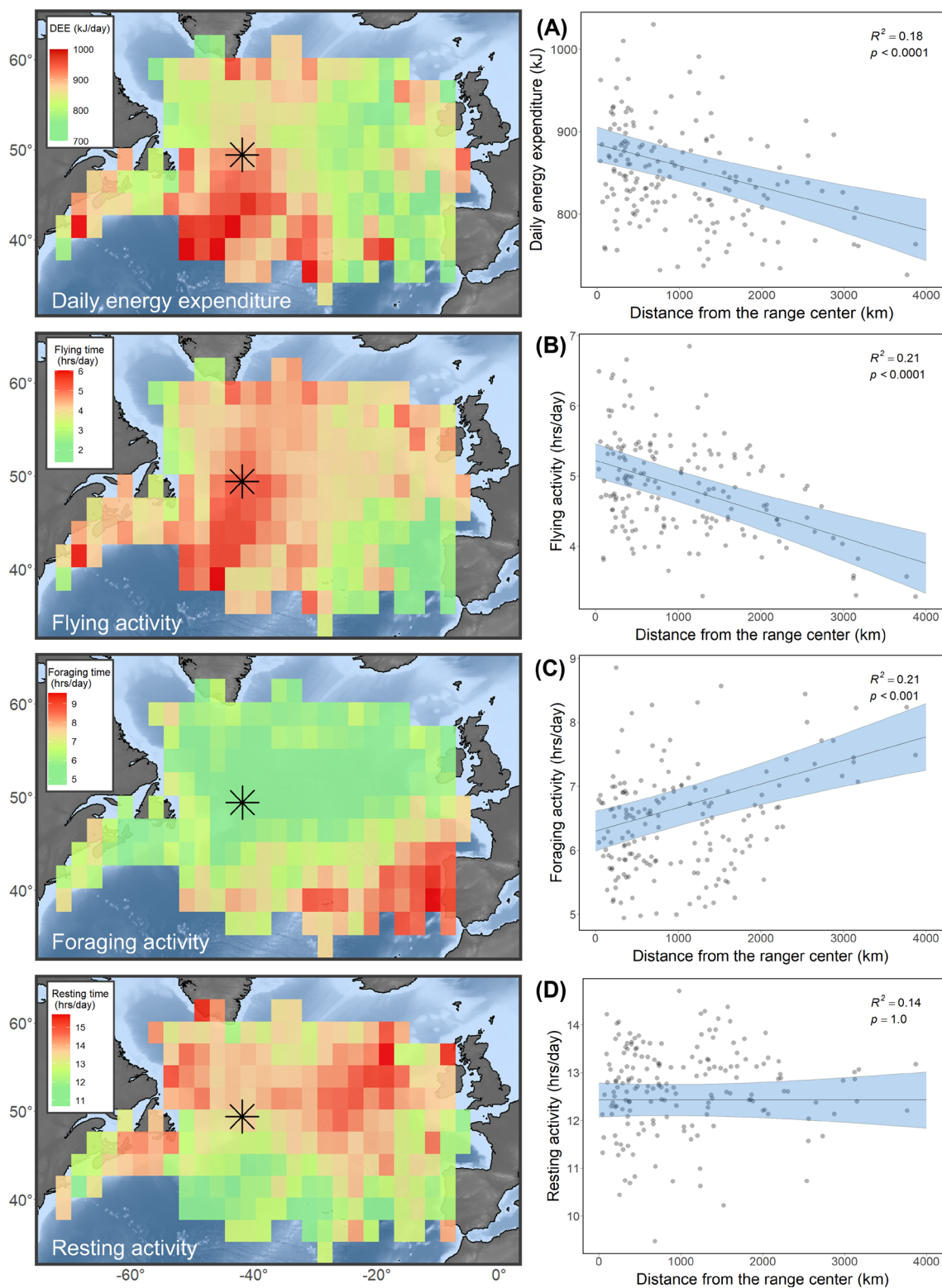


Figure 5. Heat maps illustrating the spatial heterogeneity in (A) daily energy expenditures (kJ day^{-1}), (B) time spent flying (h day^{-1}), (C) time spent foraging (h day^{-1}) and (D) time spent resting (h day^{-1}) experienced by individuals during winter, with corresponding model predictions over the distance from the centroid of the population's winter distribution. Darker grid cells (2.5° latitude \times 2.5° longitude) indicate areas of higher values for each variable. The black star (*) shows the centroid of the population's winter range ($n = 21$ 510 positions).

the assumption of the abundant centre hypothesis that individuals' performance decrease towards the range periphery. DEE was best predicted by the spatial proximity to the core of the population's wintering range, and not by the home range size or movement rate of wintering individuals. This spatial variation in winter energy expenditure, however, did not translate into consequences on the annual fitness of individuals in the following breeding season, as we did not find differences in the reproductive success of individuals wintering at the centre versus the periphery of the wintering range. We suggest that conditions at the centre of the range likely provide high energy intake, allowing individuals to compensate for higher energy expenditure, as the difference in energy expenditure between the centre and edge of the range (-117 kJ day^{-1}) would lead to rapid mass loss and mortality at the centre within a few days if not offset by higher energy intake. Thus, we argue that the dense centre of the range is characterized by high resource acquisition, high competition, high time spent flying and high energy expenditure compared to the edge.

Spatial variation in reproductive success

Annual fitness (reproductive success) did not vary over the winter range. Even if higher energy expenditure in winter can lead to lower body mass upon arrival, this is presumably buffered by the conditions experienced at the colony site during the pre-laying and the breeding season, allowing individuals to still invest successfully into breeding by building up stores during that period, and explaining the absence of an impact on reproductive success (Grecian et al. 2019, Pelletier et al. 2020). For instance, common eiders *Somateria mollissima* compensate for harsh winter conditions via positive effects on body condition, arrival date and earlier breeding onset, so that overwintering conditions do not negatively impact reproductive success (Steenweg et al. 2022). As income-breeders, kittiwakes are particularly reliant on energy available at the vicinity of the colony to be directly invested into reproduction, with favourable feeding conditions advancing the endocrine preparation for breeding (Whelan et al. 2021). Overall, and in opposition to the premise of the abundant centre hypothesis, the centre of the range does not necessarily provide more favourable conditions, but can rather result in both higher energy loss and gain than at the range periphery.

High population density at the range centre

Wintering individuals were clustered around the centre of the kittiwake population's range and decreased towards the edge, as predicted by the abundant centre hypothesis. The range centre, in the western part of the North Atlantic, overlaps with a biologically productive area where the oceanographic circulation is believed to provide favourable foraging conditions (Scales et al. 2014, Hátún et al. 2016). This area is a wintering hotspot for multiple species with similar diet, including an estimated 4.5 million wintering kittiwakes (Frederiksen et al. 2012, Davies et al. 2021). Such high density of predators

can create competition potentially depleting local prey density and force individuals to increase the time searching for food, and consequently their DEE (Fayet et al. 2021). While individuals in the centre of the range spent less time actively foraging, they spent more time flying each day. A similar scenario plays out during the breeding season when competition for marine resources can be particularly strong near the colony site, creating growing 'halo effects' when preferred prey are gradually depleted from closer foraging areas (Ashmole 1963, Elliott et al. 2009). However, competition is expected to decrease after the breeding season when individuals are not under the central-place foraging constraint anymore and can move freely to more favourable locations (Jessopp et al. 2020). The ideal free distribution theory predicts that competitors should disperse to higher-quality foraging areas due to increased competition under higher density (Sutherland 1983). In marine systems, however, individual distribution rarely reaches this equilibrium, notably because of constraints on information of prey movement and individuals using the foraging behaviour of other predators as visual cues to locate prey patches (the 'local enhancement' strategy; Fauchald 2009). Regardless, the spatial variation in energy expenditure implies that survival, and thus population demography, may be linked to wintering conditions, as originally proposed by Lack (1966), rather than by population regulation during the breeding season (but see Ashmole 1963).

Decreasing energetic performance towards the range centre

Wintering towards the centre of the population's range entailed higher energy expenditure, implying that individuals at the centre are potentially more vulnerable to changes in feeding conditions than those at the edge, if they lead to elevated energy expenditure or reduced energy intake. As up to 80% of Atlantic kittiwakes are wintering near the centre of the range where energy expenditure is higher (Frederiksen et al. 2012), a decrease in prey availability could have strong consequences on the species demography, without necessarily constraining the range limits. Indeed, it has been suggested that edge individuals may still benefit from patches of favourable habitat, even if the favourable habitat is sparse towards the range's margins (Sexton et al. 2009). Alternatively, more experienced, or higher-quality individuals may be more efficient at extracting energy from their environment when resources are scarcer, while still maintaining low energy expenditure (van Noordwijk and de Jong 1986). Lower energy expenditure at the edge of the range could then reflect lower food supply, limiting the ability of individuals to spend energy, potentially driving range limits. Overall, the absence of spatial variation in breeding success across the wintering range suggests that individuals at the margins are able to use alternative strategies to exploit environments with different energy constraints. This could facilitate the population's resilience to eventual changes in feeding conditions over the wintering range, for instance through a potential range shift towards alternative wintering areas at the range's

margin. Such range shift has not yet been observed in that population, as a previous study on the same dataset showed that individuals remained faithful to their wintering areas during the 11 years of the study period (Léandri-Breton et al. 2021).

The higher energy expenditure of individuals wintering at the centre of the range is partly driven by the higher flying activity in this area, with individuals spending nearly twice more time in flight than at the range edge. Flight is inherently a locomotion mode associated with elevated energy expenses (Pennycuick 1975, Elliott et al. 2013), but with costs that are highly dependent on wind conditions experienced in flight. Oceans are open environments characterized by stronger wind than over land (Felicísimo et al. 2008), and seabirds are adapted to these conditions (Watanabe 2016). Although kittiwakes can benefit from prevailing wind during directional movements such as during migration (Amélineau et al. 2023), they primarily rely on flapping flight, making them less able to capitalize on varying wind conditions compared to dynamic soaring species (Collins et al. 2020, Kempton et al. 2022). For species using flapping flight, unfavourable winds, such as headwinds or crosswinds, demand increased flying effort through either stronger wingbeats or longer flight times (Hedenström and Alerstam 1995, Hedenström et al. 2002). Similar to other flapping birds like gulls and terns, kittiwakes adapt to high wind speeds by intensifying wingbeat effort (Ainley et al. 2015, Collins et al. 2020). Consequently, higher wind intensities in oceanic staging areas likely lead to increased flight effort to counteract headwinds or drift. Consistent with this, our findings show that kittiwake flight activity corresponds spatially with regions of higher wind intensity, suggesting increased flying time in these areas.

Individuals at the centre of the range were flying more, but also spending less time in active foraging compared to those at the edge of the range. Potentially, this indicates favourable foraging conditions at the range centre, as individuals required less foraging time to maintain energy balance, whereas the extended period of active foraging at the range's edge suggests lower energy gain per unit of foraging time in this area. However, the persistent winds at the range centre can also affect seabirds' ability to forage, with increased wave height and seawater turbidity affecting the detectability and accessibility of prey (Real et al. 2022). For instance, European shags *Phalacrocorax aristotelis* forage less under high wind speed conditions (Lewis et al. 2015), with a potentially strong impact on winter mortality (Frederiksen et al. 2008). We indeed found a decrease in foraging activity at the centre of the population's range where individuals are experiencing higher wind intensity. Starvation through inability to forage effectively has been pointed out as the main cause of mass mortality events of wintering seabirds during prolonged periods of severe weather in the North Atlantic Ocean (Clairbaux et al. 2021). These 'winter wrecks' disproportionately affect species relying on flapping flight, with alcids, cormorants and kittiwakes being the most abundant seabirds found dead in an emaciated condition (Harris and Wanless 1996, Gaston 2004, Morley et al. 2016). In the North Atlantic, the highest exposure of seabirds to cyclones occurs in the western part of

the oceanic basin (Clairbaux et al. 2021), directly overlapping with the core of the kittiwake population range.

Latitudinal variations in environmental factors

Kittiwakes also experienced contrasting environmental conditions along a latitudinal gradient, with the northern wintering distribution characterized by stronger wind and colder sea surface temperatures. Furthermore, the shorter day length in winter at these high latitudes can limit their ability to balance their energy budget due to less time available for foraging. This is because kittiwakes are diurnal and their foraging and flying activity is essentially restricted to the daylight and twilight periods, while the night period at sea is spent resting on the water (Daunt et al. 2002, McKnight et al. 2011). Moreover, the prolonged night duration can entail substantial additional energy costs while kittiwakes are resting on the water (Humphreys et al. 2007). For endothermic species, heat loss via conduction is indeed significantly higher in the water than in the air (Croll and McLaren 1993) and thermoregulation costs of resting on the water were thus included in our energy expenditure formula. Consequently, the higher wind intensity, colder temperature and reduced day length at high latitudes can contribute to constraining the northern limit of the population's range through both a reduced time available to forage and increased thermoregulation costs while resting (Garthe et al. 2012). Meanwhile, the southern edge of the wintering distribution corresponds roughly to the beginning of the warm, highly stratified waters of the central Atlantic, south of approximately 35°N, which are characterized by low biological productivity (Vereshchaka et al. 2023). Although this could contribute to limiting foraging ability of kittiwakes at the southern edge, no such effects were detected in the estimates of DEE or activity estimates, which showed no distinct spatial patterns in this region.

In this study, we used an approach based on the activity budget of free-ranging animals to track individuals' energy expenditure over an 11-year period, therefore incorporating the behavioural response of individuals to biotic and abiotic constraints they are experiencing. Our results illustrate that performance does indeed differ predictably between the centre and the periphery of the wintering range, although the centre of the range does not necessarily provide better performance overall, but can rather result in a strong tradeoff between high energy loss and potentially high energy gain. This suggests that potential deteriorations in feeding conditions could have disproportionate consequences on individuals at the dense range centre, leading to dire effects on the population demography. However, we did not find differences in reproductive success between individuals wintering at the centre versus at the edge of their wintering range during the study period. Maintaining their energy balance is critical for all organisms and is particularly challenging for those living in harsh and unpredictable environmental conditions. Our study provides empirical indications to rethink the common assumption that individuals at the centre of the range benefit from better conditions overall and are consequently less vulnerable than those living at the periphery.

Acknowledgements – We are thankful to the Norwegian Institute for Nature Research, and the Norwegian Polar Institute, as well as the French Polar Institute and Alfred Wegener Institute for Polar and Marine Research (AWIPEV) for their logistical support in the field and to the Centre de la Science de la Biodiversité du Québec for their help with travel logistics. We are very grateful to Dr Anna Hargreaves and Dr Dominique Gravel for their revisions of preliminary versions of this manuscript and to the Krykkjefjellet field teams without whom this study would not have been possible, including Alexandre Corbeau, Céline Clément Chastel, Pauline Dhainaut, Hilde Dørum, Anna Lippold and Solveig Nilssen.

Funding – This study was financially and logistically supported by the French Polar Institute (IPEV project 330 to OC) and the Norwegian Research Council (Arctic Field Grant no. 310662 to DJLB) with additional funding provided by the Polar Knowledge Canada (Northern Scientific Training Program), the Fonds de Recherche du Québec Nature et Technologies – FRQNT (International Internship no. 294040 to DJLB), Mitacs (Globalink Research Award no. IT27173 to DJLB), SEATRACK-project (Norway, <https://seapop.no/en/seatrack/>), the Fram Centre flagship ‘Climate Change in Fjord and Coast’ (grant no. 232019 to BM) and McGill University (GREAT Award; Mobility Award; PGSS – Graduate Excellence Award to DJLB). DJLB was funded by the Weston Family Foundation (Northern Research Award), the Natural Sciences and Engineering Research Council of Canada – NSERC (Canada Graduate Scholarship – Doctoral; Michael Smith Supplement) and the FRQNT (Doctoral Scholarship).

Permits – This study was approved by the Norwegian Food Safety Authority (FOTS ID 2086, 3319, 4169, 6291, 6348, 8482, 15603, 15611, 19970), the Governor of Svalbard and the McGill University Animal Care Committee.

Author contributions

Don-Jean Léandri-Breton: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Kyle H. Elliott:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (supporting); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (lead). **Arnaud Tarroux:** Data curation (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Pierre Legagneux:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **William Jouanneau:** Investigation (lead); Methodology (supporting); Writing – review and editing (equal). **Françoise Amélineau:** Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Frédéric Angelier:** Investigation (supporting); Writing – review and editing (equal). **Pierre Blévin:** Investigation (supporting); Writing – review and editing (equal). **Vegard Sandøy Bråthen:** Data curation (equal); Writing – review and editing (equal). **Per Fauchald:** Data curation (equal); Writing – review and editing (equal). **Geir W. Gabrielsen:** Project administration (supporting); Resources (supporting); Writing – review and editing (equal). **Aurélié Goutte:** Investigation (supporting); Writing – review and editing (equal). **Sabrina Tartu:** Investigation

(supporting); Writing – review and editing (equal). **Børge Moe:** Data curation (equal); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Writing – review and editing (equal). **Olivier Chastel:** Conceptualization (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07498>.

Data availability statement

Data are available from the Norwegian Polar Institute: <https://doi.org/10.21334/npolar.2024.ffb156cc> (Léandri-Breton et al. 2024b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Ainley, D. G., Porzig, E., Zajanc, D. and Spear, L. B. 2015. Seabird flight behavior and height in response to altered wind strength and direction. – *Mar. Ornithol.* 43: 25–36.
- Alexander, J. M., Atwater, D. Z., Colautti, R. I. and Hargreaves, A. L. 2022. Effects of species interactions on the potential for evolution at species’ range limits. – *Philos. Trans. R. Soc. B* 377: 20210020.
- Amélineau, F. et al. 2023. Multi-colony tracking of two pelagic seabirds with contrasting flight capability illustrates how wind-scapes shape migratory movements at an ocean-basin scale. – *Ecography* 2023: e06496.
- Anderson, C. E. and Alexander, K. A. 2020. Uncharted waters: climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals. – *Global Change Biol.* 26: 4284–4301.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. – *Ibis* 103b: 458–473.
- Bartoń, K. 2023. Mumin: multi-model inference. – R package ver. 1.47.05.
- Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Blévin, P., Tartu, S., Ellis, H. I., Chastel, O., Bustamante, P., Parenteau, C., Herzke, D., Angelier, F. and Gabrielsen, G. W. 2017. Contaminants and energy expenditure in an Arctic seabird: organochlorine pesticides and perfluoroalkyl substances are associated with metabolic rate in a contrasted manner. – *Environ. Res.* 157: 118–126.
- Bråthen, V. S., Moe, B., Amélineau, F., Ekker, M., Fauchald, P., Helgason, H. H., Johansen, M. K., Merkel, B., Tarroux, A., Åström, J. and Strøm, H. 2021. An automated procedure (v2.0) to obtain positions from light-level geolocators in large-scale

- tracking of seabirds. A method description for the SEATRACK project. NINA report 1893. – Norwegian Institute for Nature Research.
- Brooks, M. E., Kristensen, K., Benthem, K. J. V., Magnusson, A. S., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378.
- Brower, L. P., Kust, D. R., Rendon-Salinas, E., Garcia-Serrano, E., Kust, K. R., Miller, J., Fernandez del Rey, C. and Pape, K. 2004. Catastrophic winter storm mortality of monarch butterflies during January 2002. – In: Oberhauser, K. S. and Solenskyj, M. J. (eds), *The monarch butterfly: biology and conservation*. Cornell Univ. Press, pp. 151–156.
- Calenge, C. 2006. The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Modell. 197: 516–519.
- Camphuysen, C. J., Berrevoets, C. M., Cremers, H. J. W. M., Dekinga, A., Dekker, R., Ens, B. J., Van Der Have, T. M., Kats, R. K. H., Kuiken, T., Leopold, M. F., Van Der Meer, J. and Piersma, T. 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. – Biol. Conserv. 106: 303–317.
- Clairbaux, M. et al. 2021. North Atlantic winter cyclones starve seabirds. – Curr. Biol. 31: 3964–3971.e3.
- Collins, P. M., Green, J. A., Elliott, K. H., Shaw, P. J. A., Chivers, L., Hatch, S. A. and Halsey, L. G. 2020. Coping with the commute: behavioural responses to wind conditions in a foraging seabird. – J. Avian Biol. 2020: e02057.
- Coulson, J. C. and Porter, J. M. 1985. Reproductive success of the kittiwake. – Ibis 127: 450–466.
- Croll, D. A. and McLaren, E. 1993. Diving metabolism and thermoregulation in common and thick-billed murre. – J. Comp. Physiol. B 163: 160–166.
- Dallas, T., Decker, R. R. and Hastings, A. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. – Ecol. Lett. 20: 1526–1533.
- Daunt, F., Benvenuti, S., Harris, M. P., Dall’Antonia, L., Elston, D. A. and Wanless, S. 2002. Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. – Mar. Ecol. Prog. Ser. 245: 239–247.
- Davidson, S. C. et al. 2020. Ecological insights from three decades of animal movement tracking across a changing Arctic. – Science 370: 712–715.
- Davies, T. E. et al. 2021. Multispecies tracking reveals a major seabird hotspot in the North Atlantic. – Conserv. Lett. 14: e12824.
- Dingle, H. and Drake, A. V. 2007. What is migration? – BioScience 57: 113–121.
- Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P. and Green, J. A. 2020. A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. – Sci. Rep. 10: 5993.
- Dunn, R. E., Green, J. A., Wanless, S., Harris, M. P., Newell, M. A., Bogdanova, M. I., Horswill, C., Daunt, F. and Matthiopoulos, J. 2022. Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle. – Funct. Ecol. 36: 1612–1626.
- Elliott, K. H., Woo, K. J., Gaston, A. J., Benvenuti, S., Dall’Antonia, L. and Davoren, G. K. 2009. Central-place foraging in an arctic seabird provides evidence for Storer–Ashmole’s halo. – Auk 126: 613–625.
- Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R. and Davoren, G. K. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. – Proc. Natl Acad. Sci. USA 110: 9380–9384.
- Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. – Mar. Ecol. Prog. Ser. 391: 139–151.
- Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M. and Guilford, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. – Behav. Ecol. 27: 1061–1072.
- Fayet, A. L., Clucas, G. V., Anker-Nilssen, T., Syposz, M. and Hansen, E. S. 2021. Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. – J. Anim. Ecol. 90: 1152–1164.
- Felicísimo, A. M., Muñoz, J. and González-Solis, J. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. – PLoS One 3: e2928.
- Fort, J., Porter, W. P. and Grémillet, D. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. – J. Exp. Biol. 212: 2483–2490.
- Frederiksen, M., Daunt, F., Harris, M. P. and Wanless, S. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. – J. Anim. Ecol. 77: 1020–1029.
- Frederiksen, M. et al. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. – Divers. Distrib. 18: 530–542.
- Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. – J. Avian Biol. 30: 116.
- Gabrielsen, G. W., Mehlum, F. and Karlsen, H. E. 1988. Thermoregulation in four species of arctic seabirds. – J. Comp. Physiol. B 157: 703–708.
- Garthe, S., Ludynia, K., Hüppop, O., Kubetzki, U., Meraz, J. F. and Furness, R. W. 2012. Energy budgets reveal equal benefits of varied migration strategies in northern gannets. – Mar. Biol. 159: 1907–1915.
- Gaston, A. J. 2004. *Seabirds: a natural history*. – Yale Univ. Press.
- Gaston, K. J. and Sheffield, S. 2009. Geographic range limits: achieving synthesis. – Proc. R. Soc. B 276: 1395–1406.
- Goutte, A., Barbraud, C., Herzke, D., Bustamante, P., Angelier, F., Tartu, S., Clément-Chastel, C., Moe, B., Bech, C., Gabrielsen, G. W., Bustnes, J. O. and Chastel, O. 2015. Survival rate and breeding outputs in a high Arctic seabird exposed to legacy persistent organic pollutants and mercury. – Environ. Pollut. 200: 1–9.
- Grecian, W. J., Williams, H. J., Votier, S. C., Bearhop, S., Cleasby, I. R., Grémillet, D., Hamer, K. C., Le Nuz, M., Lescroël, A., Newton, J., Patrick, S. C., Phillips, R. A., Wakefield, E. D. and Bodey, T. W. 2019. Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. – Front. Ecol. Evol. 7: 214.
- Greenberg, R. and Marra, P. P. 2005. *Birds of two worlds: the ecology and evolution of migration*. – Johns Hopkins Univ. Press.
- Grosbois, V. and Thompson, P. M. 2005. North Atlantic climate variation influences survival in adult fulmars. – Oikos 109: 273–290.
- Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. and Perrins, C. 2011. A dispersive migration in the Atlantic puffin and its implications for migratory navigation. – PLoS One 6: e21336.

- Guo, Q., Taper, M., Schoenberger, M. and Brandle, J. 2005. Spatial-temporal population dynamics across species range: from centre to margin. – *Oikos* 108: 47–57.
- Hargreaves, A. L., Samis, K. E. and Eckert, C. G. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. – *Am. Nat.* 183: 157–173.
- Harris, M. P. and Wanless, S. 1996. Differential responses of guillemot *Uria aalge* and shag *Phalacrocorax aristotelis* to a late winter wreck. – *Bird Study* 43: 220–230.
- Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. and Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. – *J. Anim. Ecol.* 80: 4–18.
- Hátún, H., Lohmann, K., Matei, D., Jungclaus, J. H., Pacariz, S., Bersch, M., Gislason, A., Ólafsson, J. and Reid, P. C. 2016. An inflated subpolar gyre blows life toward the northeastern Atlantic. – *Prog. Oceanogr.* 147: 49–66.
- Hedenström, A. and Ålerstam, T. 1995. Optimal flight speed of birds. – *Philos. Trans. R. Soc. B* 348: 471–487.
- Hedenström, A., Ålerstam, T., Green, M. and Gudmundsson, G. A. 2002. Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. – *Behav. Ecol. Sociobiol.* 52: 308–317.
- Hengeveld, R. and Haeck, J. 1982. The distribution of abundance. I. Measurements. – *J. Biogeogr.* 9: 303.
- Hijmans, R. 2024. Geosphere: spherical trigonometry. – R package ver. 1.5-14.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – *Proc. Natl Acad. Sci. USA* 106: 19659–19665.
- Humphreys, E. M., Wanless, S. and Bryant, D. M. 2007. Elevated metabolic costs while resting on water in a surface feeder: the black-legged kittiwake *Rissa tridactyla*. – *Ibis* 149: 106–111.
- Jessopp, M., Arneill, G. E., Nykänen, M., Bennison, A. and Rogan, E. 2020. Central place foraging drives niche partitioning in seabirds. – *Oikos* 129: 1704–1713.
- Jodice, P. G. R., Roby, D. D., Suryan, R. M., Irons, D. B., Kaufman, A. M., Turco, K. R. and Visser, G. H. 2003. Variation in energy expenditure among black-legged kittiwakes: effects of activity-specific metabolic rates and activity budgets. – *Physiol. Biochem. Zool.* 76: 375–388.
- Kautz, T. M., Belant, J. L., Beyer, D. E., Strickland, B. K. and Duquette, J. F. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: evidence for a late-winter survival bottleneck. – *Ecol. Evol.* 10: 1666–1677.
- Kempton, J. A., Wynn, J., Bond, S., Evry, J., Fayet, A. L., Gillies, N., Guilford, T., Kavelaars, M., Juárez-Martínez, I., Padgett, O., Rutz, C., Shoji, A., Syposz, M. and Taylor, G. K. 2022. Optimization of dynamic soaring in a flap-gliding seabird affects its large-scale distribution at sea. – *Sci. Adv.* 8: eabo0200.
- Kock, R. A., Orynbayev, M., Robinson, S., Zuther, S., Singh, N. J., Beauvais, W., Morgan, E. R., Kerimbayev, A., Khomenko, S., Martineau, H. M., Rystaeva, R., Omarova, Z., Wolfs, S., Hawotte, F., Radoux, J. and Milner-Gulland, E. J. 2018. Saigas on the brink: multidisciplinary analysis of the factors influencing mass mortality events. – *Sci. Adv.* 4: eaao2314.
- Lack, D. 1966. Population studies of birds. – Clarendon Press.
- Léandri-Breton, D. J., Tarroux, A., Elliott, K. H., Legagneux, P., Angelier, F., Blévin, P., Bråthen, V. S., Fauchald, P., Goutte, A., Jouanneau, W., Tartu, S., Moe, B. and Chastel, O. 2021. Long-term tracking of an Arctic-breeding seabird indicates high fidelity to pelagic wintering areas. – *Mar. Ecol. Prog. Ser.* 676: 205–218.
- Léandri-Breton, D. J., Elliott, K. H., Tarroux, A., Moe, B., Jouanneau, W., Amélineau, F., Angelier, F., Blévin, P., Sandøy Bråthen, V., Fauchald, P., Gabrielsen, G. W., Goutte, A., Parenteau, C., Tartu, S., Legagneux, P. and Chastel, O. 2024a. Individual quality overwrites carry-over effects across the annual cycle of a long-distance migrant. – *J. Anim. Ecol.* 93: 1197–1211.
- Léandri-Breton, D.-J., Elliott, K. H., Tarroux, A., Legagneux, P., Jouanneau, W., Amélineau, F., Angelier, F., Blévin, P., Bråthen, V. S., Fauchald, P., Gabrielsen, G. W., Goutte, A., Tartu, S., Moe, B. and Chastel, O. 2024b. Data from: Low energy expenditure at the edge of a seabird's winter range suggests energy underpins the Abundant Centre Hypothesis. – Norwegian Polar Institute. <https://doi.org/10.21334/npolar.2024.fbb156cc>
- Lewis, S., Phillips, R. A., Burthe, S. J., Wanless, S. and Daunt, F. 2015. Contrasting responses of male and female foraging effort to year-round wind conditions. – *J. Anim. Ecol.* 84: 1490–1496.
- Lovvorn, J. R. 2007. Thermal substitution and aerobic efficiency: measuring and predicting effects of heat balance on endotherm diving energetics. – *Philos. Trans. R. Soc. B* 362: 2079–2093.
- McKnight, A., Irons, D. B., Allyn, A. J., Sullivan, K. M. and Suryan, R. M. 2011. Winter dispersal and activity patterns of postbreeding black-legged kittiwakes *Rissa tridactyla* from Prince William Sound, Alaska. – *Mar. Ecol. Prog. Ser.* 442: 241–253.
- Morley, T. I., Fayet, A. L., Jessop, H., Veron, P., Veron, M., Clark, J. and Wood, M. J. 2016. The seabird wreck in the Bay of Biscay and South-Western Approaches in 2014: a review of reported mortality. – *Seabird* 29: 22–38.
- Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R. and Steinheim, G. 2001. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. – *Nature* 410: 1096–1099.
- Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – *Methods Ecol. Evol.* 4: 133–142.
- Newman, S. H., Chmura, A., Converse, K., Kilpatrick, A. M., Patel, N., Lammers, E. and Daszak, P. 2007. Aquatic bird disease and mortality as an indicator of changing ecosystem health. – *Mar. Ecol. Prog. Ser.* 352: 299–309.
- Newton, I. 2008. The migration ecology of birds. – Elsevier Academic Press.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. and Ratcliffe, L. M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. – *Proc. R. Soc. B* 271: 59–64.
- O'Connor, C. M., Norris, D. R., Crossin, G. T. and Cooke, S. J. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. – *Ecosphere* 5: 1–11.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Patterson, A. 2022. seabiRds: prepares biologging data for analysis and upload to the lab database. – R package ver. 0.1.0.
- Pelletier, D., Seyer, Y., Garthe, S., Bonnefoi, S., Phillips, R. A. and Guillemette, M. 2020. So far, so good... Similar fitness consequences and overall energetic costs for short and long-distance migrants in a seabird. – *PLoS One* 15: e0230262.
- Pennycook, C. J. 1975. Mechanics of flight. – In: Farner, D. S. and King, J. R. (eds), *Avian biology*, vol. 5. Academic Press, pp. 1–75.
- Pironon, S., Papuga, G., Villellas, J., Angert, A. L., García, M. B. and Thompson, J. D. 2017. Geographic variation in genetic

- and demographic performance: new insights from an old biogeographical paradigm. – *Biol. Rev.* 92: 1877–1909.
- Real, E., Orol, D., Bertolero, A., Igual, J. M., Sanz-Aguilar, A., Genovart, M., Hidalgo, M. and Tavecchia, G. 2022. It's not all abundance: detectability and accessibility of food also explain breeding investment in long-lived marine animals. – *PLoS One* 17: 1–15.
- Sagarin, R. D., Gaines, S. D. and Gaylord, B. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. – *Trends Ecol. Evol.* 21: 524–530.
- Santini, L., Pironon, S., Maiorano, L. and Thuiller, W. 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. – *Ecography* 42: 696–705.
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W. and Votier, S. C. 2014. On the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. – *J. Appl. Ecol.* 51: 1575–1583.
- Schmidt-Nielsen, K. 1997. *Animal physiology: adaptation and environment.* – Cambridge Univ. Press.
- Schneider, J. E. 2004. Energy balance and reproduction. – *Physiol. Behav.* 81: 289–317.
- Sexton, J. P., McIntyre, P. J., Angert, A. L., Rice, K. J., Sexton, J. P., McIntyre, P. J., Angert, A. L. and Rice, K. J. 2009. Evolution and ecology of species range limits. – *Annu. Rev. Ecol. Evol. Syst.* 40: 415–436.
- Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. 2013. Energy landscapes shape animal movement ecology. – *Am. Nat.* 182: 298–312.
- Steenweg, R. J., Crossin, G. T., Hennin, H. L., Gilchrist, H. G. and Love, O. P. 2022. Favorable spring conditions can buffer the impact of winter carryover effects on a key breeding decision in an Arctic-breeding seabird. – *Ecol. Evol.* 12: e8588.
- Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. – *J. Anim. Ecol.* 52: 821.
- van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. – *Am. Nat.* 128: 137–142.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*, 4th edn. – Springer.
- Vereshchaka, A. L., Mikaelyan, A. S., Piontkovski, S. A. and Lunina, A. A. 2023. A mesoplankton biomass decline in the central Atlantic coupled with an increase of surface temperature and an expansion of low-productive zones. – *Global Ecol. Biogeogr.* 32: 1365–1376.
- Watanabe, Y. Y. 2016. Flight mode affects allometry of migration range in birds. – *Ecol. Lett.* 19: 907–914.
- Whelan, S., Hatch, S. A., Benowitz-Fredericks, Z. M., Parenteau, C., Chastel, O. and Elliott, K. H. 2021. The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. – *Horm. Behav.* 127: 104874.
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., Yovovich, V. and Hebblewhite, M. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. – *Ecology* 96: 1741–1753.
- Woodworth, B. K., Wheelwright, N. T., Newman, A. E., Schaub, M. and Norris, D. R. 2017. Winter temperatures limit population growth rate of a migratory songbird. – *Nat. Commun.* 8: 14812.