Seasonal interactions and migratory behaviour across the annual life cycle of an Arctic-nesting seabird

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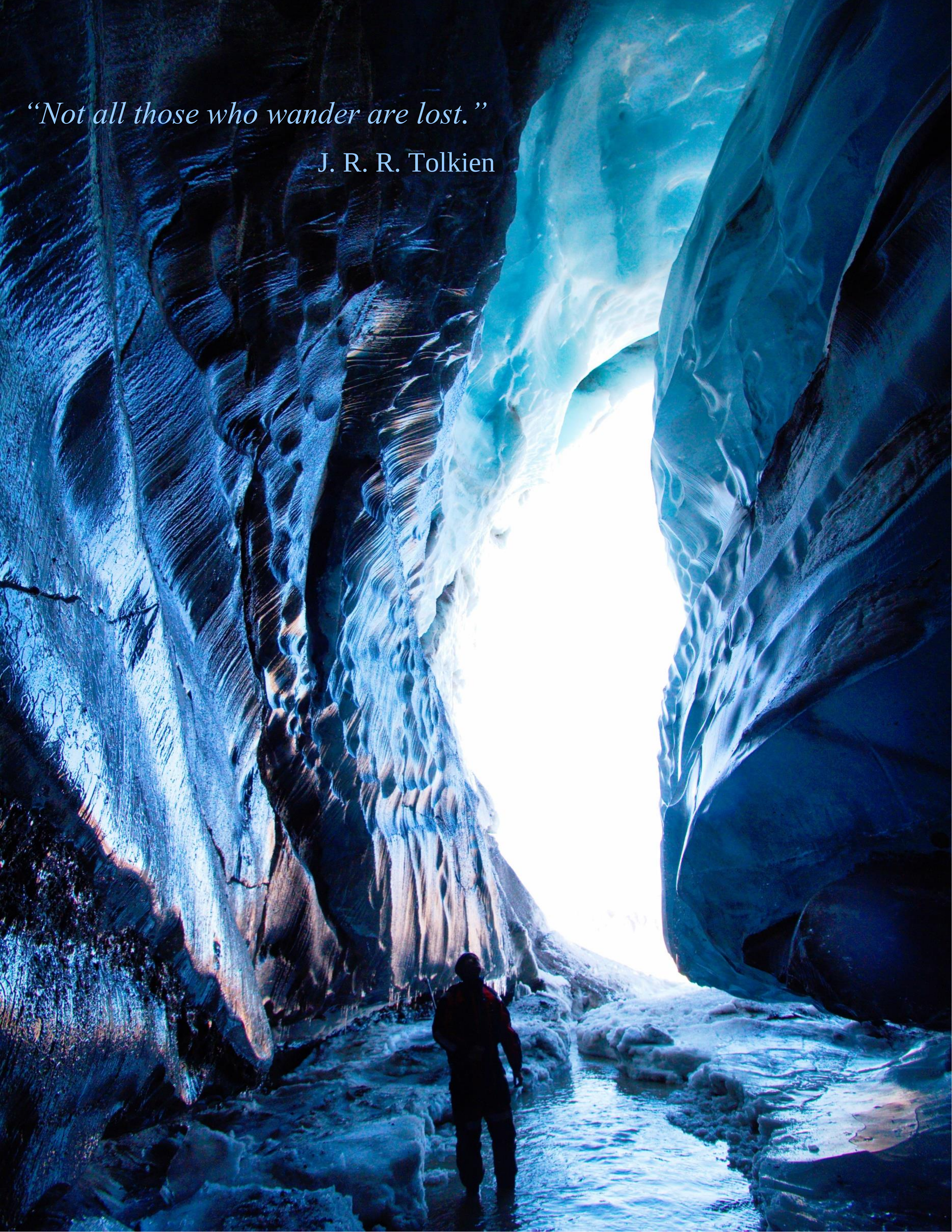

“Not all those who wander are lost.”

J. R. R. Tolkien

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ABSTRACT

Migration is one of nature's most impressive phenomena, with billions of animals travelling each year, sometimes over tremendous distances. By doing so, migrants are linking ecosystems as they transport energy, nutrients and contaminants between separate locations and change trophic interactions and energy flow within resident communities. Migrants typically have sequential life-history stages throughout their annual life cycle, with breeding and non-breeding stages connected by the migratory movement, and the fitness and survival of individuals relies on a successful integration of these stages across seasons. Decisions taken by individuals during one season can thus have downstream consequences on subsequent life stages and strongly impact population dynamics. However, the underlying mechanisms of such carry-over effects remain unclear, partly due to difficulties of tracking and monitoring individuals across their whole annual life cycle. In this thesis, I use up to 13 years of annual movement tracking and breeding monitoring to investigate seasonal interactions potentially leading to carry-over effects in a long-distance migrating seabird population of black-legged kittiwakes (*Rissa tridactyla*) breeding in the High Arctic (Svalbard, Norway). First, I estimate the movement consistency during the overwintering stage and show that the study population is characterized by high individual movement repeatability (site fidelity). Such specialization for key wintering areas suggests vulnerability to perturbations affecting environmental and feeding conditions and for carry-over effects to be structured spatially. Second, I assess the consequences of such site fidelity on the energy expenditure of individuals during winter using a time-activity budget approach. Individuals wintering closer to the population range centre had higher energy expenditure than those at the edge, but the higher energy expenditure did not carry consequences into fitness, suggesting it was compensated by higher energy intake. Third, I explore whether levels of poly- and perfluoroalkyl substances (PFAS) at the breeding site reflect the exposure during the previous wintering stage. The contamination burden was primarily acquired at lower latitudes and brought to the Arctic, suggesting that kittiwakes contribute to the biotransport of contaminants from more contaminated southern regions, with winter exposure carrying over to impact breeding. Finally, I combine a longitudinal approach with an experimental approach (experimentally induced reproductive failure) to separate true carry-over effects from cross-seasonal consistency in individual performance associated to individual quality. Piecewise path analyses revealed that individuals with better breeding performances (successful breeders) were also performing better in winter (lower energy expenditure), with positive interactions between breeding success in a given year, winter distribution and breeding success the subsequent year. Individual quality was thus dominant in determining seasonal interactions, although controlling experimentally for individual quality also revealed underlying carry-over effects. Thus, in this thesis I demonstrate that seasonal interactions in migratory animals are determined by a complex interplay between the costs of decisions taken by individuals at each stage of their annual cycle and their intrinsic quality influencing their ability to cope with these costs. By using a highly integrative approach, this thesis provides a unique perspective on the full annual cycle of migrants and the importance of individual processes in linking its different parts through spatial, phenological, energetic, physiological, and ecotoxicological processes. These results contribute to unravelling the multifaceted constraints migrants are facing, an essential step towards understanding the role of migration in connecting geographically distant ecosystems.

RÉSUMÉ

La migration est l’un des phénomènes naturels les plus impressionnants avec des milliards d’animaux voyageant chaque année, parfois sur des distances considérables. Les migrateurs ont un cycle de vie séquentiel, avec des étapes distinctes de reproduction et d’hivernage liées par des mouvements migratoires. La fitness et la survie des individus dépendent ainsi d'une intégration réussie de ces étapes dans le temps et les décisions prises par les individus au cours d'une saison peuvent donc avoir des conséquences sur les étapes de vie suivantes. Cependant, les mécanismes sous-jacents de ces effets reportés (« *carry-over effects* ») demeurent mal compris, en partie en raison des difficultés à suivre les individus tout au long de leur cycle de vie annuel. Dans cette thèse, j'utilise jusqu'à 13 années de suivi des mouvements annuels et de reproduction pour étudier les interactions saisonnières susceptibles d’entraîner des effets reportés au sein d'une population d'un oiseau marin migrateur, la mouette tridactyle (*Rissa tridactyla*) se reproduisant dans le Haut Arctique (Svalbard). Premièrement, j'estime la répétabilité de leurs mouvements hivernaux et démontre que la population étudiée est caractérisée par une forte fidélité spatiale. Une telle spécialisation pour des zones d'hivernage clés suggère une vulnérabilité aux perturbations affectant les conditions environnementales. Deuxièmement, j'évalue les conséquences de cette fidélité spatiale sur les dépenses énergétiques des individus pendant l'hiver en utilisant une approche de budget temps-activité. Les résultats indiquent que les individus hivernant plus près du centre de l'aire de répartition de la population ont des dépenses énergétiques plus élevées que ceux situés à la périphérie. Ces dépenses énergétiques plus élevées n'ont cependant pas de conséquences sur la fitness, ce qui suggère qu'elles sont compensées par un apport énergétique plus élevé. Troisièmement, j'étudie si les niveaux de substances poly- et perfluoroalkyles (PFAS) des individus sur le site de reproduction reflètent l’exposition sur le site d’hivernage. Je démontre que la charge en contaminants est principalement acquise à des latitudes basses et apportée en Arctique, les mouettes tridactyles contribuant donc au biotransport de contaminants provenant de régions méridionales plus contaminées. Enfin, je combine les approches longitudinale et expérimentale (c-à-d, un échec de reproduction induit expérimentalement) pour séparer les véritables effets reportés des interactions saisonnières émergeant de différences dans la qualité des individus. Des analyses de pistes démontrent que les individus ayant de meilleures performances reproductrices sont également plus performants en hiver (dépenses énergétiques plus faibles), révélant ainsi des interactions positives entre le succès reproducteur d'une année donnée, la distribution hivernale et le succès reproducteur de l'année suivante. La qualité individuelle est donc le principal facteur déterminant les interactions saisonnières, bien que le contrôle expérimental de la qualité individuelle révèle également des effets reportés sous-jacents. Dans son ensemble, cette thèse démontre que les interactions saisonnières chez les animaux migrateurs sont déterminées par une interaction complexe entre les coûts des décisions prises par les individus à chaque étape de leur cycle annuel et leur qualité intrinsèque influençant leur capacité à faire face à ces coûts. Grâce à une approche hautement intégrative, cette thèse offre une perspective unique sur le cycle annuel complet des migrateurs et sur l'importance des processus individuels reliant ses différentes parties à travers des processus spatiaux, phénologiques, énergétiques, physiologiques et écotoxicologiques. Ces résultats contribuent à démêler les contraintes multiples auxquelles les migrateurs sont confrontés, une étape essentielle pour comprendre le rôle majeur de la migration dans la connexion d'écosystèmes géographiquement éloignés.

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CONTRIBUTION TO KNOWLEDGE

Living with the consequences of our choices is something with which we are all familiar. In this thesis, I investigate how the decisions made by migratory animals in one life stage can have lasting consequences in subsequent stages of their annual cycle. I employ an integrative and experimental approach to explore the potential mechanisms behind such carry-over effects, combining movement ecology, phenology, energetics, ecotoxicology, endocrinology, and long-term population monitoring.

A strength of this thesis stems from taking advantage of the long-term seabird monitoring program in Svalbard (High Arctic Norway), led by the Centre d'Études Biologiques de Chizé (CEBC-CNRS, France), and the Norwegian Polar Institute (Tromsø, Norway). Geolocation tracking of the non-breeding movements of seabirds began at this site in 2008 and, since 2014, has been integrated into the SEATRACK international initiative, a collaborative project focused on tracking North Atlantic seabird wintering movements. Analyzed here as a whole for the first time, this dataset now spans 13 years, making it one of the world's longest tracking programs of avian non-breeding movement. This thesis, therefore, focuses on the non-breeding spatial ecology, a period of a migratory species' annual cycle about which little is known.

In the context of carry-over effects, the use of long-term data is essential to encompass a wide range of environmental variability, notably because carry-over effects are likely to emerge only in years when resources are particularly limited, preventing individuals from increasing their resource intake to mitigate these trade-offs. Furthermore, I use data from an original experiment involving breeding investment manipulation, which allows me to test some underlying mechanisms of carry-over effects. From the long-term dataset, I also estimate the repeatability in the behaviour and performance of individuals. Repeated measurements of the same individuals across years and experimental approaches are critical for disentangling true carry-over effects and repeatability in individual performance and behaviour across seasons.

Here, I highlight some of the most relevant findings of each chapter:

High movement consistency in space, but not in time, suggests that deep-water areas over the ocean can provide predictable resources stimulating winter site fidelity. In Chapter 2, I used 11 years of geolocation tracking data to investigate the spatiotemporal consistency in non-breeding movements in a pelagic seabird population of black-legged kittiwakes.

Site fidelity is driven by predictability in resources. Marine environments are highly dynamic and characterized by patchily distributed resources, so marine predators usually rely on predictable habitats such as upwelling zones and shelf edges. However, our results revealed that kittiwakes also displayed site fidelity over highly pelagic areas of the North Atlantic, thus challenging the belief that deep-water areas cannot provide enough predictability in resources to stimulate site fidelity in marine predators.

Moreover, consistency in non-breeding movement was stronger in space than in time, suggesting that it was driven by consistent resource pulses that may vary in time more so than in space. Spatial consistency was also higher within than among individuals, suggesting that site fidelity might emerge from individuals’ memory to return to locations with predictable resource availability. Such specialization for key wintering areas suggests vulnerability to perturbations affecting environmental and feeding conditions and that carry-over effects emerging from the wintering stage can be spatially structured among individuals.

Energetic performance and fitness are not necessarily higher towards the centre of the distribution range. In Chapter 3, I tested the predictions of a central hypothesis in theories for range limitations 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’). I tested these predictions over the non-breeding distribution of kittiwakes, using 11 years of tracking and saltwater immersion data to estimate the energy expenditure of individuals during winter as a proxy of energetic performance, and estimated their reproductive success after their return to the colony during summer.

While range limits are usually studied for resident or breeding species, range limits are equally important for migratory species in winter when population limitation may occur due to limited resources. To the best of my knowledge, this is the first time that range limits are investigated over a migratory species’ non-breeding distribution or where hypotheses for range limits are tested using empirical data from tracking of individual energy expenditure, a key currency in nature.

Contrary to the predictions, the energy expenditure of individuals was higher at the centre of the range and decreased towards the edge. This suggests that deteriorations in feeding conditions could have disproportionate consequences on individuals at the range centre, leading to dire effects on the population demography. However, this variation in energetic performance did not carry over to the individual fitness in the following summer as we found no spatial differences in the reproductive success of individuals wintering at the centre versus at the edge of their range. This 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.

Winter burden of per- and polyfluoroalkyl substances can carry over into breeding, potentially outweighing local exposure at the breeding site. In Chapter 4, I tested whether the winter distribution of individuals leads to differences in exposure to pollutants that can carry over to the following breeding stage. Migratory species are exposed to various and geographically distinct sources of anthropogenic contamination as they travelled between regions during their annual cycle. Knowledge of the migratory patterns of animals is thus essential to assess the threats contamination exposure imposes on migratory species throughout their annual cycle. Per- and polyfluoroalkyl substances (PFAS) are a group of contaminants raising increasing concerns because of their worldwide distribution, high toxicity and highly stable chemical structure that earned them the name of “forever chemicals”. However, it remained unknown whether PFAS burden can carry across life stages.

In this study, I show that the PFAS burden of breeding kittiwakes was primarily obtained on the wintering area thousands of kilometres away and brought to the Arctic. The concentrations varied with the wintering latitude, showing that migratory decisions can impact exposure, leading to different contamination burdens that carry into breeding. Moreover, this latitudinal gradient in PFAS winter exposure was related to the carbon chain length of the compound tested. The latitudinal gradient reported in this study is thus the first clear support in wildlife exposure to the hypothesis that longer carbon chain PFAS molecules have a greater dispersal propensity than shorter carbon chain PFAS molecules.

Although seabirds are widely utilized as bioindicators, these results call for caution when using a migratory species as indicators of local PFAS concentration as they can carry contaminants through time and space, which can hinder our ability to draw conclusions on the exposure and bioaccumulation these animals are facing as well as biomagnification processes in the local food web.

Differences in individual quality can mask underlying carry-over effects. Chapter 5 is an original field experiment where I induced reproductive failure via a clutch removal experimental to separate consistency in individual breeding performance (individual quality) from true carry-over effects of breeding costs. I use a very integrative approach combining movement ecology, phenology, energetics, endocrinology, and long-term population monitoring to investigate carry-over effects across the full annual life cycle of individuals.

I found that individuals with better breeding performance (successful breeders) were also performing better in winter (lower energy expenditure), leading to positive correlations across seasons between current reproduction, winter distribution and future reproduction. It is only after controlling experimentally for consistency in breeding performance (individual quality) that I could conclude these correlations were attributed to differences in individual quality, and also reveal underlying carry-over effects into the winter energetics and the breeding phenology that were otherwise masked by quality.

These results highlight the necessity to use an experimental approach to separate costs and quality effects as they can both have important, but different, evolutionary and demographic consequences on animal populations. This is one of the very few studies on carry-over effects able to discriminate between those confounding factors.

CONTRIBUTION OF AUTHORS

Chapter 2 is published by John Wiley & sons in:

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I formulated the research question and developed the methodology design under the guidance of Kyle Elliott, with input from Pierre Legagneux, Arnaud Tarroux, and Olivier Chastel. I conducted the fieldwork and data collection over two years in collaboration with William Jouanneau and benefited from the long-term data gathered over the years by Olivier Chastel, Frédéric Angelier, Pierre Blévin, Aurélie Goutte, and Sabrina Tartu. Access to the long-term tracking data was provided by Børge Moe through the SEATRACK program. Arnaud Tarroux generously hosted me at the Norwegian Institute for Nature Research to provide training in spatial analytical methods and the use of the geolocation processing algorithm he developed with Per Fauchald. Vegard S. Bråthen and Børge Moe carried out the preliminary processing and curation of the raw geolocation data. I conducted all spatial and statistical analyses and wrote the manuscript. All authors contributed to the drafts and gave their final approval for publication. Stephen C. Votier handled the manuscript for publication, and F. Raphael Ceia, along with two anonymous reviewers, provided recommendations that enhanced the quality of the manuscript. Funding was obtained by Olivier Chastel, Børge Moe, and myself.

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I developed the research question and the methodology design under the guidance of Kyle Elliott, with valuable input from Pierre Legagneux and Olivier Chastel. William Jouanneau and I conducted fieldwork and data collection in 2019 and 2021, while the long-term data were collected by Olivier Chastel, Frédéric Angelier, Pierre Blévin, Aurélie Goutte, and Sabrina Tartu. Geir W. Gabrielsen provided expert advice and logistical support in the field. Access to the long-term population monitoring was facilitated by Olivier Chastel, and the tracking data were provided by Børge Moe. Vegard S. Bråthen and Børge Moe carried out the preliminary processing and curation of the raw geolocation data. I analyzed the data and drafted the manuscript. All authors contributed to the drafts and gave their final approval for publication. Anna Hargreaves and Dominique Gravel provided insightful reviews of the manuscript. Funding was secured by Olivier Chastel, Børge Moe, and myself.

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I developed the research ideas and study design under the guidance of Kyle Elliott and Olivier Chastel, with input from Pierre Legagneux. All fieldwork and data collection were conducted by Olivier Chastel, William Jouanneau, Pierre Blévin, and me, with invaluable logistical support from Geir W. Gabrielsen. PFAS analyses were performed at the Norwegian Institute for Air Research by Dorte Herzke, William Jouanneau, and Vladimir A. Nikiforov. Vegard S. Bråthen and Børge Moe handled the preliminary processing and curation of the raw geolocation data. I analyzed the data and wrote the manuscript with support from William Jouanneau. All authors contributed to the drafts and provided their final approval for publication. Funding was secured by Olivier Chastel, Børge Moe, and myself.

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I conceived the research question and designed the methodology with Kyle Elliott, Olivier Chastel, and Pierre Legagneux. I conducted the field experiment and all fieldwork activities, along with William Jouanneau and Pierre Blévin, with invaluable logistical support from Geir W. Gabrielsen. Long-term data was collected over the years by Olivier Chastel, Françoise Amélineau, Frédéric

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AUTHORSHIP DECLARATION FOR PHOTOGRAPHS

All photographs included in this thesis were taken by the author. The author asserts full ownership and authorship rights over these visual representations, which serve to enhance and support the content presented in this academic work.

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OTHER PUBLICATIONS CONNECTED TO THIS THESIS

Amélineau, A., A. Tarroux, S. Lacombe, V. S. Bråthen, S. Descamps, M. Ekker, P. Fauchald, M. K. Johansen, B. Moe, T. Anker-Nilssen, M. I. Bogdanova, I. S. Bringsvor, O. Chastel, S. Christensen-Dalsgaard, F. Daunt, N. Dehnhard, K. Einar Erikstad, A. Ezhov, M. Gavrilo, E. S. Hansen, M. P. Harris, H. H. Helgason, M. Langset, **D.-J. Léandri-Breton**, S.-H. Lorentsen, B. Merkel, M. Newell, B. Olsen, T. K. Reiertsen, G. H. R. Systad, T. L. Thorarinsson, J. Åström and H. Strøm (2023) *Multi-colony tracking of two pelagic seabirds with contrasting flight capability illustrates how windscapes shape migratory movements at an ocean-basin scale*. Ecography, e06496. https://doi.org/10.1111/ecog.06496

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GENERAL INTRODUCTION

Migration is one of nature's most impressive phenomena, with billions of animals travelling each year, sometimes over tremendous distances. These seasonal and predictable movements have evolved across major branches of the Animal kingdom, involving crustaceans, insects, amphibians, reptiles, mammals, and birds (Bowlin et al. 2010) showcasing some of the most incredible endurance feats and natural spectacles. Among these remarkable migrations, the Arctic terns (*Sterna paradisaea*) are renowned for covering up to 80,000 km annually, a distance equivalent to three round trips to the Moon in their lifetime (Egevang et al. 2010). But the achievements of migratory animals extend beyond this. When flying over the Himalayas, bar-headed geese (*Answer indicus*) reached 7000 km of elevation where oxygen drop to 40% of that of sea level (Hawkes et al. 2013). Until recently, over 1 million saiga antelopes (*Saiga tatarica*) were swiping the steppes of Central Asia during their migratory movements (Bekenov et al. 1998). Despite their seemingly stout appearance, great snipe can achieve speeds of nearly 100 km/h during non-stop flights without relying on wind support (Klaassen et al. 2011). With complete disregard for continent drift, shorebirds connect some of the most remote regions on Earth by performing extreme transoceanic flights linking the Americas with Africa and Oceania (Gill et al. 2009, Léandri-Breton et al. 2019). Even feather-light dragonflies, the Globe skimmer (*Pantala flavescens*), are able to cross the ocean during their migration between India and Africa (Ranjan et al. 2023). Meanwhile, leatherback turtles (*Dermochelys coriacea*) swim 12 000 km every year before going back to the beach where they were born (James et al. 2005). Furthermore, swarms of 43 million terrestrial red crabs (*Gecarcoidea natalis*) crawl out of the forest when the wet season arrives, covering Christmas Island overnight (Adamczewska and Morris 2001).

It is no surprise that animal migrations have long captivated the imagination of philosophers, naturalists, and scientists, even before detailed descriptions of these movements were possible. However, comprehending the scale of these movements and the seasonal disappearance of so many animals have remained a considerable challenge. For example, Aristotle proposed the concept of transmogrification, suggesting that species present during summer, like cuckoos, transformed into those found in winter, such as sparrowhawks. Folklore also offered stories suggesting that swallows hibernated at the bottom of muddy ponds and small birds migrated on the backs of geese. It wasn't until the last two centuries that scientists have been able to provide clear evidence of long-distance avian migration. In 1899, Hans Christian Cornelius Mortensen attached the first ring to a starling’s leg, thereby marking the beginning of the scientific use of rings to follow individuals over time. But it was with the pioneering work of David Lack in the 1960s that modern concepts of migration were formulated. Lack emphasized the role of natural selection in shaping migration patterns and proposed the concept of "optimal migration," where individuals aim to maximize their fitness by choosing the most advantageous routes and timings for migration (Lack 1968). Nonetheless, ecologists predominantly directed their focus toward the breeding stage, logistically easier to monitor. Meanwhile, our understanding of migration ecology continued to rely heavily on Mortensen's ringing methodology even though it could provide essentially no data on remote locations (e.g., middle of the ocean), thereby fuelling speculations regarding destinations, movement repeatability, and the interconnection between breeding and non-breeding grounds. However, during the last two decades, we entered a golden age of migration research (Davidson et al. 2020). New technologies have enabled tracking the movement of animals of various sizes and shapes, from colossal blue whales to delicate butterflies. More than ever, it is now possible to follow migrants across seasons and regions to unravel the intricacies of animal migration.

In this thesis, I investigate the seasonal interactions among life stages and their potential carry-over effects throughout the full annual life cycle of a migratory species. In my first chapter, I argue that life stages of migratory species cannot be studied in isolation and that the annual life cycle should be considered as a whole. My second chapter uses long-term tracking data to investigate the relative importance of time and space in determining non-breeding movement repeatability. My third chapter investigates how energetics can influence the non-breeding distribution and migratory decisions, as well as their consequences on annual fitness. My fourth chapter assesses whether carry-over effects into breeding can arise from anthropogenic sources through exposure to contaminants on the wintering site. In my fifth chapter, I investigate seasonal interactions over the full annual cycle and the relative importance of carry-over effects and individual quality in determining cross-seasonal interactions and fitness consequences. Finally, in my sixth chapter, I discuss the main conclusions of each chapter and future research directions. Aristotle, Mortenson and even Lack would have no doubt been astonished by the degree that birds can link ecosystems that were beyond the Known World not long ago, moving molecules and energy from the depths of the Atlantic Ocean to Polar Regions.

CHAPTER 1 – LITTERATURE REVIEW

Annual Life Cycle of Migrants

Migration has evolved in response to seasonality and the spatiotemporal fluctuations in environmental conditions and resources it creates (Berthold 2001). Every year, animals from around the world migrate across regions and habitats to follow seasonal changes in temperature, prey abundance, predation risk or precipitation (Alerstam et al. 2003). Whales follow predictable plankton blooms (Abrahms et al. 2019). Geese surf the green wave of plant phenological development in spring (Kölzsch et al. 2015). Shorebirds cross continents during latitudinal migrations to benefit from the long daylight and reduced nest predation risk of the Arctic summer (McKinnon et al. 2010). Bats perform altitudinal migrations to follow seasonal variations over the orographic gradient (McGuire and Boyle 2013). Elephants move across the savannah to follow regional patterns in rain precipitation (Bohrer et al. 2014). Migrants are thus under a particularly tight schedule to track the seasons across time and space and match their energy requirements across their annual cycle with the timing of seasons.

While some migratory species like monarch butterflies complete their migration cycle over several generations (Flockhart et al. 2013), most migrants are iteroparous, breeding multiple times in their life and moving across life stages in annual circles following the seasonal cyclicity (Stearns 1992). The result is that the annual life cycle of migrating species is highly sequential and typically organized in well-defined life history stages as they move between breeding and non-breeding periods (Harrison et al. 2011). Although those stages are temporally and often geographically separated, they are closely interconnected and cannot be considered in isolation. Indeed, a growing body of literature demonstrates that events occurring during one stage often continue to influence individuals and populations during subsequent stages (O’Connor et al. 2014). Such seasonal interactions act on individuals and populations with profound consequences on ecological and evolutionary processes (Marra et al. 2015). Our understanding of these processes, however, has been limited by a strong research bias towards the breeding stage. In response to this, there is a call to move from single season research towards the full annual life cycle and its seasonal interactions (Marra et al. 2015).

Carry-Over Effects

At the individual level, seasonal interactions imply that decisions taken during one stage (e.g., habitat selection, breeding investment) can have downstream consequences into the next life-history stages (Harrison et al. 2011). The fitness of individuals thus relies on a successful integration of these stages in time, and failing to do so can lead to non-lethal carry-over effects affecting their future performance (Norris et al. 2004, Norris and Marra 2007). This notion of carry-over effects, interconnecting non-breeding and breeding stages, was introduced to the field of ecology through the early work of Peter Marra and Ryan Norris (Marra et al. 1998, 2000, Norris et al. 2004, Norris 2005, Norris and Marra 2007). Using habitat-specific isotopic signature, they demonstrated that non-breeding habitat quality determined the physical condition of wintering American redstarts (*Setophaga ruticilla*), which in turn determined their arrival date and condition on the breeding ground (Marra et al. 2000). Harrison *et al*. further developed this concept by defining carry-over effects as “events and processes occurring in one season that result in individuals making the transition between seasons in different states (levels of condition) consequently affecting individual performance in a subsequent period” (Harrison et al. 2011). The study of carry-over effects in the 2000s was, however, limited by the difficulty to track migrants across seasons (O’Connor et al. 2014). This field of research thus benefited greatly from the technological advancement of lighter tracking devices in the 2010s that could be fitted on a wider range of species to track their movements over their full annual life cycle. New Global Positioning Systems (GPS) devices can now weigh as little as 1 g, allowing tracking small passerines and bats, although this technology is still expensive and limited by the short battery lifespan (Weller et al. 2016, Fleming 2019, Pedersen et al. 2019). Automated radio-telemetry tags (e.g., MOTUS) are small enough to be attached to flying insects, but provides only sporadic locations along the migration path (Knight et al. 2018, Bégin-Marchand et al. 2021). Light-level geolocators are arguably one of the most used technologies for smaller migratory animals due to their size and weight (3 to < 1 g), affordability and long battery lifespan (up to three years) allowing to follow animals across multiple annual life cycles (Fig. 1.1) (McKinnon and Love 2018). Geolocators estimate geographic locations from the timing of variations in the ambient light (e.g., twilight, solar zenith, sunset and sunrise) with an accuracy to the order of 200 or 300 km (Lisovski et al. 2020, Halpin et al. 2021). They are thus adequate for tracking large-scale movements of animals over their full annual cycle, including smaller species (e.g., Fayet et al. 2016, Briedis et al. 2018, Léandri-Breton et al. 2019).

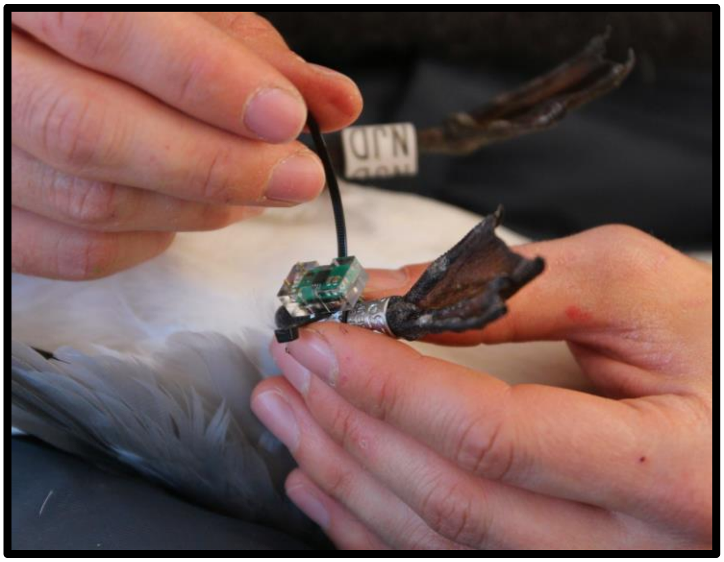

Figure 1.1: Attachment geolocator on the leg ring of a black-legged kittiwake in Svalbard. Photo credits: Don-Jean Léandri-Breton.

The development of these technologies resulted in a recent boost of studies on animal movements, giving further support that processes occurring during the non-breeding stages can carry over to affect the subsequent breeding stage, notably via winter food availability constrained by habitat quality, weather and competition (O'Connor et al. 2014). For capital breeding species (e.g., geese), relying on endogenous reserves for breeding, this may reflect the relationship between resource acquisition during winter and utilization in summer, as those individuals that gain more resources over the winter will have more endogenous reserves available for breeding (Williams et al. 2017). Thus, some individuals may have a better body condition or higher nutrient reserve levels, which then contribute directly to the reproductive outcome (Legagneux et al. 2012, Jean-Gagnon et al. 2018). In income breeders, however, the relationship between wintering environment and breeding outcome is potentially less mediated by resource-based factors as the energy required for breeding is mostly obtained locally (i.e., on the breeding area) (Jönsson 1997, Drent and Daan 2002). Instead, the timing of arrival at the breeding site might be an important factor mediating carry-over effects as earlier onset of reproduction is widely associated with higher breeding success in a wide array of species, although arriving too early may also have costs (Smith and Moore 2003, Bêty et al. 2004, Morrison et al. 2019, Whelan et al. 2021, Seyer et al. 2023). Higher resource acquisition in winter and during stopovers can indeed allow for an earlier departure or faster migration, and subsequently, to an earlier arrival on the breeding site and onset of reproduction (Bêty et al. 2003).

The most reported carry-over effects remain the costs of reproduction, with the breeding investment in one season leading to costs paid during the subsequent stages (Williams 2012). Reproduction requires high energy investment and, because resources are limited, the "resource-allocation trade-off" theory predicts that energy directed towards one function can no longer be allocated to other traits or functions such as self-maintenance (Williams 1966, Reznick 1992, Harshman and Zera 2007). Trade-offs resulting in differential resource or energy allocation between reproduction and other functions such as moult or migration can thus carry consequences, at least over short-term periods (Langston and Rohwer 1996, Dawson 2006, Monaghan et al. 2009, Fowler and Williams 2017). Such allocation trade-offs can also entail long-term effects with, for instance, a high level of reproductive investment earlier in life associated with faster senescence and lower reproductive value later in life, indicative of lasting effects a reproduction and somatic maintenance conflict (Reed et al. 2008). Indeed, life history theory predicts that costs of reproduction can have long-lasting effects paid in terms of reduced future reproductive value (Williams 1966, Stearns 1992), and negative correlation between reproductive allocation in a given year and reproductive output the next has been widely described among long-lived mammal and bird species (Hamel et al. 2010, Bleu et al. 2016).

Individual Quality and Cross-Seasonal Consistency

Despite expected trade-offs between current and future reproduction, animals often show a positive correlation between consecutive reproductive attempts (Reznick et al. 2000, Hamel et al. 2009). Resource acquisition can vary according to individual quality so that some individuals will always have more resources than others to allocate into all functions in a given annual life-history stage (see Fig. 1.2) (Noordwijk and Joung 1986, Reznick et al. 2000, Hunt et al. 2004). Seasonal interactions could thus reflect inter-annual consistency in the individual’s breeding success and overwintering strategies (Bogdanova et al. 2011). Individual quality in this context implies consistency in performance and refers to inter-individual heterogeneity that correlates with fitness traits, usually reproductive success (Wilson and Nussey 2010, Bergeron et al. 2011). Links between individual quality and life-history decisions can therefore lead to cross-seasonal correlations in breeding and wintering performance with, for instance, better breeders also consistently accessing better quality wintering habitats (Gunnarsson et al. 2005). Such variations in individual quality could notably arise from larger individuals being able to better compete for resources (Ronconi and Burger 2011), and interact with age as more experienced adults have refined their foraging behaviour and locations over the years (‘exploration-refinement hypothesis’) (Guilford et al. 2011). This poses the challenging question of differentiating between seasonal interactions arising from genuine carry-over effects and inter-annual consistency in within-individual performance associated with intrinsic factors such as individual quality (Harrison et al. 2011, Daunt et al. 2014). For example, associations between winter habitat quality, derived from stable isotope analysis, is often associated with breeding parameters, and interpreted as reflecting a carry-over effect (Marra et al. 1998), while it could also indicate that higher quality individuals access better quality habitats. Because variations in costs and in quality are likely both present in a population, it is not possible to predict the sign of the covariance between traits. Moreover, it is not possible to assess the strength of carry-over effects if the covariance is negative, nor to conclude that underlying costs are absent if the covariance is positive. Experimental approaches, and repeated measurements from the same individuals, are required to separate costs and quality effects as they can both have important, but different, evolutionary and demographic consequences on animal populations (Harrison et al. 2011, Williams 2012). However, experimental evidence of carry-over effects remains uncommon.

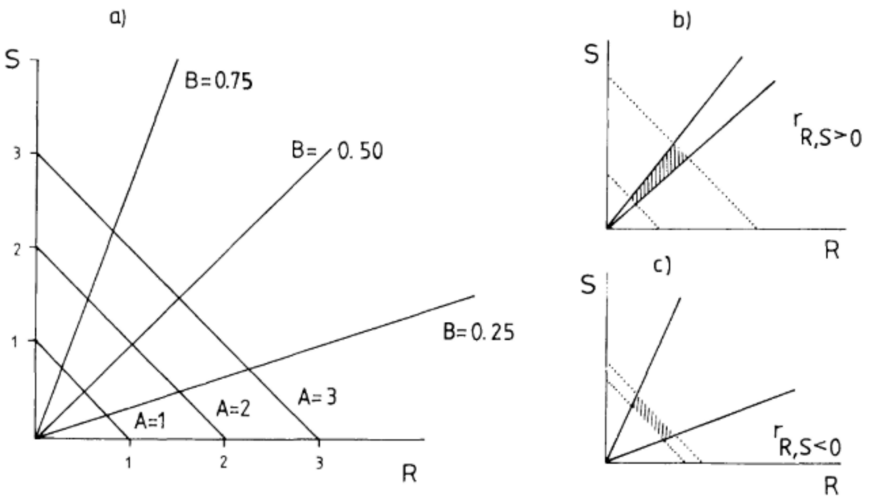

Figure 1.2: The allocation/acquisition model from (Noordwijk and Joung 1986) illustrating a) the trade-off between two life-history traits (here S for Survival and R for Reproduction) at different levels of resource acquisition (A) and for different investment (allocation, B). The relationship observed between S and R (hatched area) in a population can be b) positive when there is high variance in resource acquisition among individuals (and low difference in resource allocation between traits) or negative relation when there is low variance in resource acquisition among individuals (and high difference in resource allocation between traits).

Proximal Mechanisms of Carry-Over Effects

Despite the development of new tracking technologies, the proximal mechanisms underlying carry-over effects are still unclear and so diverse that drawing an integrative explanation remains challenging. For instance, carry-over effects can emerge from higher muscular activity and energy expenditure required for breeding which can result in greater oxidative damage to tissues (Monaghan et al. 2009). This can lead to exercise-induced injuries in post-breeding birds, constraining their ability to migrate or the onset of migration (Guglielmo et al. 2001, Jimenez et al. 2019). Carry-over effects can also emerge from the overlap between reproduction and another energy-costly function such as moult because of limitations in resources needed for feather production (e.g., specific amino-acids; Murphy 1996, Vézina et al. 2009) or direct physiological conflict between those two functions. It has been suggested that that high level of prolactin required for chick-rearing inhibits the onset of moult (Dawson 2006). This pleiotropic effect of prolactin could then cause a delay in moulting until after parental care resulting either in delaying the post-breeding migration or in the production of low-quality feathers associated with rapid moulting (Dawson et al. 2009, Williams 2012). Overall, studies provide a wide range of avenues of potential mechanisms of carry-over effects, most of which are correlational and remain to be tested. Some experimental studies, however, started to unravel underlying mechanisms of carry-over effects. Fruit flies exposed to the scent of a predator provided evidence that fear can affect survival and subsequent offspring quality via body mass loss (Elliott et al. 2016). The manipulation of the individual state in spring-staging snow geese (*Anser caerulescens*) affected their reproductive success on the Arctic breeding grounds (Legagneux et al. 2012). Experimentally enlarged brood size resulted in increased energy expenditure in breeding common kestrels (*Falco tinnunculus*) and lower survival the following winter (Daan et al. 1996). Food supplementation in banded mongoose (*Mungos mungo*) showed that energetic loss from breeding effort inhibits future investment via elevated levels of glucocorticoid hormones (Sanderson et al. 2014). These studies illustrate that the physiological processes regulating energy could provide a general mechanism for carry-over effects.

The allostasis model gives an integrative explanation of how individuals can achieve stability in their energy (and nutrients) needs throughout life-history stages (McEwen and Wingfield 2003a). Allostatic overload occurs when energy requirements during a given life stage exceed energy acquisition, potentially leading to carry-over effects. The “stability through change” principle of allostasis is regulated by key physiological mediators, notably glucocorticosteroid hormones. Corticosterone, the principal glucocorticosteroid hormone in birds, regulates carbohydrate levels and a short-term up-regulation of this hormone stimulates foraging behaviour necessary to successfully meet increased energy demands during costly life stages like chick rearing (Love et al. 2004, Crossin et al. 2012). However, environmental stressors and unpredictable events (e.g., storms, food shortage) can trigger an acute stress response mediating physiological and behavioural changes to redirect energy towards self-feeding, self-maintenance and long-term survival (Wingfield et al. 1998). This “emergency life-history stage” can result in stress-induced inhibition of reproductive behaviours with consequences on breeding success through parental attendance (Kitaysky et al. 2001) and foraging behaviour during chick rearing (Angelier et al. 2007). Therefore, secretion of corticosterone is considered an adaptative response to variation in seasonal energy demands, but long-term elevated levels or acute stress response can have negative effects on life-history stages (McEwen and Wingfield 2003a). Additionally, corticosterone is a potential mediator of carry-over effects through a stress-induced inhibition of the physiological pathway leading to reproductive behaviours. Acute secretion of this glucocorticosteroid is expected in individuals facing environmental challenges like food depletion or inclement weather (Bonier et al. 2009). Through a cascade of effects along the hypothalamic–pituitary–gonadal axis (HPG), corticosterone can inhibit the production of the luteinizing hormone as shown in kittiwakes (Goutte et al. 2010a) which, in turn, disrupts the release of sex steroids hormones. This can result in the inhibition of sex steroid dependent behaviours associated with the onset of reproduction, such as mating, nest building and courtship (Ball 1993). These examples highlight the pleiotropic effect of corticosterone as elevated levels needed to face increased energy demands can create physiological conflicts with other functions such as feather growth or production of reproductive hormones (Williams 2012). Therefore, endocrine mechanisms regulating stress response of individuals have a strong potential to mediate environmental conditions and individual behaviour in the context of carry-over effects (Bonier et al. 2009).

Carry-Over Effects from Chemical Pollution

One set of environmental conditions that can potentially create carry over effects are chemical pollutants. As we have entered the Anthropocene, an era with major anthropogenic transformation, wildlife and ecosystems are facing novel and exceptionally severe threats (Steffen et al. 2011, Dirzo et al. 2014). Habitat loss and degradation, climate changes, invasive species, over-exploitation and exposure to noise pollution, new pathogens and contaminants are among the global challenges behind the ongoing biodiversity extinction crisis (Dirzo et al. 2014, Pyšek et al. 2020, Persson et al. 2022). The decision process of animals, optimized via adaptation to their natural environment, now entails new potential consequences arising from human activity. These novel environmental conditions are thus expected to create carry-over effects emerging from these anthropogenic threats. Climate warming induced changes in winter conditions, such as the frequency of freeze-thaw events, can carry effects into the phenology, reproduction and survival of animals wintering in temperate latitudes (Sutton et al. 2021, Dinh et al. 2023). Habitat degradation on winter grounds and key stopover sites impacts body condition and reproduction of migratory species (Cooper et al. 2015, Taylor and Stutchbury 2016, Studds et al. 2017). In some cases, human activities can also have positive carry-over effects with, for instance, winter food subsidies from agricultural crops or bird feeders leading to a better energetic condition in spring and reproductive success in species like the greater snow goose (*Anser caerulescens caerulescens*) and the great tit (*Parus major*) (Fowler et al. 2020, Broggi et al. 2022).

Environmental pollution is yet another major human-induced impact on ecosystems, posing a global threat to wildlife. Currently, more than 350,000 chemicals have been registered for commercial production and use (Wang et al. 2020), and new compounds are continually being introduced each year. This rate of production, along with the volume of chemicals, surpasses society's ability to conduct safety-related assessments and monitoring (Persson et al. 2022). Environmental contaminants can now be found in even the most remote ecosystems, from the Himalayan Plateau to the ocean floor and the Arctic wilderness (Wang et al. 2019, Chen et al. 2019). The importance of environmental pollution risk assessment, regulation, and mitigation has been emphasized as a priority in environmental policies such as the Stockholm Convention.

Because they are highly mobile, migratory species are exposed to various and geographically distinct sources of contamination during their annual cycle (Flack et al. 2022). The exposure to contamination is thus particularly difficult to assess in these species as their pollutant burden can reflect local contamination at the breeding site or exposure far away on the wintering grounds (e.g., Leat et al. 2013, Bourgeon et al. 2013, Fort et al. 2014, Albert et al. 2019). Several studies have highlighted the critical need for a better understanding of exposure to pollutants during the wintering stage to assess the risk that migratory species are facing throughout their annual cycle (Blais et al. 2005, Fort et al. 2014). For example, in an experimental study on great skua (*Stercorarius skua*), food supplementation of chicks accelerated their development but did not alleviate their organochlorine burden, which was still 50% higher for chicks whose mothers wintered in Europe than those whose mothers wintered in West Africa (Bourgeon et al. 2013). This shows that the contamination load in chicks was more influenced by the mother’s exposure on the wintering site, via maternal transfer into the egg, than by local contamination at the breeding site.

Similarly, mercury burden carries over from the wintering stage into the breeding stage in other migratory seabirds such as auklets, guillemots, cormorants and terns (Lavoie et al. 2014, Fort et al. 2014, Shoji et al. 2021, Bertram et al. 2022).

The propensity of contaminants to carry-over from one stage to the next depends on the compound-specific turnover rate. For compounds with a short turnover rate, tissues collected on the breeding site should reflect more recent uptake and exposure at the wintering site would rapidly become less apparent via depuration processes (Pacyna-Kuchta 2023). In contrast, for compounds with long half-lives, concentrations may represent a larger accumulation period mostly reflective of the winter exposition (Yoo et al. 2009, Yeung et al. 2009, Tarazona et al. 2015), likely due to a lower excretion rate (Zhang et al. 2013). The turnover rate also varies among tissues, with blood associated to the shortest half-life (Pacyna-Kuchta 2023). However, blood concentrations can also partly result from the remobilization of contaminants from other tissues in periods when individuals rely on their endogenous reserves (Bustnes et al. 2017, McPartland et al. 2020, Kebke et al. 2022). Notably, migratory species often deposit body reserves before engaging in long migratory movements, reserves that are depleted during the journey, potentially contributing to recirculation in the blood of contaminants assimilated during winter (Hitchcock et al. 2019). Seabirds, such as kittiwakes, rely less on body reserves for migration and tend to adopt a “fly-and-forage” strategy when migrating (Amélineau et al. 2021), but the pre-laying stage remains nutritionally stressful as individuals engaging in activities such as courtship and nest-defence behaviour reduce their foraging time and rely more on endogenous reserves during this period (Tremblay et al. 2022, Jackson et al. 2023). Thus, there is the potential for contaminants to be remobilized during that period.

Among contaminants raising increasing concerns are per- and polyfluoroalkyl substances (PFAS). These compounds have very stable chemical structures with strong carbon-fluorine bonds that earned them the nickname of “forever chemicals” (Evich et al. 2022). While their high chemical and thermal stability make PFAS particularly useful in a wide array of manufactured goods (e.g., metal coating, food packaging, firefighting foam; Glüge et al., 2020), these properties also make PFAS highly resistant to degradation and very persistent in the environment (Evich et al. 2022). Moreover, PFAS are found worldwide and are prone to large dispersion despite having an overall low volatility (Yeung et al. 2017, Kurwadkar et al. 2022).

Because of their high persistence in the abiotic environment and their high water solubility, the oceans act as major sinks for PFAS (Yamashita et al. 2005, 2008). Consequently, marine species can be particularly exposed to PFAS, especially long-lived top predators like seabirds that occupy a high trophic level and can accumulate high concentrations of contaminants in their tissues (Ankley et al. 2021, De Silva et al. 2021, Sun et al. 2023). High PFAS concentrations in breeding seabirds have been associated with several endpoints in correlative studies including reproductive success, incubation behaviour, integument coloration, metabolism, oxidative stress, telomere dynamics, immune and endocrine systems (Tartu et al. 2014, Blévin et al. 2017b, Costantini et al. 2019, Sebastiano et al. 2020, 2023, Jouanneau et al. 2023). Despite PFAS abundance and high toxicity, most work on migratory species has focused on the breeding stage and, as far as I know, no studies have yet looked into whether PFAS burden at the breeding site reflects exposure in previous non-breeding life stages.

Seabirds and their eggs are widely used as indicators of the local contamination of the breeding area (Furness and Camphuysen 1997, Burger and Gochfeld 2004, Bianchini et al. 2022, Sun et al. 2023). However, since most species are migratory they can carry contaminants through time and space, which can hinder our ability to draw conclusions on the exposure and bioaccumulation these animals are facing as well as biomagnification processes in the local food web (Lavoie et al. 2014). Blood and eggs are generally assumed to reflect short-term, local exposure to contaminants and feathers to reflect exposure on the wintering site, although this requires knowledge on the moulting schedule which is often lacking (Pacyna-Kuchta 2023). A thorough understanding of the migratory patterns of animals and propensity of contaminants to carry-over are essential to assess the threats contamination exposure imposes on migratory species throughout their annual cycle. By doing so, migratory species can be used to monitor the exposure and pollutant concentrations in remote regions of the Globe, such as the oceans where sampling is otherwise difficult.

Carry-Over Effects in Seabirds

Seabirds are also considered important indicators of the marine environmental conditions (Furness and Camphuysen 1997, Piatt et al. 2007, Durant et al. 2009, Ramos and Pereira 2022). Because of their position at the higher level of the food web they are highly responsive to changes in prey availability and in environmental conditions (Cairns 1988, Frederiksen et al. 2006, Iverson et al. 2007). Moreover, their wide distribution means that they can be used to track these conditions across broad ecosystems, including pelagic regions of the oceans difficult to monitor otherwise. As long-lived species, they are good models to investigate carry-over effects as they are likely to respond to environmental stressors by modulating their behaviours, such as their breeding effort, to promote their own survival and their lifetime fitness over the survival of their current offspring (Erikstad et al. 1998, Bókony et al. 2009). For instance, inducing breeding failure in male Cory's shearwater (*Calonectris borealis*) decreased their propensity in engaging in long-distance migration compared to successful breeders (Catry et al. 2013). Individuals 'released' from their breeding commitment also left the colony earlier in fall and arrived earlier the following spring

(Catry et al. 2013). Kittiwakes that were supplementary fed during breeding travelled shorter distances and contracted their winter distribution compared to unfed individuals (Whelan et al. 2020). Failed breeders also left their colony earlier and travelled further to reach the Northwest Atlantic Ocean, while most successful breeders departed later and wintered closer to the colony along the European coasts (Bogdanova et al. 2011). A chick crossfostering experiment also showed that individuals with reduced parental investment spent more time away from the breeding site compared to those with increased breeding investment (Fayet et al. 2016). Reduced parental investment via a clutch removal experiment, however, resulted in earlier return to the colony site the following year (Gatt et al. 2021). Corticosterone implants stimulating exposure to an environmental stressor caused individuals to depart from the breeding site earlier and to spend more time on the wintering grounds (Schultner et al. 2014). The winter activity has also been found to be a good predictor of breeding success the following year in seabirds. For instance, higher winter flying activity in long-tailed jaeger (*Stercorarius longicaudus*) was associated in lower breeding propensity (Seyer et al. 2023). Higher foraging activity in winter was associated to lower breeding performance in European shags (*Gulosus aristotelis*) and Manx shearwaters (*Puffinus puffinus*), suggesting that individuals were not able to compensate for harsher foraging conditions experienced during winter. Together, these studies illustrate strong resource allocation trade-offs in seabirds between reproduction and self-maintenance.

Consequences of breeding investment can, however, weaken over the course of the non-breeding stage, a period in the annual life cycle potentially less time-constrained and during which breeding costs can be buffered rather than accumulated (Briedis et al. 2018). For instance, previous studies on kittiwakes showed that the time spent on the wintering site was associated to a reduce telomere shortening while higher energy expenditure during breeding had no detrimental effect on the return rate of individuals the following year (Schultner et al. 2014a). This highlights the need to use multiple years of data encompassing a wide range of environmental variability as carry-over effects are likely to emerge only in years when resources are particularly limited or when competition is important so that individuals cannot increase their resource intake to mitigate these trade-offs. Most carry-over effects studies, however, rely on one or very few years of data.

Study System

The black-legged kittiwake (*Rissa tridactyla*) is a colonial seabird extensively studied in research, resulting in a comprehensive understanding of its life history, behaviour and physiology. More specifically, and particularly relevant for this thesis, its hormonal profile (e.g., (Kitaysky et al. 1999, Angelier et al. 2009, Whelan et al. 2021) and activity-specific metabolic rates (Gabrielsen et al. 1987, Jodice et al. 2003, Blévin et al. 2017a) are relatively well known. Moreover, kittiwakes are medium-size gulls (365-400g). Consequently, they are large enough so that they can easily be fitted with small tracking devices, such as geolocators (Hatch et al. 2009).

As income breeders, kittiwakes mostly rely on local food availability at the colony site to cover the extra cost of reproduction (Jönsson 1997) and would time the onset of breeding according to the food availability (Gill et al. 2002, Whelan et al. 2021, 2022). In Svalbard, individuals spend nearly two months in the colony area prior to laying eggs (Goutte et al. 2014). Such prolonged pre-laying periods can be devoted to physiological and behavioural preparation for breeding such as maturation of the reproductive system, acquiring energy reserves for breeding, finding and guarding the nest site, pair bonding and nest building (Jönsson 1997, Williams 2012, Whelan et al. 2021). The body condition of kittiwakes during the pre-laying period influences breeding propensity, and, for those that do breed, lay date, which in turn affects the reproductive outcome (Goutte et al. 2014). Resource is a limiting factor for the onset of egg laying (Whelan et al. 2021) and individuals arriving on the breeding site with an energy deficit would presumably have to delay breeding to acquire the resources needed. As demonstrated by a clutch removal experiment, reproductive costs in kittiwakes translate in a reduced survival rate the following year, potentially mediated by a body mass loss during chick-rearing (Golet et al. 1998, 2004). However, such effects may only be apparent in years of poor local feeding conditions at the colony or at the wintering site (Golet et al. 2004). In this species, body condition has been related to baseline corticosterone levels (Kitaysky et al. 1999, but see Golet et al. 2004), as well as circulating persistent organic pollutants contaminant levels (Nordstad et al. 2012). Indeed, body condition index, as well as levels of corticosterone and endocrine disruptive contaminants (e.g., mercury), vary greatly among individuals arriving at the colony (Goutte et al. 2010b, a, 2014, 2015, Tartu et al. 2013). Corticosterone levels upon arrival at the colony site were negatively associated to laying propensity (Lanctot et al. 2003). A short-term experimental elevation of corticosterone also resulted in females leaving the colony earlier and spending a longer period at the wintering grounds than control birds (Schultner et al. 2014). However, little is known about how physiological condition (nutritional and stress condition) at the arrival at the colony is influenced by individuals' behaviour during the previous non-breeding season.

The Krikkjefjellet colony of kittiwakes in Kongsfjord, Svalbard (High-Arctic, Norway, see Fig. 1.3) has been closely monitored during the last decades by the Centre d'Études Biologiques de Chizé (CEBC-CNRS, France) and the Norwegian Polar Institute for research on foraging and breeding behaviour, endocrine disruptive contaminants and physiological processes (e.g., (Tartu et al. 2013, Goutte et al. 2014, Jouanneau et al. 2023). Moreover, kittiwakes from this colony have been tracked year-round with geolocator devices since 2008. The colony is part of the SEATRACK international initiative (https://seapop.no/en/seatrack/), a collaborative project focused on tracking

North Atlantic seabird movements, and engaging researchers from eight countries. Svalbard holds the northernmost colonies of this species, and this population's main wintering site is situated on the Grand Banks of Newfoundland, off Eastern Canada (Frederiksen et al. 2012). Kittiwakes breeding in Svalbard are therefore long-distant migrants travelling across contrasting environmental conditions during their annual movement. This long migration and the short breeding window during the High-Arctic summer have the potential to impose a strong time constraint on the annual life cycle of Svalbard's kittiwakes. In winter, the productive waters of the Grand Banks are largely shared by kittiwakes breeding in colonies across the Atlantic Ocean (Frederiksen et al. 2012). This high degree of overlap during winter among colonies indicates that the overall Atlantic population could be sensitive to changes in winter environmental conditions off Atlantic Canada (Frederiksen et al. 2012), although the inter- and intra-individual repeatability in movements have never been tested. Moreover, high Arctic waters around Svalbard are subject to changes in oceanographic features (e.g., change from an Arctic ecosystem with high sea ice cover to a warmer Atlantic-like ecosystem), so-called "Atlantification", that affect kittiwakes' food quality during reproduction season (Vihtakari et al. 2018).

The movement and demography monitoring program of kittiwakes from Svalbard will provide me access to one of the most extensive non-breeding tracking datasets available, allowing for the investigation of seasonal interactions and their potential carry-over effects. Twenty years after the introduction of the concept of carry-over effects in the field of Ecology, we now have greater opportunities than ever to study interactions among the life stages of migratory species. The limitations highlighted by Marra, Norris, and Harrison, in terms of access to long-term tracking data covering many years of environmental conditions and multiple annual cycles for the same individuals, are now being lifted as long-term tracking programs mature. Throughout this thesis, I take advantage of such datasets to elucidate different facets and underlying mechanisms of seasonal interactions across the entire annual life cycle of migrants.

Figure 1.3: Seabird monitoring at the “Krykkjefjellet” colony in Svalbard. Photo credits: Don-Jean Léandri-Breton.

CHAPTER 2 – LONG-TERM TRACKING OF AN ARCTIC-BREEDING SEABIRD INDICATES HIGH FIDELITY TO PELAGIC WINTERING AREAS

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ABSTRACT

Site fidelity is driven by predictable resource distributions in time and space. However, intrinsic factors related to an individual's physiology and life-history traits can contribute to consistent foraging behaviour and movement patterns. Using 11 yr of continuous geolocation tracking data (fall 2008 to spring 2019), we investigated spatiotemporal consistency in non-breeding movements in a pelagic seabird population of black-legged kittiwakes *Rissa tridactyla* breeding in the High Arctic (Svalbard). Our objective was to assess the relative importance of spatial versus temporal repeatability behind inter-annual movement consistency during winter. Most kittiwakes used pelagic regions of the western North Atlantic. Winter site fidelity was high both within and across individuals and at meso (100−1000 km) and macro scales (>1000 km). Spatial consistency in non-breeding movement was higher within than among individuals, suggesting that site fidelity might emerge from individuals' memory to return to locations with predictable resource availability. Consistency was also stronger in space than in time, suggesting that it was driven by consistent resource pulses that may vary in time more so than in space. Nonetheless, some individuals displayed more flexibility by adopting a strategy of itinerancy during winter, and the causes of this flexibility are unclear. Specialization for key wintering areas can indicate vulnerability to environmental perturbations, with winter survival and carry-over effects arising from winter conditions as potential drivers of population dynamics.

KEYWORDS:

Spatial distribution, Individual consistency, Migration, Repeatability, Nearest neighbour distance, Biologging, Global Location Sensors,·GLS

INTRODUCTION

Site fidelity, the propensity of organisms to return to previously occupied locations, is a common form of behavioural consistency across taxa (Switzer 1993, Börger et al. 2008, Piper 2011). Such spatial consistency is closely related to resource quality and predictability over space and time (Switzer 1993). Site fidelity for foraging patches may be favoured by individuals living in unpredictable environments, notably when resources are patchily distributed but spatially and temporally predictable (Switzer 1993). Returning to the same high-quality patch is reinforced by individuals' acquisition of local knowledge during previous journeys, likely facilitating foraging efficiency (the 'always-stay' strategy; Switzer 1993, Irons 1998, Piper 2011). However, if changes in resource predictability and availability occur, fluctuations in behavioural consistency of individuals are expected to generate a decrease in site fidelity over time (the 'win-stay, lose-shift' strategy; Kamil 1983, Switzer 1993). The spatiotemporal predictability in resources is also a strong driver of migratory movements during which individuals follow consistent seasonal changes in environmental conditions (Mueller & Fagan 2008). Examples of individuals tracking predictable resources along a migratory pathway, sometimes over remarkable distances, include whales following planktonic blooms or geese following the 'green wave' of plant phenological development in spring (Alerstam & Hedenström 1998, Kölzsch et al. 2015, Abrahms et al. 2019). Resource tracking across space and time is likely driven by a trade-off between (1) memory of location and timing of profitable patches and (2) exploration of novel environments when memory is unable to locate profitable patches, with repeatability governed by both extrinsic and intrinsic factors that generate or constrain profitability (Fagan et al. 2013).

In marine systems, top predators, such as seabirds, are dependent on patchily distributed resources (Weimerskirch 2007, Fauchald 2009). Because predictability in pelagic resources is habitat- and scale dependent, seabirds often rely on specific higher quality foraging zones (e.g., shelf edges, frontal zones, upwellings) that are predictable at meso (100−1000 km) and macro scales (>1000 km; Weimerskirch 2007). Specialization in foraging behaviour would be optimal when resources are predictable, thus stimulating site fidelity in high-quality patches that show consistency in productivity over time (Barraquand & Benhamou 2008, Carroll et al. 2018). Extrinsic factors related to interactions with other species or the environment (e.g., competition, prey availability, heterogeneity in resources) can therefore have a profound influence in determining individuals' movements across landscapes and distribution (Fayet et al. 2017). However, oceans are dynamic environments and currently undergoing major changes that can affect resource predictability (Cury et al. 2008, Polovina et al. 2008, Hoegh-Guldberg & Bruno 2010). Temporal and spatial changes in marine resource predictability and availability can lead to shifts in the distribution of seabirds (Hamer et al. 2001, 2007, Ceia et al. 2014, Orben et al. 2015). The resilience and adaptability of populations to such changes are closely related to phenotypic plasticity and variability in behavioural traits of individuals, with populations showing high specialization in distribution, foraging behaviour, and diets being more sensitive to an alteration of their environment (Canale & Henry 2010, Patrick et al. 2015, de Grissac et al. 2016). Although seabirds often show within-individual wintering site fidelity (Ceia & Ramos 2015 and references therein), some species like the Cory's shearwater *Calonectris borealis* or the long-tailed skua *Stercorarius longicaudus* are highly flexible with some individuals shifting their winter distribution at the ocean scale (e.g., from the western to the eastern Atlantic Ocean; Dias et al. 2011, van Bemmelen et al. 2017). Flexibility in movement behaviour that is affected by extrinsic factors may only be measurable over large time scales, stressing the need for long-term movement tracking.

Intrinsic factors related to physiological or life-history traits, such as sex, age, nutrition state, or breeding status and investment, can also contribute to individual variation in foraging and movement patterns (Phillips et al. 2017). Failed breeders often depart on migration earlier than successful breeders, and this difference sometimes persists into the overwintering period with the previous breeding status affecting the winter distribution and the timing of the arrival at and departure from the wintering site (Phillips et al. 2005, Catry et al. 2013, Bogdanova et al. 2017). Personality can also influence movement patterns, with bold individuals typically displaying higher foraging site fidelity, while shy individuals are shifting sites and travelling farther (Patrick & Weimerskirch 2014, Krüger et al. 2019, Harris et al. 2020). Moulting patterns, flight capabilities, and levels of stress hormones can affect the migration timing and an individual's ability to engage in long migratory flights (Dawson et al. 2000, Guglielmo et al. 2001, Schultner et al. 2014, Cherel et al. 2016). Moreover, important life history stages that compose the annual life cycle such as migration or reproduction are controlled by physiological processes whose timing or duration is regulated internally by an individual's biological clock (the endogenous processes behind the biological rhythms) in response to temporally fixed cues (e.g., photoperiod; Kumar et al. 2010). Therefore, movement patterns driven by intrinsic factors with strong biological clock control (e.g., changes in physiology, body condition, moult) will tend to occur consistently between years over an individual's life (Kumar et al. 2010, Wascher et al. 2018). Overall, the mechanisms underlying inter-annual movement consistency involve complex interplay between extrinsic and intrinsic factors, and the relative contributions of those factors is likely to vary over time (Phillips et al. 2017).

Using a long-term tracking dataset of 11 yr of continuous non-breeding movement data (fall 2008 to spring 2019) of black-legged kittiwakes *Rissa tridactyla* breeding in Svalbard (High Arctic

Norway), we investigated inter-annual variations in space utilization and movement phenology during the nonbreeding period. The North Atlantic populations of kittiwakes largely congregate in winter at a shared staging area in the Western Atlantic Ocean (Frederiksen et al. 2012). Although the high degree of overlap in winter suggests site fidelity among and within populations, these results rely on 2 yr of data only (Frederiksen et al. 2012). Moreover, other studies showed that kittiwakes may alter their winter distribution according to intrinsic factors (e.g., stress hormone levels, breeding statuses, or reproductive investment; Schultner et al. 2014, Bogdanova et al. 2017, Whelan et al. 2020), which highlights the importance of multiple years of tracking data to assess the consistency of movement over time. We estimated inter-annual consistency in movement among and within individuals (2 to 7 yr repeated per individual) and how this consistency varied over the course of the non-breeding period across a decade. Our main objective was, therefore, to assess the relative importance of spatial versus temporal repeatability underlying inter-annual movement consistency. Site fidelity can emerge from resource specialization where resources are predictable so that individuals would show high distribution repeatability for consistent high-quality foraging areas (Switzer 1993). Higher repeatability for space utilization would then suggest that individuals are specialized on certain resources and are more vulnerable to extrinsic factors (e.g., environmental conditions, resource availability). Timing of climatic events (e.g., sea ice breakup, peak in primary productivity) can show high interannual variations associated with fluctuations in strength of large-scale climatic and oceanographic systems like the North Atlantic Oscillation (NAO; Visbeck et al. 2001) or ocean gyres (Polovina et al. 2008). Individual specialization driven by individuals following consistent patches learned on previous winters might thus be expected to show consistency in space over time. In contrast, higher repeatability in time than space would suggest that individual specialization is driven by factors occurring consistently at the same time each year in relation to the individual biological clock. The temporal and spatial consistency in movement patterns can thus inform about the relative importance of extrinsic versus intrinsic parameters behind the site fidelity observed in a given population, but intrinsic and extrinsic factors often remain related to one another (i.e., hormonal clocks may change with foraging success driven by environmental variation), and the dominance of one factor over the other does not preclude the interaction or importance of both.

MATERIALS & METHODS

Logger deployment and geolocation processing

From 2008 to 2018, we deployed 276 geolocators (light-loggers or Global Location Sensors, GLS) on black-legged kittiwakes *Rissa tridactyla* to track their non-breeding movements (Table S2.1 and online at www.int-res.com/articles/suppl/m676p205_supp.pdf). Adults were captured using a nylon loop attached to a fishing rod at the colony site in Kongsfjorden, Svalbard (High Arctic Norway; 78° 54’ N, 12° 12’ E) between May (pre-breeding) and July (chick-rearing) and equipped with geolocators. We used mk18 and mk13 (British Antarctic Survey), mk4083 and mk4093 (Biotrack) and Intigeo F100 and C65 (MigrateTechnology) mounted on a Darvic leg band. Devices measured light intensity every minute and recorded the maximum light intensity every 5 or 10 min. They also measured conductivity (as proxy for bird immediate environment, i.e., immersion) every 3 or 30 s and stored the number of wet measurements for every 10 min period. We recaptured 83% of the individuals at their return to the colony and recovered the geolocator (Table S2.1). Only complete annual tracks were used in the analyses after filtering out partial tracks caused by device failure or battery discharge. Overall, we acquired 200 complete tracks from 130 different individuals (see Fig. 2.1), covering 11 non-breeding seasons, continuously (fall 2008 to spring

2019). We tracked 33 individuals across multiple years (from 2 to 7 years) providing a total of 104 repeated tracks that were used to investigate within-individual consistency in movement. This repeated tracking was not always continuous, with gaps of 1 to 5 yr for 14 out of 33 individuals.

To infer geographic positions, geolocator data were processed according to the procedure developed for the SEATRACK project (Bråthen et al. 2021) and based on the threshold method calculating positions from twilight events (‘coord’ function from *GeoLight* package; Hill & Braun 2001, Lisovski & Hahn 2012, Lisovski et al. 2020). The procedure automatically identifies twilight events from raw light data (‘twilightCalc’ function from *GeoLight* package; Lisovski & Hahn 2012) and applies a set of filters to twilight events (removing or moving events from false day/night detections or noise) and positions (speed, distribution limits, angle filter). Thus, all the geolocator data were processed automatically and consistently for all years of the study. Because light sensors from different geolocator models may differ, each track was calibrated individually. As such, the calibration method avoided systematic bias in latitude related to potential differences in light sensors among geolocator models or years of production. Based on the approach by Hanssen et al. (2016) and van Bemmelen et al. (2019), the calibration method used a set of criteria that allowed calibration of tracks from kittiwakes breeding in the Arctic (79° N), where constant daylight prevents calibration at the time of deployment and recapture. By plotting the latitude against time for a range of sun elevation angles and for each track (Fig. S2.1 in the Supplement), the sun elevation angle that was manually selected (1) minimized the amplification of the latitudinal error close to the equinoxes, (2) resulted in matching latitudes at both sides of the equinox, (3) resulted in positions that fitted the latitude of the colony at the beginning and the end of the track and (4) fitted the shape and position of the oceans and continents when plotting the positions on a map (Fig. S2.2). The resulting sun elevation angle varied from −4.5 to −2.5° (mean angle −3.3°). The method also included rooftop calibration of geolocator models, with the purpose to select model specific thresholds that would result in approximately the same sun elevation angles among geolocator models. The mk-series geolocators from the British Antarctic Survey and Biotrack were as signed a threshold of 1 unit, while Intigeo geolocators from Migrate Technology were assigned a threshold of 11 units.

Although longitudes can still be determined reliably around the equinoxes, estimation of latitudes is inherently imprecise during this period, because day length is similar around the globe (Lisovski et al. 2012). Therefore, locations around equinoxes were excluded (8 Sep−20 Oct, 20 Feb−3 Apr; Bråthen et al. 2021). Additionally, continuous daylight during the polar summer (or continuous night during polar winter) does not allow geolocation-based tracking using light-level sensors. To fill these gaps and reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm that was specifically developed for SEATRACK (Fauchald et al. 2019), based on a method originally proposed by Technitis et al. (2015). In short, this algorithm is based on the determination of so-called space-time prisms, which are 3-dimensional volumes defined by the coordinates *(x,y)* and time *(z)*. The space-time prism delineates all the potential paths that can be followed by an individual moving from point A to point B, given 3 parameters: the distance from A to B, the time budget available, and the maximum rate of movement (Miller 1991). When projected onto a 2-dimensional plane, the space-time prism becomes the potential point area (hereafter *Ppa*; Technitis et al. 2015). Although the 3-dimensional representation of the space-time prism is useful to understand its concept (Neutens et al. 2007), it is naturally more convenient to work with only 2 dimensions when dealing with discrete time steps, as is the case in tracking studies, where locations are obtained at specific time intervals. Computing the *Ppa* in this context is straightforward (Technitis et al. 2015), given that the 3 above-mentioned parameters are known. Let us consider a startpoint (A) and start time *(ti*−1), and an endpoint (B) and end time *(ti*+1). Knowing the maximum rate of movement and the time *ti* at which a new location *(Ni)* is to be created, one can determine the circle defining the maximum range *(rgi*−1) from point A to the new location and the circle defining the maximum range *(rgi*+1) to point B, centred on B. The *Ppa* corresponds to the area of overlap between those 2 circles of maximum range, i.e., the area delimiting all locations that are reachable from both A and B, given the time budget and maximum movement rate. This process can be repeated any number of times, depending on the number of new locations that need to be generated. The new locations are generated in a random order (i.e., not chronological), thus creating a sort of correlated random walk respecting the constraints set by the relative position of A and B, the time budget, and the maximum movement rate. Here, we used a dynamic value for the maximum movement rate parameter, based on the distribution of observed movement rates as a function of time elapsed between 2 locations from the dataset. To do so we calculated, based on each individual track, the movement rates for random combinations of known locations separated by varying time-intervals. We used the 75th percentile from that distribution as the maximum movement rate (Fig. S2.3). The 75th percentile was computed by quantile regression, using the function ‘rq’ from package *quantreg* (Koenker 2020). Finally, the algorithm uses additional information to constrain the new positions obtained: (1) immersion data to determine attendance at the colony and force a new location to remain close to the colony during the breeding season, (2) land masks (land filters) to constrain positions over the ocean, (3) longitudes (obtained from the geolocator data, as longitude can still be estimated during the equinoxes), and (4) light levels to determine whether the new position was north of the latitudinal limit of the polar day in summer or night in winter (i.e., continuous day/night recorded by the loggers).

In all further analyses, an annual track refers to the non-breeding period extending from the colony departure in fall to the return to the colony area the following spring. Departure from the colony and return to the colony were identified using Lavielle partitioning algorithm (‘ts.LaviellePart’ function from R package *adehabitatLT* v.0.3.25; Calenge 2006, Barra quand & Benhamou 2008) over a 5 d running maximum of the saltwater immersion data indicating a transition between land use (mostly dry) and continuous pelagic behaviour (mostly wet). Departure and arrival dates were adjusted according to visual inspection of the individual’s locations right after the behavioural transition from land use to pelagic in fall, and right before the transition from pelagic to land use in spring. In spring, foraging trips after the first visit to the colony area were excluded, as individuals start to display a central place foraging behaviour, including long pre-laying trips as far as Iceland (Bogdanova et al. 2011).

Consistency in intertrack distances

To estimate the consistency in non-breeding movement over the entire annual tracks either among or within individuals, we used an approach based on the nearest neighbour analysis (for similar methods see Guilford et al. 2011, Dias et al. 2013, van Bemmelen et al. 2017). For each location of a focal track, we calculated the orthodromic distance to the nearest location on (1) a randomly selected track from another individual to estimate among-individual consistency and (2) a track from the same individual but from another year to estimate within-individual consistency. Pre-breeding movements were excluded, and positions were considered to be fixed at the colony after the first visit in the colony area in spring. This nearest neighbour distance was calculated over a large time window (60 d) to assess spatial consistency in movement. The 60 d time window was selected after running a sensitivity analysis using different time windows varying from 1 to 120 d (with 10 d intervals) to assess when apparent variation related to timing differences fades (Fig.

S2.4). The time window we selected allows spatial comparison without overlaps between fall and spring migrations that would be created if using a larger time window (i.e. >100 d). We repeated the method described above with a 1 d time window (i.e., daily comparison) to compare dissimilarities among tracks generated by both spatial and timing differences. We bootstrapped the resulting distances 10 000 times to calculate the mean intertrack distance per day among and within individuals. The results were log-transformed before further analysis to meet the assumptions of homoscedasticity and normality of residuals. We fitted linear mixed-effects models (LMER, R package *lme4* v.1.1-23; Bates et al. 2020) to determine if among- and within- individual distances differ, using the mean intertrack distance for each annual track, with individual and year as random factors. Sex had no effects on individuals with known sex (LMER; using the 60 d time window: $\beta = 0.05$, $SE = 0.05$, $df = 107.1$, $p = 0.318$; using the 1 d time-window: $\beta = 0.04$, $SE = 0.03$, $df = 116.7$, $p = 0.191$) and was therefore discarded from the final models on all individuals. Following the method used by van Bemmelen et al. (2017), the mean intertrack distance calculated over the large time window (60 d) was mapped to illustrate both among- and within-individual spatial consistency in movement during the non-breeding period.

Variability in migration schedule

To illustrate the variability in migration schedule, we extracted parameters associated to important migration phenology events: (1) the departure from the colony, (2) the start of the southward migration movement, (3) the crossing of the Arctic Circle in fall corresponding to the end of the post-breeding staging in the northern regions (Barents and Greenland Seas), (4) the start of the northward migration movement and (5) the arrival at the colony defined as the first visit to the colony area in spring. We estimated the variability in the timing of each phenological parameter at the population level. To do so, we calculated the difference between the latest date in a given year and the dates from all other individuals in the same year and then averaged these differences over the 11 yr of the study. We also estimated the within-individual variability in migration timing for each phenological parameter for individuals tracked multiple years (n = 33 individuals, 104 annual tracks). This was done by calculating the difference between the latest date for a given individual and the dates from all the other years this individual was tracked and then averaged over all individuals. Mean dates are reported with their standard deviation. Finally, we estimated the individual repeatability *r* (intra-class correlation) for the timing of each phenological parameter. This was done using the function ‘rpt’ of the R package *rptR* v.0.9.22 (Stoffel et al. 2017) and using only individuals with multiple years of tracking (see Table S2.3). We used ‘year’ as random effect only for the ‘colony departure’ to account for important interannual variation in this parameter. The repeatability estimate *r* is not a measure of absolute consistency, but the proportion of total variance accounted for by differences between groups (i.e., in our case among individuals; Nakagawa & Schielzeth 2010). All analyses were carried out in R version 4.0.2 (R Core Team 2020).

Non-breeding staging areas

We used Hidden Markov Models (HMMs; Zucchini et al. 2017) to examine at-sea behaviour of individuals and identify the sequence of discrete behavioural states that best fitted the non-breeding tracks of individuals. HMMs were fitted to all individuals at once using R package *moveHMM* v.1.7 (Michelot et al. 2016) with gamma and von Mises distributions to describe the frequency of step length and turning angle distributions, respectively. Different initial parameter values were tested to ensure numerical maximization of the likelihood through the iteration process. A 4-state model was selected after examination of the pseudo-residuals (Michelot et al. 2016) and because it better fitted the geolocation data than simpler 2- or 3-state models based on AICs and initial inspection of distribution of movement parameters (see Table S2.4 and Fig. S2.5). States 1 and 2 were defined by short steps (<85 km) with either frequent shifts in direction (angle concentration of 0; State 1) or moderately directional movement (angle concentration of 1; State 2) and attributed to periods of staging in more intensively utilized areas (see Table S2.4). States 3 and 4 were defined by long steps (>150 km) with moderate shifts in direction (angle concentration of 0.5; State 3) or highly directional movement (angle concentration of 7; State 4) that characterized transient and commuting behaviours during travelling periods (see Table S2.4). In further analyses, the first 2 states were combined into a broader 'staging state' and the last 2 states into a 'travelling state' to determine stationary and travelling positions, respectively. We were only interested in the stationary positions (staging state), which we mapped separately for the fall migration, winter, and spring migration periods to illustrate the main staging areas during each period (see Fig. 2.1). Therefore, the 'staging areas' refer to more intensively utilized areas throughout the nonbreeding period. Finally, we calculated the 80 and 50% utilization distribution kernels (UDs) over the stationary positions projected using a Lambert Azimuthal Equal Area coordinate system and the R package *adehabitatHR* v.0.4.18 (Calenge 2006) with a smoothing factor (h) of 200 km and grid cells of 50 × 50 km. We used the kernels to identify important staging areas for our study population and to illustrate the correspondence between these staging areas and the spatial consistency in the intertrack distance of individuals.

RESULTS

Individual tracking and migratory routes

The mean annual departure date from the colony varied from 27 August to 25 September (5 September ± 9 d [SD]). Individuals staged within the Arctic in the Barents and Greenland Seas (mean annual staging from 38 to 64 d, 52 ± 7 d) before migrating southwest along a corridor between East Greenland and Iceland (Fig. 2.1). The mean annual date of onset of fall migration ranged from 10 to 29 October (19 October ± 5 d). All individuals spent the winter in the North Atlantic Ocean, with the main wintering area extending from the Grand Banks of Newfoundland to the mid-Atlantic ridge. The winter distribution of the population was therefore largely pelagic, but alternative staging areas were also used along the continental shelves of Northeast America and Western Europe (Fig. 2.1 and see UDs of Fig. 2.3). The northeast movement of spring migration (mean annual starting date from 31 March to 9 April, 4 April ± 3 d) was spread over a larger front than in fall, with routes passing both north and south of Iceland (Fig. 2.1). The mean annual date of arrival in the colony area varied from 10 to 20 April (15 April ± 5 d).

Non-breeding movement consistency in space

The nearest neighbour analysis conducted over a large time window (60 d) indicated high spatial consistency during the non-breeding period in the studied population, both within and among individuals (Fig. 2.2A, see also examples of repeated tracks from several individuals in Fig. S2.6). The mean within-individual intertrack distance was 261 km (95% CI: 180−376 km), significantly lower than the mean intertrack distance of 545 km found among individuals (95% CI: 377−793 km; LMER, $\beta = 0.71$, $SE = 0.04$, 95%CI: 0.62; 0.80, $df = 218.9$, $p < 0.001$). The mean within-individual intertrack distance was consistent regardless of the number of years individuals were tracked (LM, $\beta = 12.2$, $SE = 23.7$, $t_{31} = 0.5$, p > 0.609), indicating that site fidelity persists over longer tracking periods (range 2 to 7 yr). Mapping intertrack distances (Fig. 3) showed areas of high spatial consistency among individuals in the western part of the North Atlantic Ocean as well as in the Greenland Sea (east coast of Greenland and Svalbard) and in the Barents Sea (between Svalbard and Novaya Zemlya, Fig. 2.3A). These sectors of high spatial consistency correspond to the main staging areas identified with the Hidden Markov Models (Fig. 2.1) and illustrated with 80 and 50% utilization distribution kernels (Fig. 2.3A). Similarly, areas associated with high consistency within individuals were also associated with staging areas in the Northwest Atlantic Ocean and the Greenland and Barents Seas but also with areas along the coasts of Northeast America and, to a lesser extent, Western Europe (Iberian Peninsula and British Isles, Fig. 2.3B). Across the non-breeding season, the kittiwake distribution was mostly pelagic with 73% of the locations (32 327 out of 44 071 locations in total) in areas deeper than 500 m. High spatial consistency within individuals was also found in coastal areas and shallow waters of the Barents Sea (see Fig. 2.3), but the use of these areas was limited. The utilization of deeper waters was even more evident during the winter period (mid-November to mid-March), with only 12% of the locations found in areas of 0−500 m depth (2816 out of 24 034 winter locations). Overall, spatial consistency within individuals remained high over deeper waters (Fig. S2.7), indicating that site fidelity was also common in pelagic areas.

Non-breeding movement consistency in time

The nearest neighbour distance analysis conducted over a short time window (daily comparison to include variations associated with timing effects) also showed higher consistency in mean intertrack distances (Fig. 2.2B; LMER, $\beta = 0.39$, $SE = 0.02$, 95% CI: 0.35; 0.44, $df = 204.9$, $p < 0.001$) within (847 km, 95% CI: 694−1026) than among individuals (1257 km, 95% CI: 1034−1546). Using a short time window in the analysis revealed peaks in timing variability during fall (October to mid-November) and spring (mid-March to mid-April) associated with migratory stages (Fig. 2.2B). Individual repeatability estimation of phenological parameters during migration stages (Fig. 2.4B) showed low individual repeatability in timing of post-breeding colony departure ($r = 0.20$, 95% CI: 0.02; 0.39, $p < 0.001$) driven by a relatively high intra-individual variability (see Fig. 2.4A and Table S2.4), high repeatability in the onset of the fall migration movement (r = 0.80, 95% CI: 0.65; 0.88, p < 0.001), and moderate repeatability in the timing of the crossing of the Arctic Circle after the post-breeding staging in the Barents and Greenland Seas (r = 0.54, 95% CI: 0.33; 0.69, p < 0.001). In spring, the very low repeatability estimates in the timing of the onset of the migration movement (r = 0.36, 95% CI: 0.12; 0.55, p = 0.002) and the arrival in the colony area (r = 0.28, 95% CI: 0.04; 0.49, p = 0.016) were driven by high consistency in the timing of these events among individuals (see Fig. 2.4B and Table S2.3). Overall, the timing of phenological events, both within and among individuals, showed higher variability during the fall period than during the spring period (Fig. 2.4A and Table S2.2), indicating the spring migration occurred during a shorter time interval.

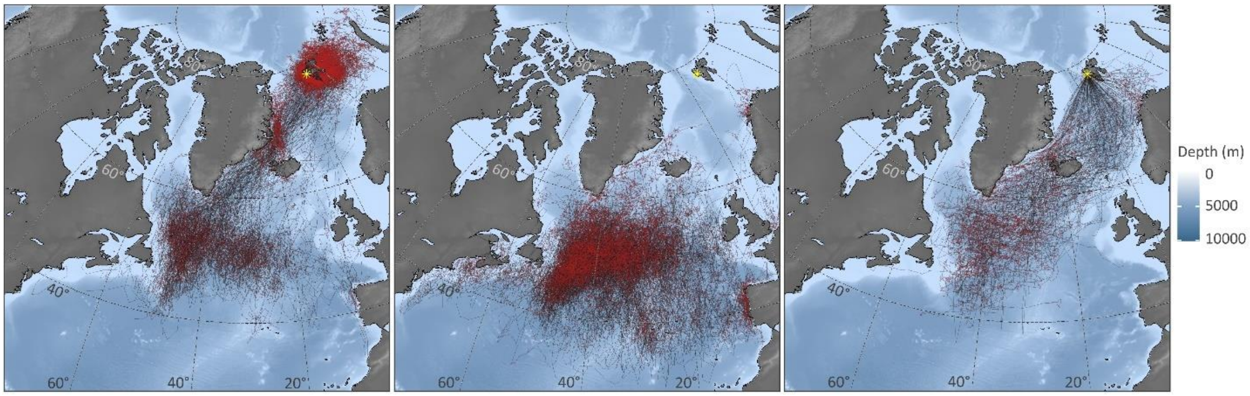

Figure 2.1: Non-breeding distribution of black-legged kittiwakes (*Rissa tridactyla*) during the fall migration period (left panel, colony departure to mid-Nov), winter period (middle panel, mid-Nov to mid-Mar) and spring migration period (right panel, mid-Mar to the first visit to the colony area) with staging locations (red dots) from Hidden Markov Models and movement paths (grey lines) for all individuals tracked between fall 2008 and spring 2019. The yellow star indicates the colony location. Plotted over a bathymetry map and using a Lambert Azimuthal Equal Area projection.

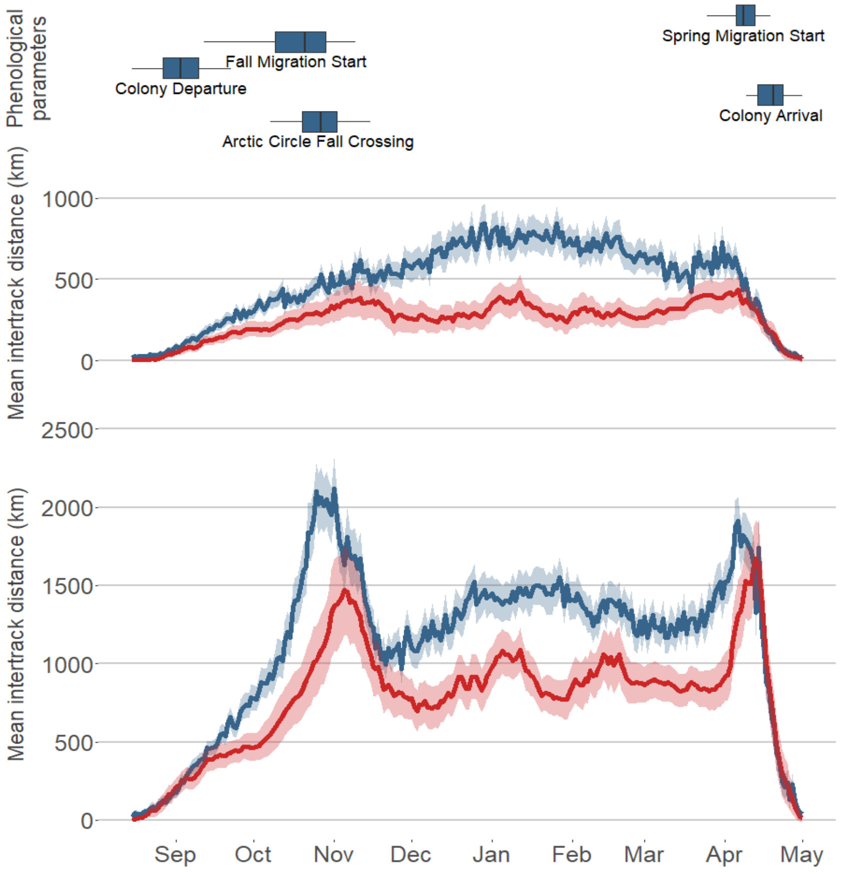

Figure 2.2: Consistency in non-breeding movements of black-legged kittiwakes (*Rissa tridactyla*) from bootstrapped mean intertrack distance estimated among (blue) and within (red) individuals. The top panel shows consistency in space with distances estimated over a large time window (60 days) reducing timing effects in movement dissimilarities while the bottom panel shows consistency in space and in time with distances estimated *per* day (1-day-time window). The shaded areas represent 95% confidence intervals of the bootstrapped mean intertrack distance. Boxplots show among-individual variation in the timing of phenological events associated with the migration periods (boxes indicate 25th, 50th and 75th percentiles and whiskers show the 5th and 95th percentiles).

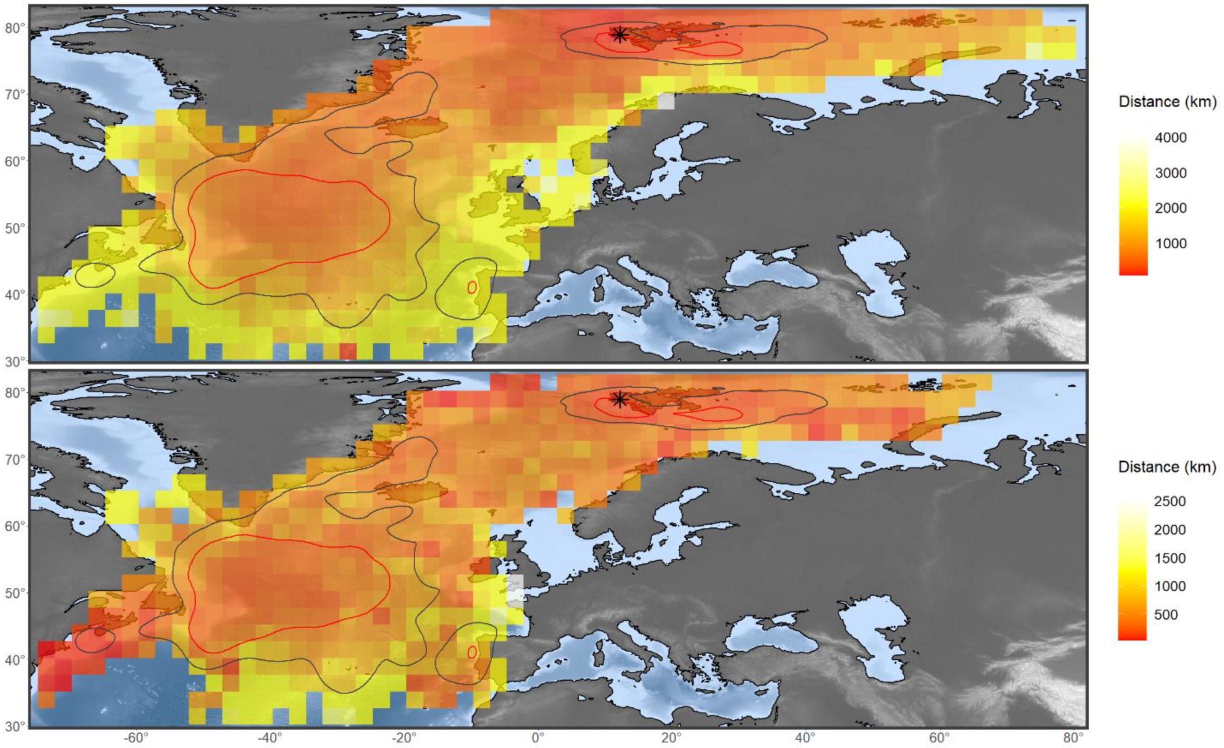

Figure 2.3: Heat maps of mean intertrack distances showing spatial consistency among individuals (top panel) and within individuals (bottom panel) during the non-breeding period. Distances are estimated with the nearest neighbour distance analysis using a large time window (60-day) to exclude most of the variability associated with timing effect and illustrate consistency in space only. Darker grid cells (2.5° latitude x 2.5° longitude) indicate areas of higher spatial consistency in movement. The polygons represent the utilization distribution (80% kernel in grey and 50% kernel in red) calculated over the stationary locations only. The black asterisk indicates the colony location.

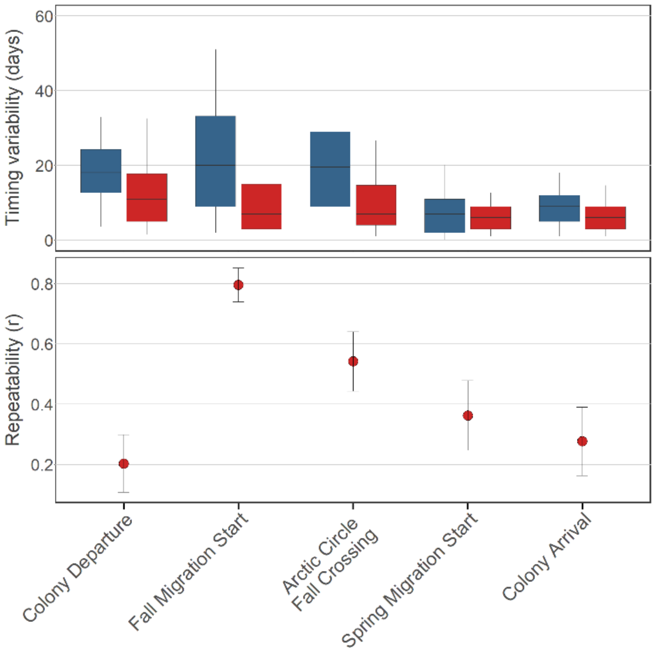

Figure 2.4: The upper panel shows observed variation in timing of phenological parameters estimated at the population level (blue boxes) and individual level (red boxes). Boxes show the 25th, 50th and 75th percentiles and whiskers show the 5th and 95th percentiles. The lower panel shows the individual repeatability in timing of phenological parameters (inter-class correlation coefficient, *r*) with standard errors, where 0 corresponds to low repeatability and 1 to high repeatability.

DISCUSSION

Kittiwakes showed high spatial consistency in nonbreeding movements at both macro (>1000 km) and meso scales (100−1000 km), suggesting that individuals benefit from predictability in resources at these coarse scales. The significantly higher consistency within individuals than among individuals indicated specialization in space-use strategy at the individual level. With a deviation in routes among years of less than 300 km on average, the inter-annual spatial consistency of individuals indicated important site fidelity at the individual level, especially when considering the coarse resolution of geolocator measurements and the wide ocean-scale distribution and long migrations of the studied population. In contrast, we found low repeatability in the timing of important phenological events in general, which suggests that those intrinsic timing mechanisms known to be repeatable across years, such as the individual's biological clock, may not have been a strong driver of the movement consistency of individuals over the years of the study (but see Section 4.3). Thus, repeatability is likely governed by memory of the location of high-quality patches relatively unconstrained by intrinsic factors. This individual spatial consistency was stable over the entire non-breeding season, with site fidelity to the wintering staging areas and also to the migratory staging sites used during fall in the Barents and Greenland Seas.

Fidelity to deep-water areas

High fidelity to staging areas outside the breeding season is not uncommon in seabirds and is often associated with more predictable areas along continental shelves and less with oceanic habitats (Weimerskirch 2007). For instance, highly productive upwelling habitats along shelf edges in the Canary and Benguela current systems were associated with site fidelity during the non-breeding period in black-browed albatrosses *Thalassarche melanophrys*, Cory's shearwaters *Calonectris borealis* and long-tailed skuas *Stercorarius longicaudus* (Phillips et al. 2005, Dias et al. 2011, van Bemmelen et al. 2017). Similarly, kittiwakes tracked in this study used the shelf edge of the Grand Banks, an area known for its high biological productivity (Heywood et al. 1994, Maillet et al. 2005, Frederiksen et al. 2012). However, many individuals also wintered in deep waters, from the edge of the Grand Banks plateau to the mid-Atlantic Ridge. Despite this highly pelagic distribution, individuals showed area fidelity, suggesting this deep-water area can provide habitats with enough coarse-scale predictability in resources to stimulate area fidelity. In comparison, black-legged kittiwakes tracked in the North Pacific also showed some degree of individual fidelity to pelagic areas (~25% of locations within 400 km grid squares; Orben et al. 2015), but to a lesser extent than what we found in the North Atlantic (~75% of locations within 400 km of mean nearest neighbour distance). However, a similar degree of spatial consistency (median nearest neighbour distance 250 to 400 km) to what we found with kittiwakes was described in long-tailed skuas for the same oceanic area west of the mid-Atlantic ridge, which they used as a staging area during migration (van Bemmelen et al. 2017).

This oceanic region is crossed by the subpolar front extending from the Newfoundland Rise to the mid-Atlantic Ridge and characterized by a strong horizontal temperature gradient, eddies, and nutrient mixing and retention inducing biological productivity enhancement (Heywood et al. 1994, Scales et al. 2014, Hátún et al. 2016). There is evidence that this mid-ocean frontal zone is an important staging site and a diversity hotspot for multiple seabirds (e.g., Guilford et al. 2009, Egevang et al. 2010, Hedd et al. 2012, Montevecchi et al. 2012, Weimerskirch et al. 2015), as well as other marine predators such as sharks (Queiroz et al. 2016), tunas (Walli et al. 2009), chelonioid turtles (Eckert 2006), and cetaceans (Doksæter et al. 2008, Skov et al. 2008). This large overlap in distribution has stressed the potential vulnerability of marine vertebrate populations relying on this area to large-scale changes in environmental conditions affecting resource predictability and availability (Frederiksen et al. 2012), such as the weakening of the subpolar gyre and warming of the North Atlantic (Häkkinen & Rhines 2004, Descamps et al. 2013, 2017, Fluhr et al. 2017, Hátún et al. 2017). Populations showing important site fidelity are expected to be more sensitive to extrinsic factors affecting resource predictability and might thus be particularly impacted by such carry-over effects (Phillips et al. 2017).

Movement strategy in space

To a certain extent, marine predators are expected to adjust their space-use strategy in response to environmental changes affecting resource predictability of foraging patches over time (Davoren et al. 2003, Wakefield et al. 2015). This ability to respond to environmental variability by using a 'win-stay, lose-shift' strategy directly depends on the flexibility and plasticity in behavioural traits intrinsic to the population and individuals (Canale & Henry 2010). Area shifting was uncommon in our study, and we found an overall high spatial consistency, even for individuals tracked up to 7 years. This long-term area fidelity could be expected to arise if individuals benefited from consistency in resource availability in known staging areas over the course of the study, thus preventing the need for important shifts in distribution at meso or macro scale. Alternatively, long-term site fidelity can be reinforced by site familiarity and the benefits of acquiring information specific to an area, leading to individuals favouring an 'always-stay' strategy (Irons 1998, Wakefield et al. 2015). Advantages of returning to a known area include increased foraging efficiency through knowledge about food location and availability, movement efficiency by using prevailing wind corridors, dominance during competitive interactions as well as avoiding potential risks of visiting unfamiliar places, such as higher risks of getting stranded (Piper 2011). In contrast, some seabird populations show high flexibility in their non-breeding distribution with individuals possibly having several preferred migratory strategies (Dias et al. 2011, van Bemmelen et al. 2017). For example, some long-tailed skuas shifted their winter distribution between years at the ocean scale, between the Benguela current and the Falkland current (van Bemmelen et al. 2017). They followed a specific route for each alternative wintering site and kept the same route over the years, indicating this shifting behaviour was not accidental but based on past experience. Similarly, Cory's shearwaters used wintering areas independently of prevailing wind currents encountered en route, suggesting the choice of using one or another alternative site was deliberate and predetermined (Dell'Ariccia et al. 2018).

We also found that some kittiwakes showed flexibility in their migratory decisions by shifting their staging areas or by displaying a more exploratory behaviour with different degrees of itinerancy, although this occurred at a more modest scale than in long-tailed skuas and Cory's shearwaters. If a decrease in resource availability can stimulate area-shifting, the cause of the flexibility observed in some individuals can emerge from a diversity of factors both extrinsic or intrinsic, and thus remains unclear. For instance, the breeding status is likely to vary across years and is known to introduce inter-annual variability in individuals' space-use strategies (Phillips et al. 2017). In some species, failed breeders engaged in longer (Bogdanova et al. 2011) or shorter migration (Phillips et al.2005) compared to successful breeders, indicating that the choice of wintering sites can be condition-dependent to the breeding investment.

Plasticity in timing of movement

The dynamics of large-scale climatic and oceanographic systems, such as the subpolar gyre, generate strong interannual variations (up to several weeks) in the timing of biological productivity (i.e., phytoplankton bloom) in the North Atlantic (Gaard et al. 1998, Henson et al. 2009), with cascading effects on higher trophic levels (Henson et al. 2009, Eliasen et al. 2011). In response to these interannual fluctuations, marine predators following foraging patches learned on past travels are expected to show higher movement consistency in space than in time. This pattern is what we observed with individuals showing high spatial consistency, suggesting that individual specialization is driven more by space utilization in relation to extrinsic factors with higher predictability in space than in time.

Similarly, when investigating phenological parameters associated with migratory movement, we observed overall low repeatability in timing across years. Notably, we found low repeatability in the timing of the colony departure, a phenological parameter often related to breeding status and reproductive investment (Bogdanova et al. 2011, Whelan et al. 2020). In another study, food supplementation enabled fed kittiwakes to initiate departure from the colony earlier than unfed kittiwakes, indicating that individuals experiencing lower breeding costs are able to transition into the non-breeding season in better condition and initiate migration earlier (Whelan et al. 2020). Interestingly, high repeatability only occurred for the timing of the onset of the fall migration. Considering the large range of departure dates in the population, this high within-individual repeatability suggests that intrinsic timing mechanisms played an important role in the phenology of the fall migration movement. This has been demonstrated with blue whales *Balaenoptera musculus*, where movement phenology was driven not by proximate environmental factors, but rather by the average timing of these factors across years at specific staging sites (Abrahms et al. 2019). This highlights the importance of memory and individual biological clock as intrinsic factors regulating the timing of individual movement in this long-lived species.

Additionally, the low individual repeatability in phenology of the spring migration was driven by low variation among individuals. This synchronicity in phenology in spring, coupled with high variation in timing of phenological parameters among individuals in fall, indicated that spring migration might be more time constrained. This is often the case for polar and subpolar migrants, as the optimal arrival date at the breeding site is a compromise between costs and benefits of an early arrival with individuals benefiting from e.g., a better nesting site or higher mating success while confronted with the risk of being exposed to harsh environmental conditions in early spring (Kokko 1999). These constraints are usually relaxed or absent in fall, leading to more variability in the timing of the fall migration (Nilsson et al. 2013), but carry-over effects arising from the breeding status and investment can also contribute to among-individual variations in post-breeding migration patterns (Harrison et al. 2011).

In conclusion, black-legged kittiwakes were remarkably consistent in their overwinter locations among years despite wintering primarily in pelagic regions of the North Atlantic. The consistency was stronger within than among individuals, implying that individuals were using memory to return to profitable locations year upon year. Consistency was also stronger in space than in time, suggesting that it was driven by consistent resource pulses that vary in time more so than space, and that intrinsic drivers (photoperiod, hormones, condition) that are known to be repeatable within individuals were somewhat less important. Of course, intrinsic and extrinsic factors often interact with one another (i.e., foraging success can influence body condition which can influence hormones), and in reality, both types of factors will be integrated by the individual to decide when to stay or go. Consistent use of key foraging locations is likely associated with foraging success, risk of starvation, and a strong driver of overwintering survival, linking variation in timing of resources to individual fitness and, ultimately, population trends.

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LINKING STATEMENT

In Chapter 2, I assessed movement repeatability in space and time. I demonstrated that kittiwakes exhibit individual repeatability in their non-breeding movements and show fidelity to specific oceanic areas during the wintering stage. Such specialization in spatial use suggests vulnerability to alterations affecting environmental and feeding conditions. Perhaps more importantly, such individual repeatability implies that potential carry-over effects arising from the wintering stage are structured spatially among individuals. I will expand on this concept throughout the thesis: individuals using different wintering areas may face distinct carry-over effects, potentially creating differential fitness potential among them over the years. In the subsequent chapters, I will explore how site fidelity leads to variations among individuals in their energy expenditure during winter (Chapter 3) and in their exposure to pollutants, specifically per- and polyfluoroalkyl substances (Chapter 4). In Chapter 5, I will test for carry-over effects emerging from such interindividual differences in winter site fidelity, movement phenology and energy expenditure.

CHAPTER 3 – HIGH ENERGY EXPENDITURE AT THE CORE OF A SEABIRD'S WINTER RANGE: METABOLIC MECHANISMS FOR RANGE LIMITS

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ABSTRACT

Understanding how geographic range limits are shaped is a central and challenging question in ecology that has become particularly critical in the context of global environmental changes. While such limits are often studied for resident or breeding species, range limits are equally important for migratory species in winter when population limitation may occur due to limited resources. A central hypothesis in several theories for range limitations 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 118 adult kittiwakes (n= 178 tracks) with geolocation devices and saltwater immersion sensors to estimate the time-activity budget and energy expenditure of individuals during winter, and estimated their reproductive success after their return to the colony during summer. 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 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

Range limits; Distribution; Animal movement; Non-breeding movement; Seabirds; *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 these range limits 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 environmental changes (Parmesan 2006, Sexton et al. 2009, Alexander et al. 2022). That question is particularly challenging for migratory species where population limitation may occur at different times of the year, and so range limits may reflect processes occurring thousands of kilometres away. Because a species' geographic range throughout its annual cycle is the expression of the ecological niche at large scales when accounting for dispersal, investigating the drivers of range limits requires defining the set of environments throughout that 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 play a key role on 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 overwinter 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, and empirical studies are therefore 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 life cycle is often spent outside the breeding range (Newton 2008). Environmental conditions experienced over the non-breeding range can lead to mass mortality events in migratory species such as butterflies (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), with subsequent impacts on population dynamics (e.g., Woodworth et al., 2017). 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 remote, offshore areas.

For species wintering at high latitudes, winter represents an energetically demanding period with deterioration in weather conditions and reduced daylight, temperature and/or food quality creating a potential “energetic bottleneck” in their annual life cycle (Fort et al. 2009, Kautz et al. 2020). Winter conditions are strongly linked to survival through their impact on energy budget, as highlighted in various studies (e.g., Grosbois & Thompson, 2005; Mysterud et al., 2001; Woodworth et al., 2017). The ability of wintering individuals to maintain their energy balance has profound consequences on life history traits, especially mortality or reproductive potential, which ultimately shape population dynamics (Schneider 2004). To traverse periods of adverse conditions, wintering animals often make important adjustments in their behaviour (e.g., nocturnal foraging, torpor; Dunn et al. 2020, Geiser 2020, Patterson et al. 2022). Maintaining the energy balance is thus under strong evolutionary pressure. This may even drive 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 life cycle (Greenberg and Marra 2005, Dingle and Alistair Drake 2007). Indeed, 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 stages of their life cycle where they are out of reach (Wilmers et al. 2015, Davidson et al. 2020).

We tested the abundant-centre hypothesis by investigating whether density, fitness and performance of individuals decreased towards the edge of the range. We used energy expenditure as a proxy for variation in foraging performance across the winter distribution range, and linked it to reproductive success during the subsequent breeding season. 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 of the distribution. If this is the case, we also hypothesized that this difference in energy expenditure in winter would lead to a decrease in fitness of individuals wintering towards the edge of the wintering range because of carry-over effects on subsequent reproductive attempts. 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 reported by 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 Atlantic kittiwake populations are panmictic in winter (Frederiksen et al. 2012) and the winter distribution of the studied population is likely representative of the subspecies (see Léandri-Breton et al., 2021). Moreover, as a pelagic species, the kittiwake’s distribution is continuous and without obvious geographical barriers that could limit their range. We used 11 years of geolocation tracking (fall 2008 to spring 2019) from 118 individuals to estimate the energy expenditure through the activity pattern 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 and investigate drivers of range limits. We combined this with reproductive monitoring data during the breeding period to estimate the reproductive success as a proxy for the individual annual fitness.

MATERIAL & METHODS

Study population and logger deployment

The studied population is a long-term monitored colony located in Kongsfjorden, Svalbard (High Arctic Norway; 78° 54’ N, 12° 12’ E). During the study period (2008 to 2019), nest content monitoring was conducted at the colony every two to six days. The success of rearing at least one chick for 10 days after hatching (hereafter ‘reproductive success’) was used as a proxy of individual fitness. It has been reported that three quarters of kittiwake chick mortality occurs within 10 days after hatching (Coulson and Porter 1985) and, in some years, nests could not be monitored until chicks fledged, so we considered this measurement to be representative of reproductive success. The sex of individuals was determined by molecular sexing (following Fridolfsson and Ellegren 1999) or through behaviour when paired with a known-sex partner.

We used 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 cable 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 minute and recorded the maximum light intensity every 5 or 10 min. They also measured saltwater immersion (that we used as a proxy for bird activity, i.e., whether or not the bird was in contact with the sea water) every 3 or 30 s and stored the number of wet measurements within every 10 min period.

We recaptured 83% of the individuals at their return to the colony and recovered the geolocators. 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. One track was discarded because the kittiwake likely spent time on land as indicated by extensive periods of low saltwater immersion associated with stationary positions along the coast. This pattern was not observed in any other tracks. Overall, we acquired 178 complete tracks from 118 different individuals (see Fig. 3.1, 55 females and 63 males), covering 11 non-breeding seasons, continuously (fall 2008 to spring 2019).

Our study does not include data on mortality as the used tracking devices require the individuals' recapture for the data to be recovered and it is not possible to confidently distinguish between mortality and breeding dispersal in an individual's failure to return to the colony. However, the link between energy expenditure and survival is clear and well studied (e.g., Grosbois & Thompson, 2005; Mysterud et al., 2001; Woodworth et al., 2017), and 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.

Geolocator processing

To infer geographic positions, geolocator data were processed according to the procedure based on the threshold method and developed for the SEATRACK project (Bråthen et al. 2021), as described in Léandri-Breton et al. (2021). To fill the gaps in the tracks associated to equinoxe periods and continuous daylight (or continuous night) at high latitudes, and to reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm that was specifically developed for SEATRACK (Fauchald et al. 2019), based on a method originally proposed by Technitis et al. (2015), and described in Léandri-Breton et al. (2021). This algorithm generates plausible locations using additional information available: 1) immersion data to determine attendance at the colony and force a new location to remain close to the colony during the breeding season, 2) land masks (land filters) to constrain positions over the ocean, 3) longitudes (obtained from the geolocator data, as longitude can still be estimated during the equinoxes), and 4) light levels to determine whether the new position was north of the latitudinal limit of the polar day in summer or night in winter (i.e., continuous day/night recorded by the loggers).

Winter range of the population

The start and end of the winter period were defined for each track as the last date in fall and the first date in spring the individual crossed the 60°N, corresponding to the northernmost extent of the winter distribution. We calculated the 95, 80 and 50% utilization distribution kernels (UDs) over the population's winter positions (from all tracks, n = 20 357 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. 3.2). The centre of the population's winter range was defined as the centroid of the 95% UD. Similarly, the centroid of each individual track was calculated over a 95% UD. The distance from the population centre was defined as the orthodromic distance between the population's winter centroid and the centroid of each individual's track.

Time-activity budget and Daily Energy Expenditure (DDE)

Saltwater immersion data were used to build a time-activity budget based on the identification of three behaviours (see similar methods in Dunn et al., 2020; Fayet et al., 2016; McKnight et al., 2011): 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 $x_{\mathrm{st}} = x/x_{\mathrm{max}}$, 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 ≥ 98%) and active foraging (0% < 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% < SSI < 100%, see Supporting information).

To calculate the daily energy expenditure, we combined the time-activity budget with the population-specific resting metabolic rate (i.e., 1.64 mL O_2 g^{-1} h^{-1}, Gabrielsen et al. 1988, Blévin et al. 2017) and the activity-specific field metabolic rates. 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 (0.1000 mL O_2 g^{-1} h^{-1} $°C^{-1}$) 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 equation (1) when the SST was below the species' thermoneutral zone (<4.5°C) and equation (2) when above it:

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

$$\textbf{(2)}\quad DEE = 7.3\, RMR\ \cdot T_{fly} +\ 4.05\, RMR\ \cdot T_{for} +\ RMR\ \cdot T_{rest}$$

Where RMR is the resting metabolic rate (in mL O_2 g^{-1} h^{-1}), β is the intercept of the RMR at 0°C, TC is the thermal conductance in water (O_2 g^{-1} h^{-1} $C^{\circ-1}$), 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 O_2 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 O_2 (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 murres (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 hrs 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 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 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. In all models, the individual and year were included as random factors. Sex was included in fixed factors, as well as the averaged day length experienced by individuals during winter to account for variations in activity duration related to day length (see Supporting information). Although the behavioural activity responses (averaged daily time flying, foraging and resting) are bounded by the 24-hr duration, we assumed a normal distribution and used 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 highly similar results. We provided the results of these models in the Supporting information. An additional linear mixed-effects model was fitted to assess if the averaged wind intensity experienced by individuals during the winter period varied non-randomly over the population’s winter range. 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 model. To do so, the explanatory variable was scaled. The resulting residuals met the homoscedasticity and normality assumptions. The revised R-squared (R^2 marginal) were estimated using ‘r.squaredGLMM’ function (package *MuMIn*, Bartoń, 2022; Nakagawa and Schielzeth, 2013). All analyses were carried out in R version 4.2.0 (R Core Team 2022).

RESULTS

The population’s winter distribution was spread across the North Atlantic Ocean with the centre of the population’s distribution situated at the edge of the Grand Banks of Newfoundland (n = 20 357 positions, Fig. 3.1). The centroids of the 178 tracks were dispersed over distances to the centre of the population’s distribution ranging from 34 to 3 813 km (Fig. 3.1). Over the entire winter period, the daily time-activity budget of individuals averaged 4.36 ± 0.81 hrs of flying time (range 1.7 to 6.5 hrs/day), 5.85 ± 1.10 hrs of foraging time (range 3.8 to 9.7 hrs/day) and 13.73 ± 1.04 hrs of resting time on the water (range 10.0 to 16.3 hrs/day). The winter DEE within the population averaged 835 ± 57 kJ daily, and was reflected in individuals’ non-breeding movement strategies (Fig. 3.2).

The winter DEE decreased by 14.3% (-116.8 kJ/day) from the centre to the edge of the population winter distribution (3820 km, Tab. 3.1). This variation in DEE was driven by the averaged flying activity of individuals, which decreased by 47.8% (-2.1 hrs/day) from the centre to the edge of the population winter distribution (Tab. 3.1). In contrast, there was a significant increase of 25.6% (1.9 hrs/day) in the averaged foraging activity towards the edge of the winter distribution, while no significant variation was detected for the averaged resting activity (Tab. 3.1). Sex had a significant but very marginal effect on the DEE, as well as foraging and resting activities, with males spending in average 2.8% (-23.4 kJ/day) less energy, 6.4% (0.7 hrs/day) less time foraging and 3.6% (0.5 hrs/day) more time resting on water than females (Tab. 3.1).

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 31.1 m s^{-1} (mean = 11.2 ± 4.3 m s^{-1}, n = 20 459 observations). The wind intensity was higher near the centre of the population's winter range (LMER, b_1 = -0.0008 m s^{-1}, *SE* = 0.0001, 95% CI[-0.0009; -0.0006], *df* = 130, , R^2 marginal = 0.38, $p < 0.0002$; see Supporting information) and decreased by 24% (-2.9 m s^{-1}) towards the edge of the range.

The reproductive success of individuals did not vary over the distance from the population's winter range centre (n = 101, GLMER, b_1 = -0.139, *SE* = 0.349, 95% CI[0.44; 1.72], R^2 marginal = 0.003, $p = 0.691$). The spatial variation in individuals' reproductive success is illustrated in Fig. 3.1.

Table 3.1: 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**	***b***	**SE**	**df**	**95% CI**	***p***	**R^2**
DEE (kJ)	**Distance (km)**	**-0.024**	**0.005**	**139**	**[-0.033; -0.014]**	**<0.0001**	**0.22**
	Day.length (hr)	**19.33**	**4.20**	**168**	**[10.89; 27.57]**	**<0.0001**	
	Sex	**-21.82**	**8.35**	**110**	**[-38.03; -5.34]**	**0.01**	
Flying activity (hr)	**Distance (km)**	**-0.0006**	**0.0001**	**155**	**[-0.0007; -0.0004]**	**<0.0001**	**0.34**
	Day.length (hr)	*-0.02*	*0.06*	*168*	*[-0.13; 0.08]*	*0.7*	
	Sex	*-0.12*	*0.11*	*117*	*[-0.34; 0.10]*	*0.3*	
Foraging activity (hr)	**Distance (km)**	**-0.0005**	**0.0001**	**122**	**[0.0003; -0.0007]**	**<0.0001**	**0.44**
	Day.length (hr)	**0.58**	**0.07**	**163**	**[0.44; 0.73]**	**<0.0001**	
	Sex	**-0.37**	**0.14**	**102**	**[-0.63; -0.09]**	**0.01**	
Resting on water activity (hr)	*Distance (km)*	*-0.0003*	*0.0001*	*122*	*[-0.0001; 0.0002]*	*0.7*	**0.30**
	Day.length (hr)	**-0.55**	**0.08**	**164**	**[-0.70; -0.40]**	**<0.0001**	
	Sex	**0.49**	**0.14**	**102**	**[0.20; 077]**	**0.001**	

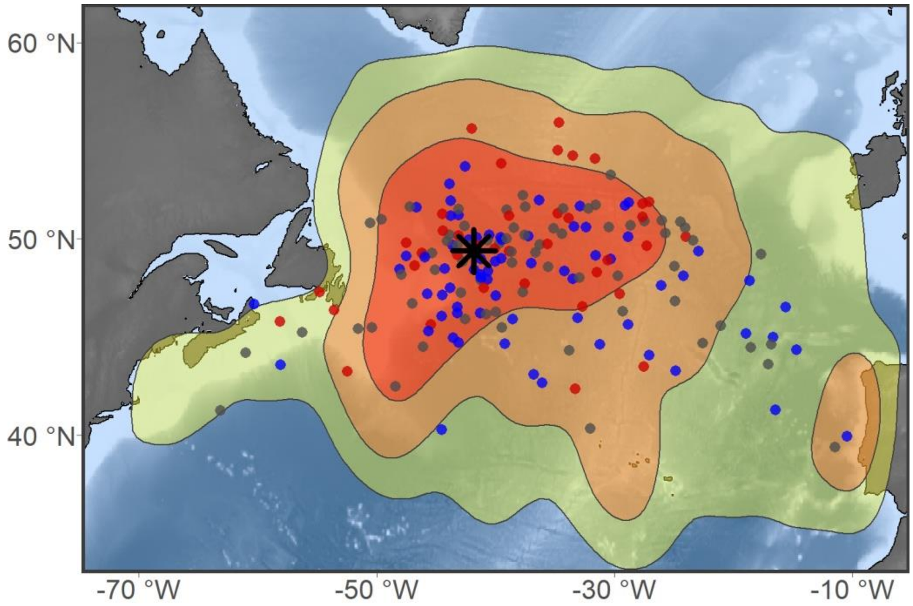

Figure 3.1: Winter distribution of black-legged kittiwakes with 95% (in yellow), 80% (in orange) and 50% (in red) utilization distribution kernels. The black star (✳) indicates the centroid of the population's range centre (n = 20 357 positions) and the dots (•) show the centroid of each individual's distribution (n = 178 tracks), with the colour coding indicating the reproductive status in the following breeding season (blue for 'reproductive success', red for 'reproductive failure' and grey 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).

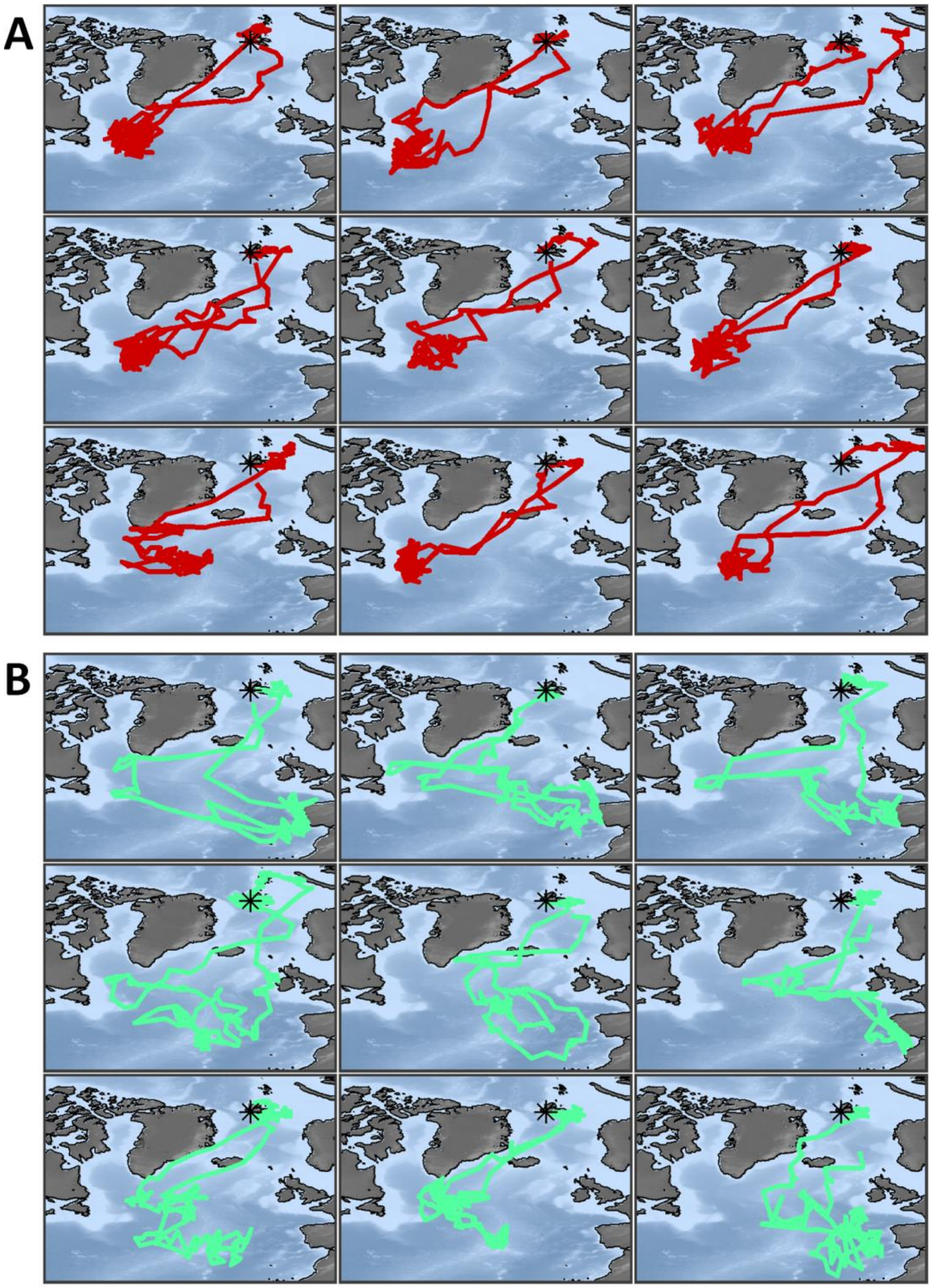

Figure 3.2: Non-breeding tracks illustrating differences in migratory strategies between A) individuals with the highest daily energy expenditure during winter and B) individuals with the lowest daily energy expenditure in winter, out of 178 tracks. The black star (✳) indicates the colony location in Svalbard, Norway.

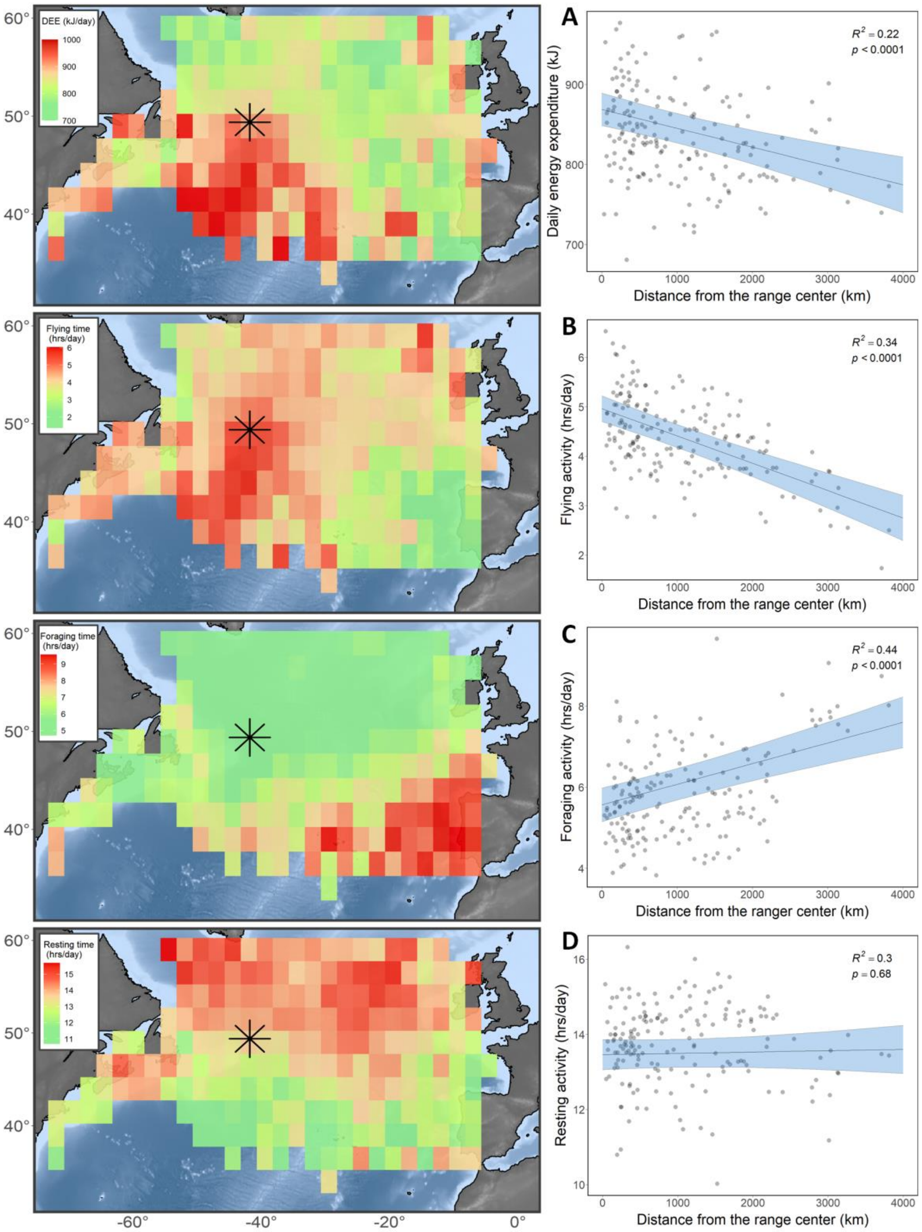

Figure 3.3: Heat maps illustrating the spatial heterogeneity in A) daily energy expenditures (kJ/day), B) time spent flying (hrs/day), C) time spent foraging (hrs/day) and D) time spent resting (hrs/day) experienced by individuals during winter, with corresponding model predictions over the distance from the centroid of the population's winter distribution. Darker grid cells (2.5° latitude × 2.5° longitude) indicate areas of higher values for each variable. The black star (✳) shows the centroid of the population's winter range (n = 20 357 positions).

DISCUSSION

Using a well-studied model species for avian migration, we tested the abundant-centre hypothesis predictions that density, performance and fitness are higher at the centre of the population range, using energy expenditure as a proxy for individual performance and 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 the assumption of the "abundant-centre hypothesis" that individuals' performance decrease towards the range periphery. These spatial variations 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 higher 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/d) would lead to rapid mass loss and mortality at the centre within a few days if not offset by higher energy intake. Thus, we suggest 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.

Annual fitness (reproductive success) did not vary over the winter range. Even if higher energy expenditure in winter leads 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. 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 during pre-laying advancing the endocrine preparation for breeding and laying phenology (Whelan et al. 2021). Overall, and in opposition to the premise of the ‘abundant-centre hypothesis”, our results suggest that the centre of the range does not necessarily provide more favourable conditions overall, but could rather result in both higher energy loss and gain than at the range periphery.

High energy expenditure at the centre of the range implies that individuals in that region 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. Oceans are undergoing major environmental changes affecting resource availability for marine predators (Hoegh-Guldberg and Bruno 2010). The consequences of these changes are already widespread: local extinction of key prey of ice-obligated seabirds, prey-switching for breeding kittiwakes in a warmer than ever Barents Sea or schooling fish depletion through fishery activities worldwide (Cury et al. 2008, Provencher et al. 2012, Vihtakari et al. 2018, Divoky et al. 2021). 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). Similarly to this, the decreasing energy expenditure towards the range edge shows that individuals at the margins are able to use alternative strategies to exploit environments with different energy constraints. Such plasticity in movement behaviour 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. However, 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).

This high winter site fidelity of the population suggests that the wintering locations used by individuals provided consistent foraging conditions during the study period, as site fidelity typically emerges when resources are predictable in time and space (Switzer 1993, Léandri-Breton et al. 2021). But can the centre of the range really provide higher feeding conditions enabling kittiwakes to compensate for their higher energy loss? The centre of the kittiwake population's range, 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 indeed a wintering hotspot for multiple species with similar diet, including an estimated 4.5 million kittiwakes congregating there in winter (Frederiksen et al., 2012; Léandri-Breton et al., 2021 and references therein). Such high density of predators can create competition potentially depleting the local prey density and force individuals to increase the time searching for prey, and consequently their daily energy expenditure (Fayet et al. 2021). 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 the closer foraging areas (Elliott et al. 2009). But 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 2008).

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 without barriers to airflow and characterized by stronger wind than over land (Felicísimo et al. 2008). Seabirds have evolved traits to specialize in flight modes allowing them to take advantage of these strong winds (Watanabe 2016). Albatrosses, petrels and shearwaters are unparalleled examples, using dynamic soaring flight to optimize their use of the airflow and fly at little or no mechanical costs over vast distances (Weimerskirch et al. 2000, Sachs et al. 2012, Kempton et al. 2022). Kittiwakes can also adjust their movement behaviour to prevailing winds and use wind corridors during directional movements such as migration (Amélineau et al. 2023.), but are predominantly reliant on flapping flight. Therefore, they are less able to benefit from various wind conditions to compensate for their higher flight costs (Collins et al. 2020). For species using flapping flight, unfavourable wind conditions (i.e., headwinds, crosswinds) need to be compensated by increased flying effort, either through greater wingbeat effort or increased flight duration (Hedenstrom and Alerstam 1995, Hedenström et al. 2002). Kittiwakes, together with similar-sized gulls and terns, are typically less selective for certain wind conditions, but increase their wing beat strength and their prevalence for flapping flight under high wind speed conditions (Ainley et al. 2015, Collins et al. 2020). It is thus expected that higher wind intensity over an oceanic staging area, such as the wintering site, would force individuals to increase their flying effort to compensate for headwinds or drift. In line with this, we found a spatial concordance between the flying activity and the wind intensity, suggesting that kittiwakes increased the time spent flying in regions characterized by higher wind intensity.

Individuals at the centre of the range were flying more, but also foraging less than those at the edge of the range. 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' disproportionally affect species relying on flapping flight, with alcids, cormorants and kittiwakes being the most abundant seabirds found dead in 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.

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). At higher latitudes, the reduced day length in winter can thus limit their ability to balance their energy budget through less time available for foraging. 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 much 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. The 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.

In conclusion, we used an approach based on the activity budget of free-ranging animals to track during 11 years the individuals' energy expenditure, 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 trade-off between high energy loss and potentially high energy gain. This suggests that deteriorations in feeding conditions could have disproportionate consequences on individuals at the 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.

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STATEMENTS

Ethics statement

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.

Conflict of interest

The authors declare that they have no competing or conflict of interests.

Data archiving

Data supporting this study will be deposited in a public repository upon acceptance.

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LINKING STATEMENT

In Chapter 3, I explored whether the site fidelity observed in individuals during the winter (as identified in Chapter 2) could result in varying energetic impacts among individuals. I found that individuals wintering closer to the population’s centre experienced higher energy expenditure compared to those wintering at the periphery of the range. This suggests that deteriorations in feeding conditions might disproportionately affect individuals at the range centre, potentially leading to significant effects on the population's demography. However, this variation in energetic performance did not translate into differences in individual fitness in the following summer, as I observed no spatial disparities in the reproductive success of individuals wintering at the centre compared to those at the edge of their range. Nevertheless, the pronounced spatial variations in the "energyscape" led to individuals incurring highly diverse energy costs. In Chapter 5, I integrated the findings from this chapter with those from Chapter 2 to investigate the seasonal interactions that connect such energy costs, as well as winter site fidelity and movement timing, with previous and subsequent annual stages.

CHAPTER 4 – MIGRATORY SEABIRDS TRANSPORT PER- AND POLYFLUOROALKYL SUBSTANCES TO THE ARCTIC

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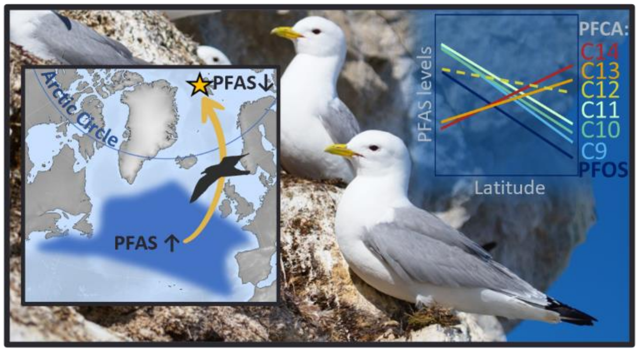
ABSTRACT

Seabirds are often considered sentinel species of marine ecosystems and their blood and eggs utilized to monitor local environmental contaminations. Most seabirds breeding in the Arctic are migratory and thus are exposed to geographically distinct sources of contamination throughout the year, including per- and polyfluoroalkyl substances (PFAS). Despite the abundance and high toxicity of PFAS, little is known about whether blood concentrations at breeding sites reliably reflect local contamination or exposure in distant wintering areas. We tested this by combining movement tracking data and PFAS analysis (nine compounds) from the blood of pre-laying black-legged kittiwakes (*Rissa tridactyla*) nesting in Arctic Norway (Svalbard). PFAS burden before egg laying varied with the latitude of the wintering area and was negatively associated with time upon return of individuals at the Arctic nesting site. Kittiwakes (n=64) wintering farther south carried lighter burdens of shorter chain perfluoroalkyl carboxylates (PFCAs, C_9-C_{12}) and heavier burdens of longer chain PFCAs (C_{13}-C_{14}) and perfluorooctanesulfonic acid (PFOS) compared to those wintering farther north. Thus, blood concentrations prior to egg laying still reflected the uptake during the previous wintering stage, suggesting that migratory seabirds can act as biovectors of PFAS to Arctic nesting sites.

Synopsis: Migratory seabirds are exposed to geographically distinct contamination sources. Tracking data suggests that exposure on distant wintering areas rather than local contamination explained PFAS burdens at the Arctic nesting site.



Graphical Abstract

KEYWORDS

PFAS, PFCA, PFSA, latitudinal gradient, winter contamination, non-breeding distribution, carry-over effects, biologging, black-legged kittiwake

INTRODUCTION

The Arctic is in most parts isolated from human industries and major settlements, and yet it is threatened by high levels of diverse pollutants that have entered the food web, causing a wide range of detrimental effects on Arctic wildlife [1–4]. In this highly seasonal environment, many animals are migratory, travelling hundreds to thousands of kilometres to reach milder wintering grounds [5]. Because they are highly mobile, migratory species are exposed to various and geographically distinct sources of contamination during their annual cycle [6]. The exposure to contamination is thus particularly difficult to assess in these species as their pollutant burden can reflect both local contamination at the Arctic breeding site and exposure far away on the wintering grounds outside the Arctic [7–12]. This also means that migratory animals contribute to the biological transport of contaminants into the Arctic from distant and potentially more contaminated, more industrialized southern regions [13].

Among the pollutants widely found in Arctic wildlife are per- and polyfluoroalkyl substances (PFAS) which have become a major environmental concern [14]. PFAS are a large group of synthetic chemicals which have a very stable chemical structure characterized by a strong carbon-fluorine bonds that earned them the nickname of “forever chemicals” [14]. While their high chemical and thermal stability make PFAS particularly useful in a wide array of manufactured goods (e.g., metal coating, waterproof clothing, food packaging, firefighting foam) [15], these properties also make PFAS highly resistant to degradation and very persistent in the environment [14]. Moreover, PFAS are ubiquitously present worldwide [16–18]. Oceanic transport is the main carrier of PFAS final products, especially closer to the emission sources (e.g., the USA, Europe, East Asia), although atmospheric currents are considered the main long-range pathways of their precursors into the Arctic[19–23]. The distribution in the environment of perfluoroalkyl carboxylates (PFCAs) has been hypothesized to vary according to the length of their carbon chain, with longer chain PFCAs (i.e. > 10 carbons) originating essentially from the degradation of their precursors either in the atmosphere or under aquatic conditions in the oceans, potentially leading to greater concentrations farther away from the emission sources [24,25]. Nevertheless, the mechanisms governing atmospheric PFAS formation and subsequent deposition remain uncertain, but it is overall anticipated that environmental concentrations decrease with distance from emission sources such as at higher latitudes, although this decrease may be less pronounced (or even reversed) for longer chain PFCAs [19,24–26].

Because of their high persistence in the abiotic environment and their mostly high water solubility, the oceans act as major sinks for PFAS [27,28]. Consequently, marine species are highly exposed to PFAS, especially long-lived top predators as several compounds biomagnify along the trophic chain and bioaccumulate over time, although concentrations presumably reach equilibrium within the organism [20,29,30]. Seabirds are particularly at risk as they occupy a high trophic level and have a long lifespan [31]. They are often considered sentinel species of the marine ecosystems and utilized as bioindicators of local environmental contamination to monitor the efficacy of environmental policies, such as the Stockholm Convention [31–33]. Their blood and eggs are widely used matrices to provide non-lethal, less invasive measurements of contaminant concentrations [34]. Because of the short turnover rate of blood, contaminant concentrations in this tissue are assumed to represent short term, local exposition [35]. Similarly, contaminant deposition in eggs is assumed to reflect recent diet at the breeding site, at least in income breeders relying more on local food intake for egg formation [35,36]. For those seabirds that migrate, however, they integrate exposure to contaminants across space and time, and unravelling contaminant sources and assessing the efficacy of regulations require being able to disentangle local signals from distant signals [37]. Retention time of contaminants can vary greatly according to sex, species and compound-specific chemical structure, with biological half-lives of PFAS in adult birds ranging widely from two weeks to up to 230 days [38–40]. Moreover, blood concentrations can also reflect recirculation from other tissues following physiological changes, notably the remobilization of energy body reserves during periods of starvation, migration and reproduction [35,41]. Despite PFAS abundance and high toxicity, little is known about the depuration rates of PFAS in wild species, and whether concentrations in eggs and blood at the breeding site reliably reflect local exposition. Furthermore, most work on migratory species has focused on the breeding stage and, to the best of our knowledge, no studies have yet looked into whether PFAS burden at the breeding site reflects exposure in previous non-breeding life stages. Yet, several studies have highlighted the critical need for a better understanding of exposure to pollutants during the wintering stage to assess the risk that migratory species are facing throughout their annual cycle [9,13].

By combining movement tracking data and PFAS measurements, we tested whether PFAS concentrations in the blood of a long-distance migratory seabird prior to egg laying (i.e., pre-laying stage) was affected by the spatial distribution of individuals during the previous winter. We investigated this in an Arctic-nesting population of black-legged kittiwakes (hereafter “kittiwakes”, *Rissa tridactyla*), breeding in Svalbard (High Arctic Norway). This population migrates for up to 5000 km to winter over the North Atlantic Ocean, with individuals spread from the North American to the European coasts [42]. Consequently, the large spatial variation in wintering locations among individuals from the same breeding population has the potential to result in contrasting exposure to contaminants. We hypothesized that PFAS concentration of kittiwakes varies according to the wintering distribution of individuals over the North Atlantic Ocean. We predicted a decrease in PFAS blood concentration over the latitude of the wintering area since PFAS concentrations in the physical environment decline along a South-North gradient in the Northern Hemisphere, but we also expected the strength of this spatial pattern to vary among PFAS compounds since they differ in their physicochemical properties [19,21,24]. More specifically, we predicted the latitudinal decline to be stronger for more water-phase-transported PFASs (PFSAs, $\leq C_{10}$ PFCAs) compared to compounds originating in greater proportion from the long-range degradation of their precursors ($> C_{10}$ PFCAs). We also predicted a negative correlation between PFAS concentrations and time spent at the colony, giving further indications that the contamination burden is mostly acquired before arriving at the Arctic breeding site.

MATERIAL & METHODS

Geolocator deployment and blood sampling

From 2018 to 2020, we deployed 127 geolocators (light-level loggers) on kittiwakes to track their movement during winter. Adults were captured using a noose attached to a fishing rod at their breeding colony in Svalbard (High Arctic Norway, 78° 54’ N, 12° 12’ E). 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 minute and recorded its maximum value every 5 or 10 min.

We recaptured 107 individuals (84% recapture rate) after their return to the colony in 2019 and 2021 to recover the geolocators. Among these, individuals recaptured during the pre-laying stage (i.e., the time of courtship and nest building, prior to egg laying) were immediately sampled for 2 mL of blood from the brachial vein and measured (skull length and body mass). Blood samples were kept on ice until centrifugation at the end of the day, and the red blood cells (RBC) and plasma were frozen at -20°C until DNA sexing (RBC) and PFAS assays (plasma). The sex of individuals was determined by molecular sexing (following Fridolfsson et al. 1999 [43]). An index of the body condition of individuals was calculated as the residuals of the linear correlation between the skull length and the body mass. Females sampled less than 10 days before laying their first egg (n=3) were removed from the dataset to minimize the biased PFAS levels due to maternal transfer into the eggs during fast follicle development [44,45]. After filtering out missing or incomplete tracks caused by device failure or battery discharge, the final dataset consists of 71 wintering tracks from 64 different individuals (23 females, 41 males) and their pre-laying PFAS concentrations.

Per-and Polyfluoroalkyl Analyses

Methods for PFAS analysis in plasma were adapted from Powley et al. (2005) [46] and extensively described in Jouanneau et al. (2022) [45]. We screened for 21 legacy PFAS and kept only compounds detected in ≥70% of the measurements with concentrations above the limit of detection (LOD, see Tab. S4.1). Nine compounds were selected this way, including both sulfonic (PFSAs): perfluorohexane sulfonic acid (PFHxS), branched (brPFOS) and linear perfluorooctanesulfonic acid (linPFOS), and carboxylic (PFCAs) PFAS: perfluorononanoic acid (PFNA), perfluorodecanoic acid (PFDcA), perfluoroundecanoic acid (PFUnA), perfluorododecanoic acid (PFDoA), perfluorotridecanoic acid (PFTriA) and perfluorotetradecanoic acid (PFTeA). Samples were analyzed for PFAS after each field season, which led to different LOD between years. We used the most conservative value for each compound (i.e., highest LOD among years for each compound), so that concentrations were comparable among years (see Tab. S4.1). Values below the LOD were set as half of the compound specific LOD. Concentrations are provided in ng g^{-1} wet weight (ww).

The quality of the measurements was evaluated by analyzing one blank and a standard reference (human serum AM-S−Y-1908 and AM-S−Y-2018 INSPQ within the Arctic Monitoring Assessment Program ring test) every 15 samples. Recovery standards were also added at the end of the sample processing to calculate the recovery of the 13C labelled internal standards. For each analysis, the LOD of each compound was defined as three times the signal-to-noise ratio, or in the case of detection in the blanks as the sum of the average of blank levels and three times the standard deviation.

Geolocation data processing and winter distribution

To infer geographic positions, geolocator data were processed according to the procedure based on the threshold method to estimate twilight events and developed for the SEATRACK project [47]. Geolocation-based-tracking generates lower accuracy for latitudes around equinox periods and no locations over continuous daylight (or night) at high latitudes. To fill these gaps in the tracks, and to reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm specifically developed for SEATRACK and described in detail in Fauchald et al. 2019 [48] and recently applied in kittiwakes in Léandri-Breton et al. 2021 [42].

The start and end of the wintering period were defined for each track as the last date in fall and the first date in spring the individual crossed the Arctic circle (66°3' N), given that the population's winter range is situated south of this demarcation [42]. For each track, the centre of the individual's winter distribution was calculated as the centroid of the 50% utilization distribution kernels (UDs) estimated over the winter positions and projected using a Lambert Azimuthal Equal Area coordinate system. This was done using the package adehabitatHR [49] with a smoothing factor (h) of 200 km and grid cells of 50 × 50 km. The latitude and longitude of the winter distribution centre were extracted for each individual.

We also estimated the time individuals spent at the breeding colony before sampling, between the return of individuals at the colony from the wintering area and the blood sampling. The timing of return to the colony area in spring was estimated using Lavielle partitioning algorithm [42]. This was done over a 5-day running maximum of the saltwater immersion data indicating a behavioural transition from a continuously pelagic behaviour during the non-breeding stage (wet) to land use at the colony (dry).

Statistical Analyses

Some PFAS compounds were highly correlated (see supp. info. Fig. S4.1) and we performed a principal component analysis (PCA, package 'FactorMineR' v. 2.8) to group co-varying compounds and facilitate the discussion and representation of the results. The first three principal components (PC) explained a high proportion of the variance (91.0% and eigenvalue above 1.0, supp. info. info Tab. S4.2) and all nine compounds significantly contributed to at least one of the first three PCs (supp. Info. Tab. S4.3) and were well represented by these PCs (supp. info. Tab. S4.4). The visualization of the distribution of PFAS over the first three PCs (supp. Info. Fig. S4.2 and S4.3) revealed four distinct groups: linPFOS, PFUnA, PFDcA, PFNA and PFDoA in group 1, PFTriA and PFTeA in group 2, PFHsX in group 3 and brPFOS in group 4. Within each of these groups, we selected the PFAS compound with the highest concentration: linPFOS, PFTriA, PFHxS and brPFOS (Tab. 4.1).

For each of the four compounds selected this way, we fitted a linear mixed-effects model to investigate the relation between the compound concentration and the spatial distribution of the birds during the previous wintering stage (see Tab. 4.2 for full models). ‘Latitude’ and ‘year’ co-varied (LMER, *coef* = 3.13° of latitude, *SE* = 0.61, *df* = 40, $p < 0.0001$) and we were interested in the wintering distribution effect, we thus removed ‘year’ from the final models but also presented the latitude effects separately per year in Fig. 4.2A and 4.2C for linPFOS and PFTriA. The ‘body condition index’ and the ‘longitude’ did not have statistically significant effects on any of four PFAS concentrations and were thus removed from the final models. The time individuals had already spent at the colony before being sampled (‘time at colony’) was also included in the models since we were interested in testing whether the PFAS concentrations vary over the time span between the return to the breeding site and the blood sampling. A decrease in concentrations over this period would give further indications that the contamination loading is mostly acquired before the return to the breeding site. The interaction between time spent at the colony and sex was included in the model with PFTriA as response factor, to account for potential male-female differences in how PFAS are uptaken, stored or excreted during the pre-laying stage. This interaction was only included in the PFTriA model since it was not significant in the other models. Sex differences in PFAS concentrations over time spent at the colony are illustrated for linPFOS and PFTriA in Fig. 4.2B and 4.2D. In all models, ‘individual’ was included as a random factor. The revised R-squared (R^2 marginal) were estimated using 'r.squaredGLMM’ (package ‘MuMIn’[50]). All analyses were carried out in R v. 4.2.2 [51].

RESULTS

The blood concentration of PFAS in pre-laying kittiwakes was associated to the distribution of individuals during the previous winter, but this relation varied greatly among the four groups of

PFAS, as tested on dominant compounds within each group: linPFOS, PFTriA, PFHxS and brPFOS. There was a strong effect of the wintering latitude on the linPFOS concentrations of individuals, with a decrease of 1.1 ng g^{-1} ww per degree of latitude north (Fig. 4.1A, Tab. 4.2) which was independent of the year of sampling (Fig. 4.2A). Across the latitudinal range of the population (42.5-56.4°), this represents a difference of 15.1 ng g^{-1} ww between individuals wintering the farthest north and those wintering the farthest south (i.e., a decrease of 38.4% in linPFOS concentration). The linPFOS concentration was also negatively correlated with the time individuals spent at the colony before sampling, with a decrease of 0.2 ng g^{-1} ww per day (Tab. 4.2) which was independent of sex differences (Fig. 4.2B). Individuals spent 48 days on average at the colony before sampling (range: 36-81 days), which corresponds to a decrease of 11.1 ng g^{-1} ww in linPFOS concentration over this period (Tab. 4.2, Fig. 4.2B).

Conversely to linPFOS, the concentration of PFTriA was positively correlated with the latitude of the individuals wintering distribution (Fig. 4.1B, Tab. 4.2), with an increase of 0.4 ng g^{-1} ww per degree of latitude representing a 6.1 ng g^{-1} increase across the latitudinal range of the population (i.e., a 35.3% increase in PFTriA concentration). This effect, however, was dependent on the year of sampling as individuals wintered on average farther north in 2019 and had higher PFTriA concentrations compared to 2021 (Fig. 4.2C). The PFTriA concentration was also negatively correlated with the time spent at the colony, with a decrease of 0.3 ng g^{-1} ww per day representing a decrease of 6.4 ng g^{-1} ww over the averaged time spent at the colony (Tab. 4.2). This negative effect was, however, driven by females (Tab. 4.2, Fig. 4.2D). Winter latitude had a small yet significant positive effect on PFHxS concentration, while it showed no effect on brPFOS concentration, with both final models accounted for a modest amount of variance (see Tab. 4.2, Fig. 4.1C-D).

The migration duration of individuals in spring, averaging 14 days (range 1 to 56 days), was not related to the wintering latitude (LME, *coef*=0.29, *SE*=0.48, *df*=69, *p*=0.5), indicating that the latitudinal gradient in PFAS concentration was independent of the migration time to reach the colony area.

Results of models testing for the effect of wintering latitude over the concentration of all nine PFAS are provided in supporting information (Tab. S4.5) and illustrated by Fig. 4.3 (rescaled concentrations for linPFOS and all PFCAs tested).

Table 4.1: Concentrations of the nine PFAS (mean, standard deviation and range) in blood of pre-laying black-legged kittiwakes (*Rissa tridactyla*) in each of the four groups determined by the principal component analysis. The compounds are further classified by carbon chain length and PFAS type (i.e., sulfonic acids, PFSA; carboxylic acids, PFCA), and the compound with the highest concentration selected in each group is shown in bold.

Groups	PFAS	Carbon chain length	Types	Concentration (ng g^{-1} ww)	
				Mean ± SD	Range
Group 1	**linPFOS**	**C_8**	**PFSA**	**21.29 ± 9.17**	**2.32 – 48.82**
	PFNA	C_9	PFCA	2.66 ± 1.14	0.33 – 5.23
	PFDcA	C_{10}	PFCA	3.65 ± 1.42	0.37 – 7.14
	PFUnA	C_{11}	PFCA	15.27 ± 5.85	1.40 – 30.57
	PFDoA	C_{12}	PFCA	2.86 ± 0.89	0.34 – 4.80
Group 2	**PFTriA**	**C_{13}**	**PFCA**	**10.05 ± 3.82**	**1.77 – 20.06**
	PFTeA	C_{14}	PFCA	1.57 ± 0.65	0.36 – 2.91
Group 3	**PFHxS**	**C_6**	**PFSA**	**0.25 ± 0.13**	**0.07 – 0.65**
Group 4	**brPFOS**	**C_8**	**PFSA**	**1.55 ± 0.72**	**0.34 – 3.90**

Table 4.2: Results of linear mixed-effects models testing the relation between concentrations of four PFAS in kittiwake's blood and the latitudinal distribution of individuals during the previous winter (i.e., latitude of the winter distribution centre), while accounting for sex and time spent at the colony before sampling. The 'individual' was included as a random factor. Significant effects are presented in bold.

Response	Predictors	Coef	*SE*	*p*-value	95% CI	R^2
linPFOS (*group 1*)	**Latitude (°N)**	**-1.082**	**0.311**	**< 0.001**	**[-1.682; -0.482]**	0.26
	Sex (male)	1.041	2.106	0.6	[-3.023; 5.106]	
	Time at colony (days)	**-0.234**	**0.098**	**0.01**	**[-0.422; -0.046]**	
PFTriA (*group 2*)	**Latitude (°N)**	**0.440**	**0.118**	**< 0.0001**	**[0.214; 0.666]**	0.38
	Sex (male)	-4.256	4.158	0.3	[-12.220; 3.709]	
	Time at colony (days)	**-0.291**	**0.084**	**< 0.001**	**[-0.452; -0.130]**	
	Sex* Time at colony	**0.188**	**0.092**	**0.04**	**[0.012; 0.364]**	
PFHxS (*group 3*)	**Latitude (°N)**	**0.011**	**0.005**	**0.03**	**[0.001; 0.021]**	0.09
	Sex (male)	0.054	0.034	0.1	[-0.014; 0.121]	
	Time at colony (days)	-0.001	0.002	0.3	[-0.005; 0.001]	
brPFOS (*group 4*)	Latitude (°N)	-0.018	0.027	0.5	[-0.086; 0.010]	0.08
	Sex (male)	**0.416**	**0.184**	**0.03**	**[0.017; 0.668]**	
	Time at colony (days)	-0.004	0.009	0.7	[-0.015; 0.016]	

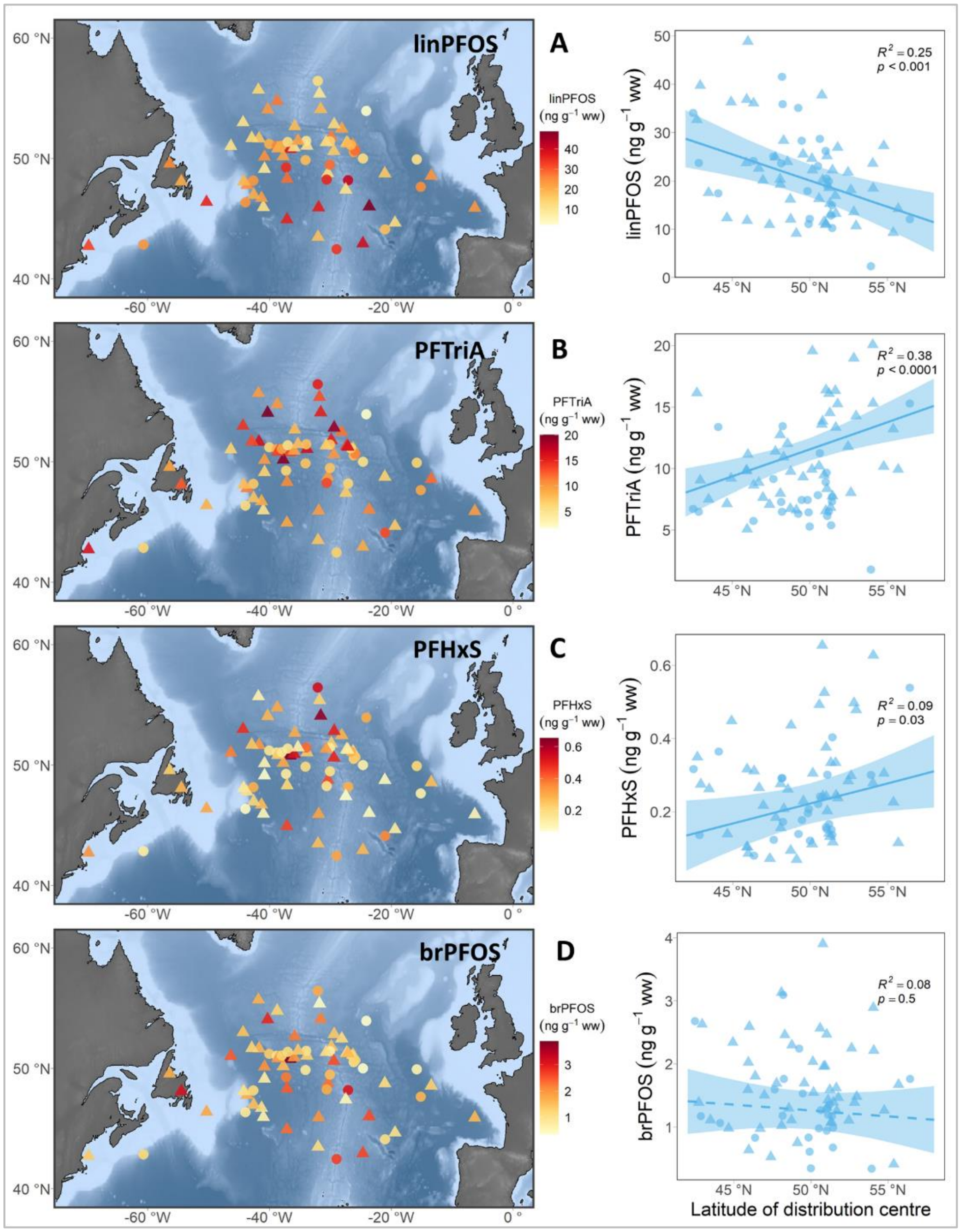


Figure 4.1: Maps (left panels) and model predictions (right panels) illustrating the winter distribution centres of male (▲) and female (●) black-legged kittiwakes (*Rissa tridactyla*) and the associated concentrations of A) linPFOS, B) PFTriA, C) PFHxS and D) brPFOS measured in blood after the return of individuals at the colony site the following spring. Solid regression lines indicate significant correlations and dashed lines nonsignificant correlations.

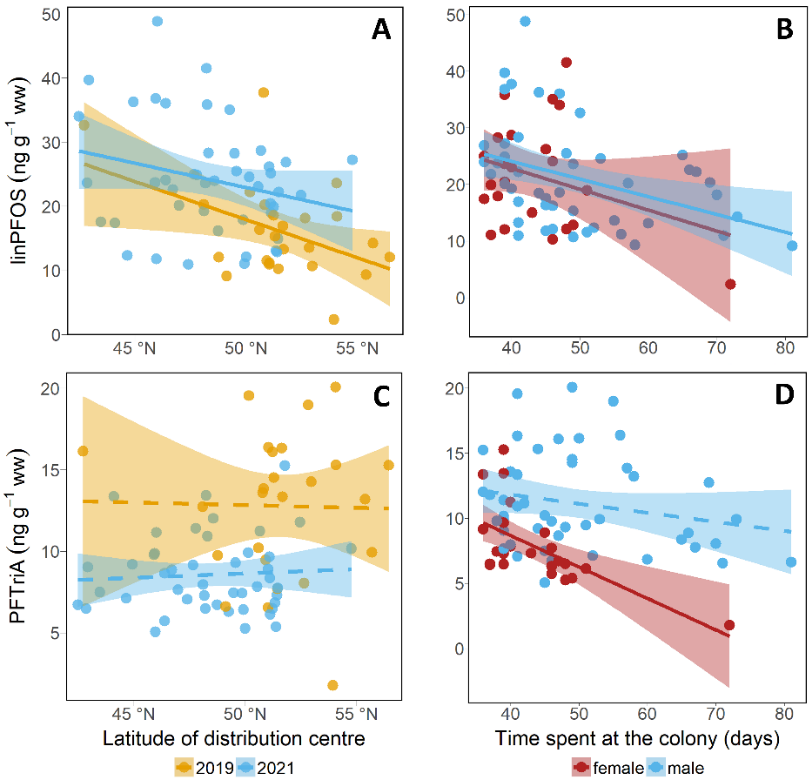


Figure 4.2: Linear regressions of linPFOS and PFTriA concentrations measured in blood of pre-laying black-legged kittiwakes (*Rissa tridactyla*) at the breeding colony in relation with the latitude of the distribution centre of individuals during the previous winter for each sampling year (A and C) and in relation with the time spent at the colony before blood sampling for females and males (B and D).

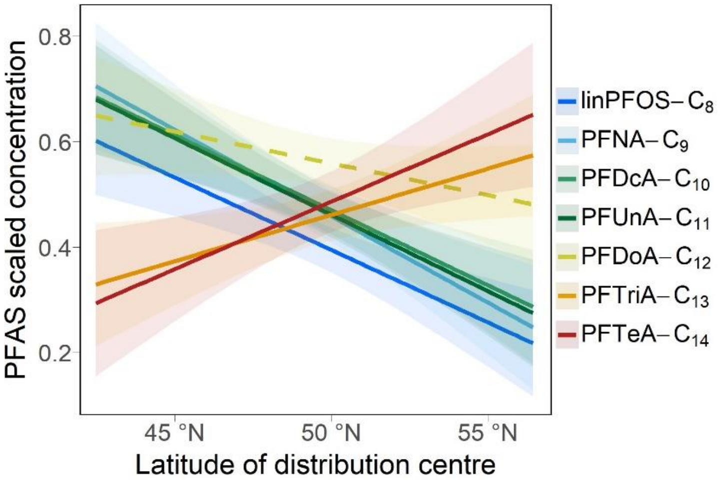


Figure 4.3: Scaled predicted concentrations (0 to 1) from linear models of linPFOS and all tested PCASs in blood of pre-laying black-legged kittiwakes (*Rissa tridactyla*) in relation with the latitude of the distribution centre during the previous winter illustrating contrasting effects depending on carbon chain length. Solid regression lines indicate significant correlations and dashed lines nonsignificant correlations.

DISCUSSION

PFAS concentration in the blood of Arctic-breeding kittiwakes could be traced to the distribution of individuals in their remote wintering areas, thousands of kilometres away. The effect of the winter distribution on the PFAS concentration varied greatly among the four groups of compounds tested, and was driven by the averaged latitude, not the longitude, at which individuals were wintering. As predicted, for the main group of co-varying PFAS (linPFOS, PFNA, PFDcA, PFUnA, PFDoA), and as tested on linPFOS, this effect was negative with a decrease of 38% in linPFOS concentration over the latitudinal gradient of the population. Conversely, for the second group of co-varying PFAS (PFTriA and PFTeA), and as tested on PFTriA, the wintering latitude had a positive effect with an increase of 35% in PFTriA concentration over the latitudinal gradient. For PFTriA, however, the latitude effect was largely dependent on the year of sampling, so that the effects of winter distribution and year were difficult to separate. Winter latitude also had a small positive effect on PFHxS concentration (third group), while no latitudinal effect was detected on brPFOS concentration (forth group). Moreover, we found that the overall PFAS burden at the population level showed a negative relation with days since arrival at the breeding site (ranging 36 to 81 days). This population-level decrease in concentrations after arrival at the Arctic-nesting site and the latitudinal gradient observed suggest that most PFAS tested were primarily obtained at lower latitudes and brought to the Arctic nesting site. This provides indications that the breeding area may have had lower background exposure of PFAS than the winter areas as kittiwakes seemed to eliminate PFAS from their bodies while at the Arctic-nesting site.

Local versus winter exposure

To the best of our knowledge, this is the first study showing a relationship between PFAS concentration measured at the nesting site and the wintering distribution of individuals, suggesting that PFAS uptake during winter can carry over into the breeding stage of a migratory species. This has been suspected, but never tested, in South Polar breeding seabirds as greater PFAS contamination load was found in trans-equatorial migratory species compared to species restricted year-round to the sub-Antarctic region [52]. Carry-over of contaminant burden has, however, been studied for other pollutants. For example, an experimental study on great skuas (*Stercorarius skua*) showed that organochlorine load in chicks was more influenced by the mother's exposure on the wintering area, via maternal transfer, than by local contamination at the breeding site 8. For DDE (DDT main metabolite), Svalbard kittiwakes had the highest concentrations in the pre-laying period, suggesting relatively high exposure in their winter areas [11]. Similarly, mercury burden carries over from the wintering stage into the breeding stage in other migratory seabirds such as auklets, guillemots, cormorants and terns [9,37,53]. Together with these studies, our results highlight the need to consider the full annual cycle when assessing exposure in a migratory species. Moreover, our study suggests adding PFAS to the list of contaminants that can be redistributed via the biovector transport to geographically distant locations [54]. By transporting contaminants from distant and more contaminated regions into the Arctic, kittiwakes along with other migratory species contribute to the contamination of the Arctic foodweb. Seabirds and their eggs are indeed important prey of the Arctic terrestrial ecosystem [55,56]. Moreover, seabird colonies can reach high densities, creating oases of biodiversity and productivity in the tundra, but also hotspots of contamination [37,54,57].

Despite the relatively short turnover rate of plasma, our results indicate that PFAS concentrations at the breeding site could still reflect the previous distribution of individuals over their remote wintering areas, not just local intake as is generally assumed. The depuration rate of the few PFSAs and PFCAs studied in adult birds varied greatly depending on species and sex, with a biological half-life ranging from two weeks to up to 230 days for compounds [38–40]. The long depuration rate in plasma of some PFAS, such as PFOS and long-chain PFCAs, may thus represent a larger accumulation period mostly reflective of the winter exposition [38,40,58–60], likely due to a lower excretion rate [61]. Moreover, blood concentrations at the nesting site can also result from the remobilization of PFAS from other tissues when individuals rely on their endogenous reserves [11,62,63]. Migratory species often deposit body reserves before engaging in long migratory movements, reserves that are depleted during the journey, potentially contributing to recirculation in the blood of contaminants assimilated during winter [64]. Kittiwakes rely less on body reserves for migration, but the pre-laying stage remains nutritionally stressful as individuals engaging in activities such as courtship and nest-defence behaviour reduce their foraging time and rely more on endogenous reserves during this period [65,66]. Moreover, the early pre-laying stage in spring can be characterized by harsh environmental conditions at the Arctic nesting site, leading to a period of food deficiency and remobilization of endogenous reserves until foraging conditions improve[67,68].

The relation between decreasing PFAS concentrations with the time spent at the Arctic breeding site for seven out of nine compounds provided further indications that the contamination burden was acquired before the arrival at the Arctic breeding site. This suggests that the breeding area had lower background exposure of PFAS than the winter areas as kittiwakes seemed to depurate their bodies over the long pre-laying period of kittiwakes (range 36 to 81 days). However, repeated intra-individual sampling timepoints over the pre-laying stage would be required to confirm that such decrease in PFAS concentration originates from depuration at the individual level. Overall, and despite the extensive duration of the pre-laying stage in kittiwakes (averaging 48 days before sampling), our study suggests that maternal transfer of PFAS into the eggs, which has been demonstrated for kittiwakes [45], likely originates in most parts from the contamination burden acquired during winter.

Latitudinal distribution of PFAS in the Atlantic

PFSAs and PFCAs have low volatility compared to many other persistent organic pollutants and they are mainly transported by ocean currents, with higher marine concentrations found closer to the direct emission sources [16,17,25]. Therefore, lower concentrations of PFAS in remote regions such as the Arctic can be expected. Indeed, the population-level decrease in the concentration of PFAS since arrival at the Arctic colony suggests a lower exposure at the Arctic breeding site with most of the uptake occurring farther south. At those high latitudes, atmospheric currents are considered to be the main pathway via long-range transport of precursors [23,24]. However, the efficiency of atmospheric transport of compounds depends on their physicochemical properties and has been hypothesized to vary according to the length of their carbon chain [24,25,69]. In line with this, we found contrasting effects of the wintering latitude on the concentration of PFAS of kittiwakes, with the main group (linPFOS and shorter-chain PFCAs: PFNA, PFDcA, PFUnA, PFDoA) negatively and the second group (longer-chain PFCAs: PFTriA, PFTeA) and third group (PFHxS) positively related to latitude on the wintering area. Environmental concentrations of > 10 carbon PFCA compounds are believed to originate essentially from the atmospheric degradation of their precursors [24,25]. In contrast, PFAS distribution models predicted that shorter chain PFCAs disperse less to higher latitudes and farther from direct emission sources because their precursors are rapidly removed by wet precipitations and therefore undergo less efficient long-range transport in the atmosphere compared to those of longer chains [26]. Although this prediction still requires empirical support, it is coherent with the latitudinal pattern we found as kittiwakes wintering farther north carried lower load of shorter chains PFCAs (C_9-C_{12}) and high load of very long chain compounds (C_{13}-C_{14}), while the reverse was found for kittiwakes wintering farther south. However, measurements in the environment and model predictions do not always reflect these latitudinal gradients in the North Atlantic, likely highlighting the uncertainty regarding the chemistry of atmospheric PFCA formation [26,70].

The latitudinal pattern we observed could also be related to marine currents in the Atlantic, notably the Gulf Stream circulation transporting PFAS discharge from direct pollution sources of the North-East American coast into oceanic regions. For instance, the distribution profile of PFOS and PFOA (perfluorooctanoic acid) in relation to the Gulf Stream circulation have shown much higher concentrations in the surface waters of the Mid-Atlantic compared to the North Atlantic, which was likely explained by longer residence times in the warm surface waters brought by the Gulf Stream and isolated from the denser, deep waters [28]. This could potentially explain that kittiwakes wintering farther south, and thus more exposed to Gulf Stream waters, carry higher burdens in PFOS and shorter chains PFCAs as both are typically associated with short-range transport closer to emission sources [17,24,25]. Further investigations on PFAS exposure in seabirds in relation to their utilization of oceanic currents are required, and would likely yield clues on latitudinal and longitudinal patterns in PFAS concentration in the Atlantic Ocean.

The small effect of latitude or time since arrival at the colony on the concentrations of PFHxS, or the lack of any notable effect on brPFOS levels, may be attributed to their exceedingly low presence in kittiwake blood (among the lowest of all compounds examined) coupled with comparatively higher limits of detection. Alternatively, their different response could be attributed to their intrinsic chemical properties. For instance, brPFOS differs from linPFOS by its much shorter half-life [71] and their sources and process of production expected to lead to different transport behaviour in the environment or fate in biota [72,73].

Movement tracking of seabirds provides valuable information on the exposure to pollution in remote regions [31–33]. This exposure, however, does not only depend on the pollutant concentrations in their environment, but also their diet. Seabirds feeding on higher trophic prey can have greater contaminant intake, resulting in inter-individual and interspecies differences in contaminant burden [74,75]. For instance, PFOS shows greater biomagnification capabilities compared to PFCA[30], so that spatial variation in main prey consumed over the winter distribution could result in different PFOS/PFCA ratio among individuals. Kittiwakes are generalist predators and their diet in winter is poorly known [76,77]. The latitudinal gradient of PFAS concentrations found over the kittiwake wintering distribution can thus emerge either through spatial differences in environmental concentration or in diet. Moreover, as this latitudinal gradient was dependent on the chain length of the compounds tested, our results suggest it can translate into a toxicity gradient over the wintering distribution in the North Atlantic, as kittiwakes show high interannual fidelity to specific wintering areas [42] and that wintering at the northern part of the distribution lead to increased concentrations of very long chain PFAS (i.e., PFTriA, PFTeA), highlighted as particularly toxic for animals in some studies [78–80]. Coupling geolocation tracking data with isotopic analysis would help to untangle trophic position and environmental contamination [9,81]. Furthermore, although we analyzed the PFAS most commonly found in biota, our study incorporates only a few compounds and other PFAS could have different distributions. The next steps would be performing the isotopic and extractable organofluorine analyses required to further investigate potential hotspots of PFAS exposition in the North Atlantic.

Conclusion

Our study suggests that the PFAS burden in migratory kittiwakes at the breeding site can reflect the uptake during the previous wintering stage, as demonstrated by 1) the latitudinal gradient in PFAS burden over the wintering area, and 2) the negative relation between PFAS concentrations and time spent at the Arctic breeding site upon return from wintering areas. Seabirds are widely utilized as bioindicators and their blood and eggs used as matrices to indicate temporal trends in local environmental contamination [82]. Our results, however, call for caution when using a migratory species as indicators of local PFAS concentration as they can carry contaminants through time and space, which can hinder our ability to draw conclusions on the exposure and bioaccumulation these animals are facing [53]. A thorough understanding of the migratory patterns of animals is essential to assess the threats contamination exposure imposes on migratory species throughout their annual cycle. By doing so, migratory species can be used to monitor the exposure and pollutant concentrations in remote regions of the Globe, such as the oceans where sampling is otherwise difficult.

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ASSOCIATED CONTENT

Supporting Information

The following files are available free of charge.

List of all PFAS screened with their detection rates (Table S4.1); Correlation matrix of selected PFAS (Figure S4.1); PCA output (Table S4.2); Contribution of PFAS to the first four principal components (Table S4.3); Quality of representation of PFAS to the first four principal components

(Table S4.4); 3D visualization of PFAS over the first three principal components (Figure S4.2); Visualization of PFAS distribution over the first three principal components (Figure S4.3); Results of linear mixed-effects models for all nine selected PFAS (Table S4.5).

Author Contributions

The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript. ‡These authors contributed equally.

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LINKING STATEMENT

I investigated whether site fidelity (assessed in Chapter 2) resulted in variations in pollutant exposure among individuals during winter. I demonstrated that the wintering distribution may affect PFAS loading, with individuals wintering farther north carrying a heavier burden of longer carbon chain compounds, which are considered more toxic, compared to individuals wintering farther south. Moreover, I established that the PFAS burden in breeding kittiwakes was primarily acquired in wintering areas located thousands of kilometres away and subsequently transported to the Arctic. Therefore, this chapter integrated ecotoxicology into the broader theme of the thesis on carry-over effects, illustrating how migratory choices can influence exposure, consequently leading to differing contamination burdens that persist into the breeding period.

CHAPTER 5 – INDIVIDUAL QUALITY OVERWRITES CARRY-OVER EFFECTS ACROSS THE ANNUAL LIFE CYCLE OF A LONG-DISTANCE MIGRANT

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ABSTRACT

1. In seasonal environments, the fitness of animals depends upon the successful integration of life stages throughout their annual life cycle. Failing to do so can lead to negative carry-over effects where individuals are transitioning into the next season in different states, consequently affecting their future performance. However, carry-over effects can be masked by individual quality when individuals vary in their efficiency at acquiring resources year after year (i.e. ‘quality’, leading to cross-seasonal consistency in individual performance.
2. Here we investigated the relative importance of carry-over effects and individual quality in determining cross-seasonal interactions and fitness consequences over the full annual cycle of a migratory seabird (black-legged kittiwake *Rissa tridactyla*).
3. We monitored the reproduction and annual movement of kittiwakes over 13 years using geolocators to estimate their fitness, distribution and winter energy expenditure. We combined this with an experimental approach (clutch removal experiment, 2 years) to manipulate the reproductive effort irrespective of individual quality.
4. Piecewise path analyses showed that successful breeders reproduced earlier and were more likely to breed successfully again the following year. This positive interaction among consecutive breeding stages disappeared after controlling for individual quality suggesting that quality was dominant in determining seasonal interactions. Moreover, controlling experimentally for individual quality revealed underlying carry-over effects that were otherwise masked by quality, with breeding costs paid in higher energy expenditure and delayed onset of reproduction.

5. We highlight the need to combine an experimental approach along with long-term data while assessing apparent carry-over effects in wild animals, and their potential impact on fitness and population demography.

KEYWORDS

Corticosterone; Energy expenditure; Geolocator; Kittiwake; Reproductive costs; Seabird; Seasonal interactions; Winter distribution.

INTRODUCTION

Seasonal environments impose strong constraints on animals, often resulting in highly sequential and well-defined life-history stages throughout the annual life cycle (Harrison et al., 2011). This is particularly true for migratory species under a tight schedule to track the seasons across time and space and match their energy requirements across their annual cycle with the timing of seasons (Harrison et al., 2011). The fitness of individuals thus relies on a successful integration of these stages in time, and failing to do so can lead to carry-over effects (individuals transitioning into the next season in different states, affecting their future performance; Norris & Marra, 2007). For instance, limited access to good quality wintering habitat (Marra et al., 1998) and reduced pre-migration nutritional condition (Bêty et al., 2003) can lead to carry-over effects from winter to the breeding season, affecting the timing of arrival at the breeding site, the onset of reproduction, and the fitness of individuals. Carry-over effects can also emerge from increased reproductive effort, leading to reduced post-breeding nutritional condition or flight-induced muscle damage (Fowler & Williams, 2017), delayed moult (Langston & Rohwer, 1996) or delayed migration (Fayet, Freeman, Shoji, Kirk, et al., 2016), constraining the ability of migrants to reach optimal winter foraging grounds (Bogdanova et al., 2011; Catry et al., 2013; Whelan et al., 2020).

Reproduction is a particularly demanding life-history stage requiring energy that cannot be allocated into other functions such as self-maintenance (the "resource-allocation trade-offs", Harshman & Zera, 2007; Stearns, 1992). When resources are limited, life-history theory predicts trade-offs between energetically costly activities with strong potential to create carry-over effects (Williams, 2012). For iteroparous species, such trade-offs lead to conflicts between the investment in current reproduction, survival and future reproduction (Reznick et al., 2000). Consequently, reproductive investment may incur lasting costs, manifested as prioritization of somatic maintenance through increased time spent at the wintering site and diminished future reproductive investment and success (Gatt et al., 2021; Golet et al., 2004; Wernham & Bryant, 1998).

Despite expected trade-offs between current and future reproduction, animals often show a positive correlation between consecutive reproductive attempts (Hamel et al., 2009; Reznick et al., 2000). Some higher quality individuals are indeed more efficient than others in acquiring resources from their environment and will consequently always have more energy to allocate in all functions in a given life-history stage (Hunt et al., 2004; van Noordwijk & Jong, 1986). Individual quality in this context implies consistency in performance and refers to inter-individual heterogeneity that correlates with fitness traits, usually reproductive success (Bergeron et al., 2011; Wilson & Nussey, 2010). Links between individual quality and life-history decisions can therefore lead to cross-seasonal correlations in breeding and wintering performance with, for instance, better breeders also consistently accessing better quality wintering habitats (Gunnarsson et al., 2005). This poses the challenging question of differentiating between seasonal interactions arising from genuine carry-over effects and inter-annual consistency in within-individual performance associated with intrinsic factors such as individual quality (Daunt et al., 2014; Harrison et al., 2011). For example, associations between winter habitat quality, derived from stable isotope analysis, is often associated with breeding parameters, and interpreted as reflecting a carry-over effect (Marra et al., 1998). Experimental approaches are necessary to separate the effects as individuals vary both in their quality and in the environmental conditions they encounter (e.g., Golet et al., 2004). A sound understanding of the relative contribution of these factors is essential as they can have different but major repercussions on individual fitness and population dynamics (Harrison et al., 2011).

Carry-over effects occur across taxa (e.g., birds: Catry et al., 2013; mammals: Sanderson et al., 2014; reptiles: Ceriani et al., 2015; amphibians: Cayuela et al., 2014; arthropods: Elliott et al., 2016). However, understanding the mechanisms behind carry-over effects is hindered, particularly in migratory species, by the necessity to track individuals across seasons and sometimes over long distances. While there is strong evidence that energy is a key currency driving such carry-over effects (Harrison et al., 2011), the physiological drivers remain unclear. A growing literature, however, points towards glucocorticosteroids as potential mediators of carry-over effects (Bonier et al., 2009). Indeed, glucocorticosteroids such as corticosterone in birds modulate energy reserves, allowing organisms to achieve stability in their energy balance throughout their life-history cycle (Angelier & Wingfield, 2013). Secretion of corticosterone is thus considered an adaptive response to variations in seasonal energy demand, but long-term elevated levels or acute stress response induced by environmental stressors or unpredictable events can cause behavioural or physiological changes to redirect energy towards self-feeding, self-maintenance and long-term survival (Wingfield et al., 1998). This can consequently create physiological conflicts with other functions such as feather growth (Romero et al., 2005) and reproduction via inhibition of reproductive behaviour (Goutte et al., 2010; Kitaysky, Wingfield, et al., 2001). For instance, a short-term experimental elevation of corticosterone caused females black-legged kittiwakes (*Rissa tridactyla*) to depart on migration earlier and extend the time spent on the wintering period (Schultner, Moe, Chastel, Tartu, et al., 2014). Moreover, years of late breeding date were associated with high corticosterone levels (Goutte et al., 2010), potentially via inhibition of sex-steroid hormone secretion in females (Goutte et al., 2014). This highlights the potential key role of glucocorticosteroids in mediating environmental conditions and the behavioural response of individuals in the context of carry-over effects (Bonier et al., 2009).

Here, we combine longitudinal and experimental approaches to disentangle carry-over effects from inter-annual consistency in individual performance (a proxy of quality, hereafter refer to as 'individual quality') in a migratory seabird, the black-legged kittiwake (hereafter 'kittiwakes'). As long-lived organisms, kittiwakes are expected to modulate their reproductive effort according to environmental conditions, promoting their own survival and future reproduction in years of poor resource availability (Stearns, 1992), a trade-off mediated by glucocorticosteroids (Angelier & Wingfield, 2013). The study site in Svalbard holds the northernmost breeding population of the species, and the short breeding window at such high Arctic latitudes has the potential to impose a strong time constraint on kittiwakes' annual life-cycle, and delayed laying date is associated with poor breeding outcome in Arctic seabirds (de Forest & Gaston, 1996; Goutte et al., 2014; Whelan et al., 2022). These characteristics make this system ideal to investigate carry-over effects affecting individual performances across their annual life-cycle. We used 13 years of annual solar geolocation tracking and breeding monitoring of kittiwakes (n=181), including up to seven years of repeated measurements of the same individuals, therefore encompassing a wide range of variation in environmental conditions. We also measured corticosterone in pre-breeding individuals to explore its potential role in mediating carry-over effects (n=54). To disentangle carry-over effects from individual quality, we manipulated the reproductive effort irrespective of individual quality by removing entire clutches during two years, thereby inducing reproductive failure in randomly selected individuals. All individuals were tracked over the non-breeding stage to determine their winter distribution and daily energy expenditure through a time activity budget, and we used piecewise structural equation models (PSEM) to assess direct and indirect causal effects between consecutive breeding stages. If seasonal interactions are dominated by carry-over effects, we expected that controlling for individual quality would show that costs of reproduction are paid in the subsequent year in lower reproductive output and are mediated by the individuals' behaviour and energetic performance during winter, such as delayed migration in fall and higher energy expenditure in winter. Alternatively, if seasonal interactions are dominated by intrinsic factors related to the individual quality, we expected a positive correlation between consecutive breeding attempts with individuals showing consistency in their breeding performance, but that this correlation would disappear once experimentally controlling for individual quality. We also predicted that carry-over effects from winter into breeding would be mediated by corticosterone levels in pre-laying kittiwakes with, notably, higher levels of corticosterone associated with higher winter energy expenditure and delayed laying date.

MATERIALS & METHODS

Study system and experimental design

The studied population is a long-term monitored colony of individually-marked black-legged kittiwakes situated in Kongsfjorden, Svalbard (High Arctic Norway; 78° 54' N, 12° 12' E). We monitored nest contents from 2008 to 2021 every two to six days to determine individual breeding success and phenology. In some years, nests could not be monitored until chicks fledged, so for all years of the study we used the success of rearing at least one chick for 10 days after hatching (hereafter 'breeding success') as a proxy of the annual reproductive success and expressed as a binary variable (failure = 0, success = 1). We considered this measurement to be representative of reproductive success as three quarters of kittiwake chick mortality occur within 10 days after hatching (Coulson & Porter, 1985). The sex of individuals was determined by molecular sexing (following Fridolfsson & Ellegren, 1999) or through behaviour when paired with a known-sex partner.

During summers 2019 and 2020, we conducted a clutch removal manipulation to relieve parents from further reproductive investment and assess potential carry-over effects while controlling experimentally for individual quality. The full clutch (one or two eggs) was removed to provoke the reproductive failure of 14 nests in 2019 and 12 nests in 2020. The eggs were collected upon laying for a parallel study on contaminants (Jouanneau et al., 2023), and replaced by dummy eggs for 10 days to avoid relaying. Nests for control and experimental groups were selected randomly, so ‘high’ and ‘low’ quality individuals should have been selected in equal proportion to their availability for the study.

Solar geolocator deployment and processing

We used geolocators (Lotek: mk18, mk13, mk4083, mk4093; Migrate Technology: Intigeo F100, C65; 3 g = 0.7% of average body mass of 411±34 g), mounted on a Darvic leg band, to track the non-breeding movement of kittiwakes. From 2008 and 2020, we deployed 363 geolocators on adults captured at their nest using a cable noose. Devices measured light intensity every minute and recorded the maximum light intensity every 5 or 10 min. They also measured saltwater immersion (whether or not the bird was in contact with the sea water) every 3 or 30 s and stored the number of wet measurements within every 10 min period. We recaptured 78% of the individuals and retrieved the geolocators. Overall, and after filtering for incomplete tracks, we acquired 277 tracks from 181 different individuals (67 females, 76 males, 38 undetermined) covering 13 non-breeding seasons (fall 2008 to spring 2021, supplementary information Table S5.1).

To infer geographic positions, geolocator light data were processed according to the procedure based on the threshold method to estimate twilight events and developed for the SEATRACK international initiative (Bråthen et al., 2021), a collaborative project focused on tracking North Atlantic seabird wintering movements, of which this study is part. Geolocation-based-tracking is inherently prone to create lower accuracy locations in latitudes around equinox periods and cannot be used over periods of continuous daylight (or continuous night) at high latitudes. To fill these gaps in the tracks, and to reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm specifically developed for SEATRACK (Fauchald et al., 2019) and recently applied in kittiwakes (Léandri-Breton et al., 2021). For detailed geolocation processing methods see supplementary information.

Breeding phenology and winter distribution

The timing of departure from the colony area in fall and return to the colony area in spring were estimated using Lavielle partitioning algorithm (see Léandri-Breton et al., 2021 and supplementary information). This was done over a 5-day running maximum of the saltwater immersion data indicating a behavioural transition between land use (dry) and continuously pelagic behaviour (wet). The foraging trips after the first visit to the colony area in spring were excluded, as individuals start to display a central-place foraging behaviour with long pre-laying trips as far as Iceland (Bogdanova et al., 2011). The wintering stage was defined for each track as the last date in fall and the first date in spring the individual crossed the 60°N, corresponding to the northernmost extent of the winter distribution (Léandri-Breton et al., 2021). The centre of the population’s winter range was defined as the centroid of the 95% utilization distribution kernel

(UD), estimated over the population's winter positions (from all tracks, n = 38 900 positions) and projected using a Lambert Azimuthal Equal Area coordinate system (Fig. 5.1, h=200 km, 50x50 km grid cells). Similarly, the centroid of each individual's track was calculated from a 95% UD over the individual's winter position. The distance from the population's range was defined as the orthodromic distance between the population's winter centroid and the centroid of each individual's winter track.

Daily energy expenditure (DEE) in winter

We used the standardized saltwater immersion data (SSI) to build a time-activity budget based on the identification of three behaviours for each 10-min periods: sustained flying (SSI = 0%), resting on water (SSI $\geq$ 98%) and active foraging (0% < SSI < 98%) which is characterized by a succession of short flights and short swimming or shallow diving bouts (Jodice et al., 2003). To estimate the daily energy expenditure during the wintering stage, we combined the time-activity budget with the population-specific resting metabolic rate (Gabrielsen et al., 1988) and the activity-specific field metabolic rates for the kittiwake flying and foraging behaviours (Jodice et al., 2003). The detailed procedures to calculate the time-activity budget and the daily energy expenditure are described extensively in the supplementary information.

Blood sampling and hormone assays

From 2019 to 2021, 92 kittiwakes (21 females, 41 males and 30 undetermined) previously equipped with a geolocator were recaptured during the pre-laying stage and sampled within 3 min (average sampling time: 129±29 sec, range: 72-180 sec) for 2 mL of blood from the brachial vein. The time before sampling had no effect on the corticosterone levels (beta regression, *coef*=0.044, *SE*=0.053, *df*=55, *p*=0.41, supplementary information). Samples were kept on ice before centrifugation and subsequently stored at -20°C until radioimmunoassays were conducted. Total baseline corticosterone concentrations (bound and free fractions) were measured in plasma via radioimmunoassay following the method validated by Lormée et al., (2003). The corticosterone was extracted from each 40 µL plasma sample by adding 3 mL of diethyl-ether. It was vortexed, centrifuged and frozen at -20°C to separate the diethyl-ether phase containing the hormone from the plasma. The solvent was evaporated in a 40°C bain-marie. The extract was then re-dissolved in a phosphate buffer and incubated overnight at 4°C with 4000 CPM of H^3-corticosterone (Perkin, Elmer, US) and a polyclonal antiserum (anti-corticosterone antibody provided by Merck, Sigma Aldrich, France). The bound and free fractions were separated using dextran-coated charcoal and the activity of the bound fraction was counted in a Tri-carb liquid scintillation counter 2810TR (Perkin, Elmer, US). All samples were assayed in duplicates. Intra- and inter-assay coefficients of variability were 11.13% and 16.88%, respectively. The lowest detectable concentration was 0.28 ng/mL.

Statistical analyses

We used piecewise structural equation models (PSEM) to assess direct and indirect causal effects between consecutive breeding stages. We formulated potential pathways based on the theoretical framework and chronology of stages of the annual life cycle of the species (Fig. 5.2) to fit linear mixed-effects (LME) and generalized linear mixed-effects models (GLME). These models were incorporated into three different PSEM using the package ‘piecewiseSEM’ (Lefcheck, 2016). They incorporated both the direct pathway between consecutive breeding stages and the indirect pathways through intermediate parameters associated to the wintering and migratory stages (Fig. 5.2). The dataset for the first model (n=141 tracks) included all individual tracks from the 13 years of the study, but excluding the individuals from experimental nests (Fig. 5.2). Therefore, with this first model we adopted a longitudinal approach with the objective of determining seasonal interactions among breeding in year *x*, non-breeding and breeding in year *x* + 1, whether they arise from potential carry-over effects or from individual quality. *Nest* (from year *x* and year *x* + 1, as both pair members were included) and *Year* were included as random factors.

A second PSEM was fitted to test directly the role of corticosterone during pre-laying as a potential mediator of carry-over effects. We used a subset of the dataset with individuals blood-sampled during the pre-laying stage and excluding individuals from experimental nests in year *x* (n=54 sampled from 2019-2021, Fig. 5.2). *Nest* was included as a random factor. (Shipley, 2009)

The third PSEM was based on an experimental approach and included experimental individuals (n=26) and control individuals (n=44) from the clutch removal experiment carried out in 2019 and 2020 (Fig. 5.2). The objective of this third model was to assess carry-over effects arising from breeding costs by manipulating the reproductive effort irrespectively of individual quality. The breeding success during the recapture year was excluded from the pathways of this model since not enough nests were monitored until breeding success in 2021. However, later laying reduces breeding success (LME, *coef*=-0.042 per day, *SE*=0.005, *df*=43, *p* <0.0001, R^2=0.47), and the results from this model are thus still reflective of the interactions from one breeding stage to the next. *Nest* was included as a random factor.

The goodness-of-fit of each SEM was evaluated from the Fisher's C-value test of conditional independencies (*d-separation*, Shipley, 2009). The *d-separation* test failed in the third model indicating the path directly linking the treatment to the winter daily energy expenditure was missing. This path was thus added to the final model. The global fit for all three final PSEM was good and the *d-separation* test indicated that no further paths were missing (PSEM 1: *C*=13.6, *df*=20, *p*=0.9; PSEM 2: *C*=19.4, *df*=14, *p*=0.2; PSEM 3: *C*=15.4, *df*=14, *p*=0.3). To achieve normality, the distance to the population's range centre was log-transformed in all models. Model predictions were reported with their standard error. The output of each PSEM is reported in supplementary information (Table S5.2).

To further investigate whether individuals showed interannual consistency in their behavioural traits, we estimated the individual repeatability *r* (intra-class correlation) of each behavioural parameter by calculating the proportion of intra-individual variance while accounting for differences among individuals. This was done using the function 'rpt' (R package 'rptR', Stoffel et al., 2017) and only individuals with multiple years of measurements. Among those, 58 individuals were tracked multiple years allowing estimation of repeatability in movement behaviour (n = 58 individuals tracked up to 7 years, 2.7±1.1 years in average, supplementary information Table S5.3). Repeated tracking of individuals was not necessarily done over consecutive years, with an average interval between first and last measurement of 3.5±1.7 years (range 2-9 years, supplementary information Table S5.3). The distance to the population's range centre was log-transformed to improve normality and models were fitted over a Gaussian distribution, with the exception of the breeding success for which we used a binary distribution. All analyses were carried out in R version 4.2.2 (R Core Team, 2022).

RESULTS

Longitudinal approach

Consecutive breeding stages were linked by direct pathways, indicating that the breeding effort in a given year *x* can have direct positive effects on the reproduction in the subsequent year *x* +1 (see Fig. 5.2). Indeed, the breeding success in year x had a strong effect on the timing of laying and the breeding success in year *x* + 1, with successful breeders laying 5 days earlier (laying date 163 ± 4 days versus 168 ± 4 days, Fig. 5.3d) and having 20% higher breeding success than failed breeders during year x + 1 (breeding success of 0.54 ± 0.09 versus 0.74 ± 0.06). Furthermore, the timing of laying in year x + 1 explained the breeding success that same year, with successful breeders laying 11 days earlier than failed breeders (averaged laying date 161 ± 0.4 days versus 172 ± 1.3 days, Fig. 5.3c). Therefore, the strongest path based on the standard coefficients linked the breeding success in year *x* to the breeding success in year *x* + 1 via the timing of laying (Fig. 5.2).

This first PSEM also revealed indirect pathways, but none of these had cascading effects persisting into the subsequent breeding stage (see Fig. 5.2). Successful breeders in year *x* left the colony 7 days later than failed breeders (departure date 249.8 ± 2.4 days versus 242.5 ± 3.1 days), but this difference had no detectable effects on the winter distribution. However, the breeding success in year *x* had a strong effect on the winter distribution of individuals, with failed breeders wintering 40% closer to the population's range centre than successful breeders (327 ± 143 km versus 810 ± 220 km, Fig. 5.3a). Furthermore, there was a decrease in daily energy expenditure of 11.0% (94.7 kJ/day) over the distance from the centre to the edge of the population's winter range (4293 km, Fig. 5.3b).

The standard coefficients from the second PSEM did not reveal any path connecting the baseline corticosterone levels of pre-laying individuals to behavioural parameters during the previous winter or the following breeding stage (see Fig. 5.2). The only significant path in this model was the effect of the timing of laying on the breeding success in year *x* +1, with successful breeders laying 14 days earlier than failed breeders (lay date: 160.5 ± 0.7 days versus 174.4 ± 1.5 days). Body condition index (i.e., residuals of the linear correlation between the skull length and the body mass) did not improve the model fit (supplementary information Table S5.4).

Experimental approach

By using data from the clutch removal experiment, hence manipulating the reproductive effort irrespectively of individual quality, the results of the third PSEM revealed paths expected to indicate true carry-over effects (see Fig. 5.2). With this third PSEM, the path linking the breeding success in year *x* to the winter daily energy expenditure was no longer mediated by the winter distribution (distance to the population's range centre) as found with the first PSEM (Fig. 5.4a and 5.4b). Instead, the breeding effort treatment had a small but direct effect on the daily energy expenditure in winter, with control individuals spending 6% more energy in winter than experimental individuals (816.5 ± 9.1 kJ versus 770.7 ± 12.4 kJ, Fig. 5.4c). The treatment also directly affected the breeding stage in the following year, with control individuals laying 2.7 days later than induced failed breeders (average laying date 162.4 ± 0.7 days versus 159.7 ± 0.9 days, Fig. 5.4d). Such delay corresponds to a decrease of 11.9% in the breeding success probability (based on population-wide breeding success, LME, *coef*=0.044 per day, *SE*=0.006, *df*=43, $p<0.0001$).

Individual repeatability in behaviour

Behavioural parameters associated with the winter distribution and energy expenditure were moderately to highly repeatable (Fig. 5.5), with 63% repeatability in the distance at which each individual is wintering to the population's range centre ($r=0.63$, 95% *CI* [0.47; 0.76], *SE*=0.07, $p<0.0001$) and 42% repeatability in the daily energy expenditure in winter ($r=0.42$, 95% *CI* [0.24; 0.57], *SE*=0.09, $p<0.0001$). This suggests that variations in these parameters are partly driven by inter-annual consistency in individuals' winter behaviour. Repeatability was, however, low for parameters associated with breeding phenology (Fig. 5.5): colony departure in fall ($r=0.22$, 95% *CI* [0.07; 0.38], *SE*=0.08, $p<0.0001$), colony arrival in spring ($r=0.16$, 95% *CI* [0.02; 0.32], *SE*=0.07, *p* <0.0001) and timing of egg laying (*r*=0.13, 95% *CI* [0.02; 0.25], *SE*=0.06, *p* <0.05). Breeding success had low repeatability (*r*=0.22, 95% *CI* [0.05; 0.41], *p* <0.001), but was associated with high variability (*SE*=0.24). We did not include this parameter in Fig. 5.5 because it is the only binary variable not directly comparable with other parameters. Overall, the breeding success in our dataset is relatively high, with 64% pairs successfully raising at least one chick to 10 days old (272 successful attempts, 97 failed attempts).

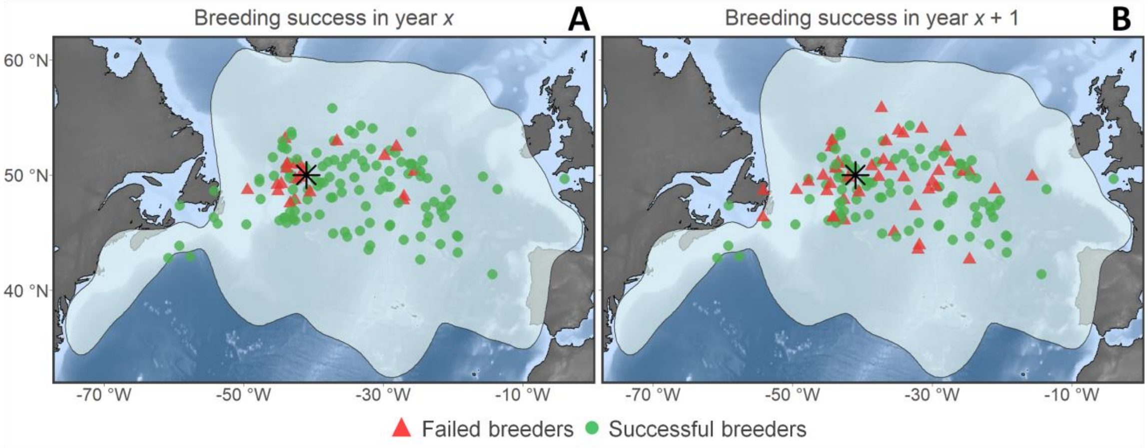

Figure 5.1: Centroids of each individual winter track (n = 141) showing the winter distribution of successful and failed breeders during consecutive breeding stages. A) Reproductive success during the previous breeding stage (year *x*), with failed breeders clustered near the population's range centre (black star ✳). B) Reproductive success during the following breeding stage (year *x* + 1), with failed breeders spread across the population's winter distribution. The grey polygon illustrates the 95% utilization distribution kernel of the population (n=38 900 positions).

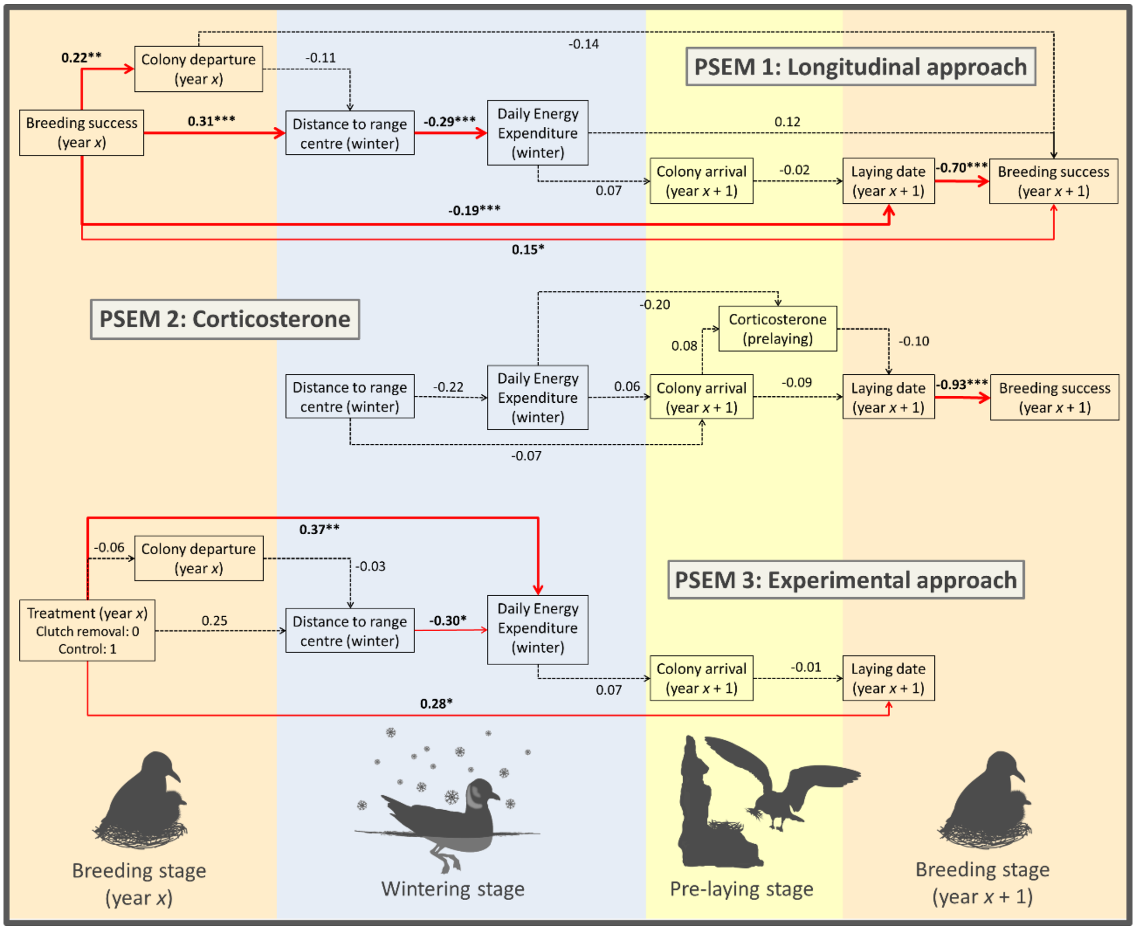

Figure 5.2: Directed acyclic graphs (DAG), showing the direct and indirect causal pathways tested in each three piecewise structural equation models (PSEM), with standardized coefficients. Arrows show the predicted directions between behavioural parameters associated to each stage of the annual life cycle of the species. Dotted arrows indicate nonsignificant pathways. Solid red arrows, bold values and stars (*) next to the coefficients indicate significant pathways.

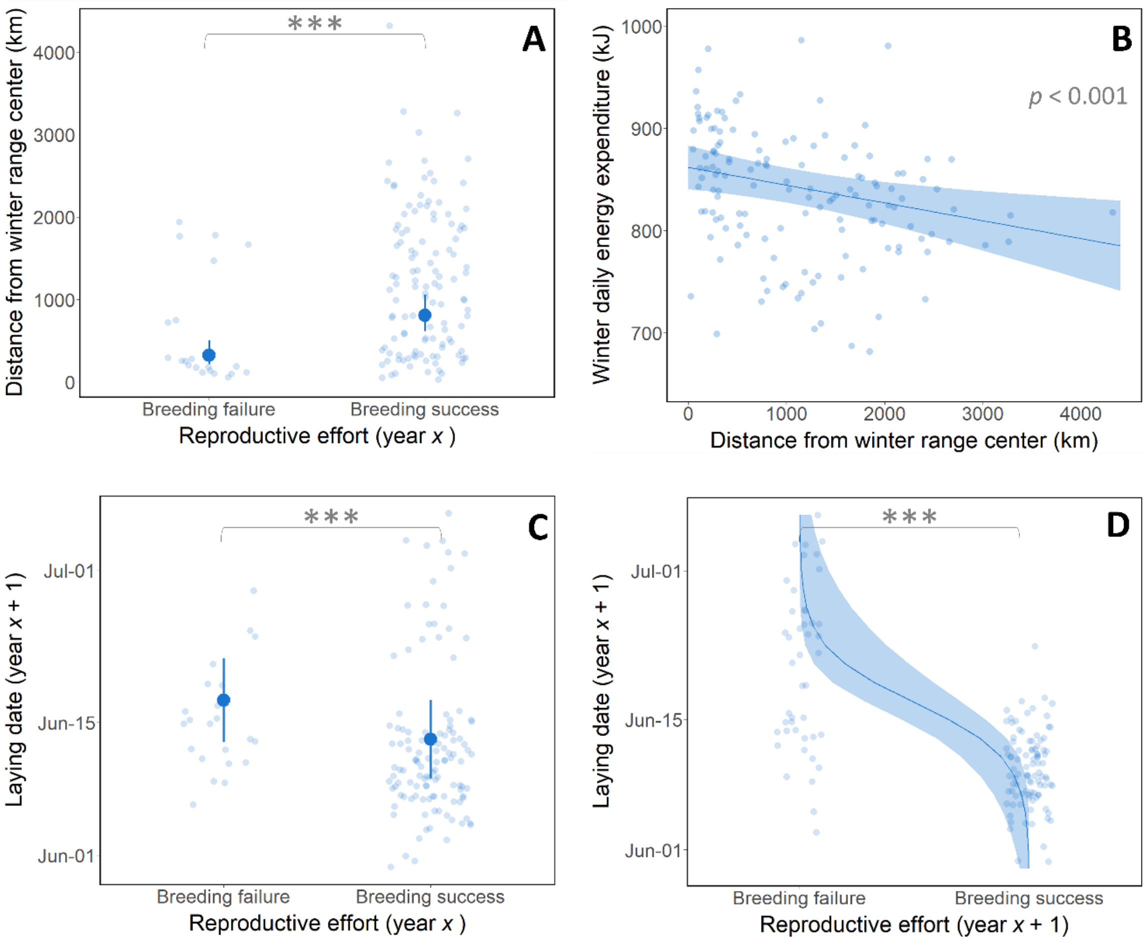

Figure 5.3: Partial residual effects of four pathways from the first PSEM (longitudinal approach) showing direct and indirect causal effects between consecutive breeding stages arising either from carry-over effects or individual quality. Plots show model predictions, with their 95% confidence intervals, over the jittered raw data. Models with log transformed predictors are plotted on the original scale.

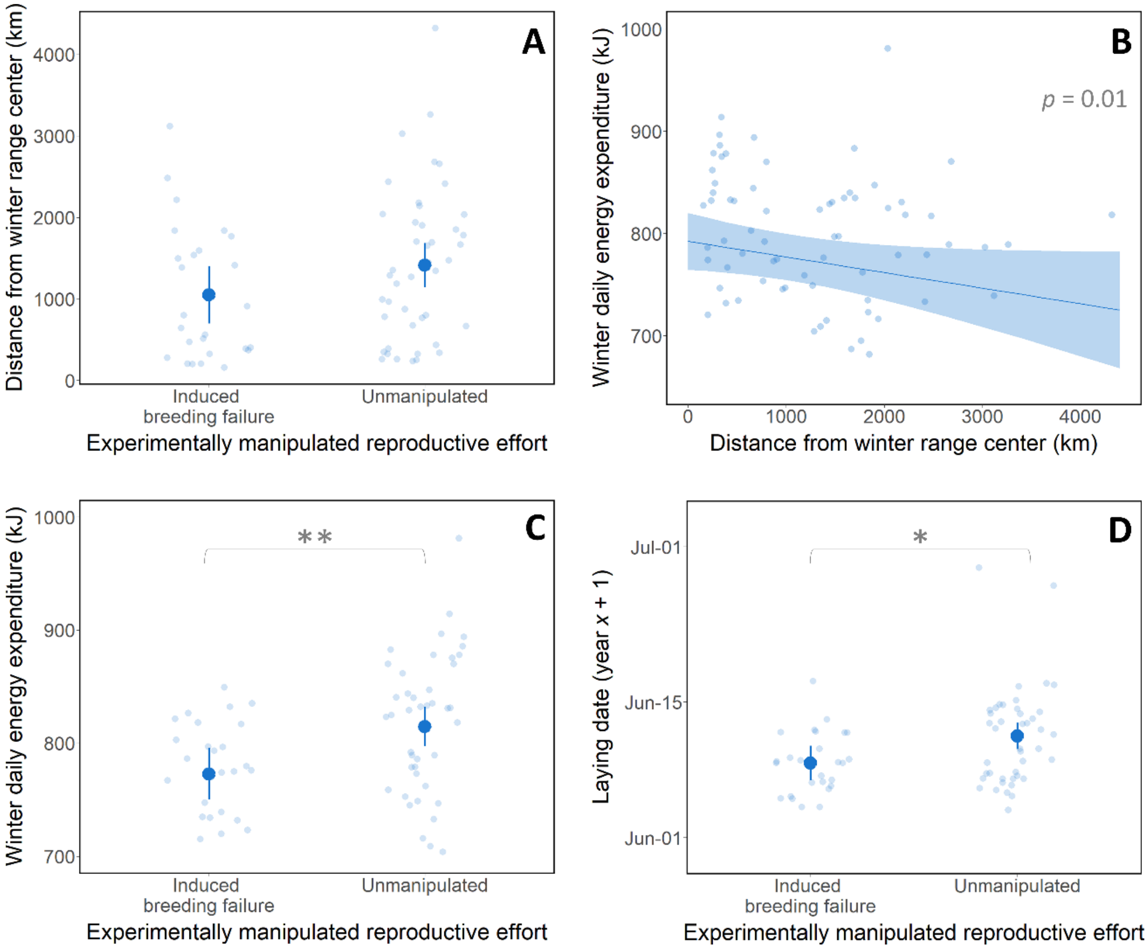

Figure 5.4: Partial residual effects of four pathways from the third PSEM (experimental approach) showing potential carry-over effects arising from the breeding effort while experimentally controlling for differences in individual quality. Plots show model predictions, with their 95% confidence intervals, over the jittered raw data. Models with log transformed predictors are plotted on the original scale.

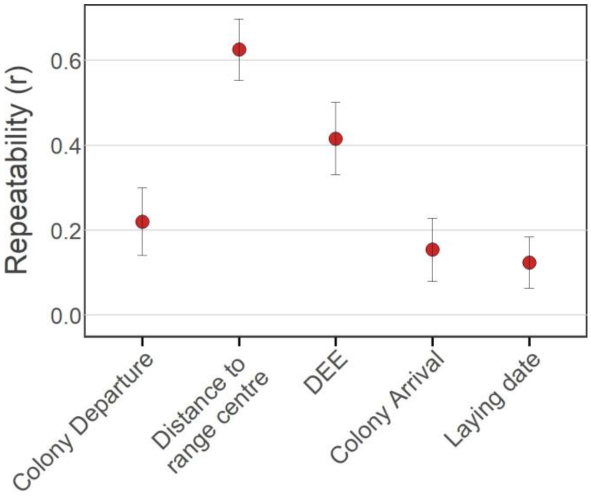

Figure 5.5: Individual repeatability (*r*) in behavioural parameters associated with different stages of the annual life cycle of black-legged kittiwakes with standard errors, where 0 = no repeatability and 1 = high repeatability.

DISCUSSION

Using a long-term dataset of a well-studied avian migrant combined with an experimental approach, we investigated the relative importance of carry-over effects and individual quality in determining cross-seasonal interactions and fitness consequences. From the longitudinal approach spanning 13 consecutive years, the breeding success was connected to the distribution of individuals during the following wintering stage, which, in turn, was connected to the energy expenditure of individuals in winter. This effect, however, did not cascade into the subsequent breeding stage. The strongest pathway directly linked consecutive breeding stages, with the breeding success in a given year resulting in an earlier onset of breeding (egg laying) the following year, which led to a 20% higher breeding success. However, when experimentally manipulating the reproductive effort irrespective of individual quality, this positive interaction between successive breeding stages disappeared. Instead, the breeding effort led to reproductive costs paid in elevated energy expenditure in winter, likely to recuperate from these costs, and a later onset of reproduction the following year associated with a 12% lower breeding success the following year (based on population-wide breeding success). The experimental approach also revealed that quality and area fidelity, rather than reproductive costs, were dominant in driving the winter distribution of individuals, masking underlying carry-over effects into the winter energy expenditure of individuals. Thus, individual quality overwrote carry-over effects, although both were present.

Individual quality

Although life-history theory is predicated on the idea that reproduction is costly, individuals often show positive correlations between current and future reproduction (Hamel et al., 2009; Reznick et al., 2000). This is what we observed in the study population with the individual breeding performance in a given year positively associated with the onset and success of reproduction the following year. Similarly to this, and despite the fact that breeding kittiwakes are operating close to their metabolic ceiling (Welcker et al., 2010), breeders from another study had higher probability of breeding again the subsequent year compared to individuals that skipped reproduction (Cam et al., 1998). Such absence of apparent allocation trade-offs between traits in a given population can arise when there is high variance in resource acquisition among individuals, with higher quality individuals being more efficient in extracting resources from their environment, consequently having more energy to allocate in all functions in a given life-history stage without impacting their future reproduction and survival (Hunt et al., 2004; van Noordwijk & Jong, 1986). Heterogeneity in individual quality can have a genetic basis, but may also arise from cohort or maternal effects which can have irreversible, long-lasting impacts on the fitness of individuals later in life (‘silver spoon effect’, Grafen, 1988; Wilson & Nussey, 2010). We found strong effects of individual quality in our system that could arise, for instance, from larger individuals being able to better compete for resources (Ronconi & Burger, 2011). Age can also be a source of differences in individual apparent quality, especially in long-lived species, with survival and reproductive output typically peaking in more experienced, mid-aged individuals, before declining with senescence (Forslund & Pärt, 1995). More experienced adults may indeed be better able to acquire resources from the environment, having refined their foraging behaviour and locations over the years (‘exploration-refinement hypothesis’, Guilford et al., 2011). Age is indeed likely associated to consistency in behaviour (i.e., winter distribution) and breeding performance in our study, since all birds were adults and those tracked over a longer period were likely older individuals. Overall, intrinsic differences in quality would lead to individuals also varying in their ability to cope with resource limitations, resulting in differential breeding costs, as observed in our study population.

Consistency in spatial movement

Breeding investment can also lead to carry-over effects influencing subsequent spatial behaviour of individuals, as shown in a few experimental studies on migratory seabirds. For instance, inducing breeding failure in male Cory’s shearwaters (*Calonectris borealis*) decreased their propensity in engaging in long-distance migration compared to successful breeders (Catry et al., 2013). Pacific kittiwakes that were supplementary fed during breeding travelled shorter distances and contracted their winter distribution compared to unfed individuals (Whelan et al., 2020). Similarly to these studies, we found a correlation between the breeding effort and the winter distribution of individuals, which in turn was connected to the energy expenditures of individuals during winter: failed breeders (reduced breeding effort) wintered closer to the population’s range centre compared to successful breeders (Fig. 5.1a). However, this link disappeared after manipulating the breeding effort irrespectively of individual quality, indicating that the winter distribution was more determined by intrinsic factors related to individual quality than by carry-over effects. In line with this, individuals from the study population show high area fidelity in winter as indicated by the repeatability in the position of the distribution centroid of individuals (>60%, Fig. 5.5) and the consistency in their overall movement in winter (mean nearest neighbour distance of 260 km between tracks; Léandri-Breton et al., 2021). Site fidelity is commonly found across taxa (Piper, 2011), suggesting that within-individual spatial consistency is likely a widespread factor masking underlying carry-over effects and needs to be taken into account.

Similarly, Bogdanova et al., (2011) found that kittiwakes failing reproduction left their colony in Scotland earlier and travelled over 3000 km to reach the same wintering area as failed breeders in our study, while most successful breeders departed later and wintered closer to the colony along the European coasts. Failed breeders may have more time and energy to engage in a long-distance migration to reach profitable winter locations (Bogdanova et al., 2011), but our results suggest that such spatial differences may also result from differences in individual quality. In line with this, fidelity to wintering areas in a population of Atlantic puffins (*Fratercula arctica*) was associated with significant differences in breeding success, indicating that individual of different quality may visit different areas (Fayet, Freeman, Shoji, Boyle, et al., 2016). Overall, we suggest that higher quality individuals with higher breeding performances are also performing better in winter as they use areas allowing them to maintain better energy performances (lower energy expenditures) throughout the wintering stage.

Underlying carry-over effects

After controlling for individual quality, the breeding investment directly determined the activity budget in winter, with individuals experimentally relieved from breeding costs experiencing reduced energy expenditure on the wintering site compared to control individuals. Control individuals may have increased their activity to compensate for poor foraging conditions on their wintering grounds, although this seems unlikely considering that wintering area selection is in great part determined by site fidelity in our study (>60% repeatability). More likely, this difference in energy expenditure suggests that control individuals increased their activity to regain condition following their higher breeding investment, while experimental individuals were able to 'take it easy' the winter following the manipulation. Likewise, chick cross-fostering in Manx shearwaters (*Puffinus puffinus*) showed that increased breeding effort led to elevated activity in winter and lower reproductive success the following year, although such differences were not apparent for individuals with reduced breeding effort (Fayet, Freeman, Shoji, Kirk, et al., 2016). Moreover, elevated winter energy expenditure was associated with lower reproductive performances in European shags (*Gulosus aristotelis*) and Manx shearwaters, suggesting that individuals adjusted their activity in response to their own immediate condition rather than in anticipation of future breeding costs (Daunt et al., 2014; Shoji et al., 2015). In our study, however, differences in energy expenditure between experimental and control birds did not persist into the next breeding stage, potentially because individuals were successful in adjusting their winter activity to compensate for breeding costs. Consequences of breeding investment can indeed weaken over the course of the non-breeding stage, a period in the annual life cycle potentially less time-constrained, allowing breeding costs to be buffered rather than accumulated (Bogdanova et al., 2017; Briedis et al., 2018; Ramos et al., 2018). For instance, previous studies on kittiwakes showed that a longer time spent on the wintering site was associated with reduced telomere shortening (Schultner, Moe, Chastel, Bech, et al., 2014) while higher energy expenditure during breeding had no detrimental effect on the return rate of individuals the following year (Welcker et al., 2010). In another clutch removal experiment, consequences of breeding costs on the following breeding propensity were buffered during winter in most years of the study, although survival costs were still entailed (Golet et al., 2004). However, breeding costs in our study were not entirely buffered by the wintering stage as controlling for individual quality revealed underlying carry-over effects paid in a delayed onset of breeding the following year, with control individuals (higher breeding investment) laying 2.7 days later compared to individuals experimentally relieved of further breeding investment. Although this difference in the breeding phenology appears small, it corresponds to a 12% decrease in breeding success (at the population level) and has the opposite direction than what was found before controlling for individual quality (i.e., breeding success in a given year positively associated to 20% increased success the following year). This indicates that controlling for individual quality revealed a potential cost of reproduction lasting into the following breeding stage. Thus, the experimental approach provided evidence that, although they are masked by individual quality and site fidelity, carry-over effects exist in the study population, with reproductive costs resulting in an elevated energy budget in winter and a delayed onset of breeding, a parameter strongly related to breeding success in our study and in birds in general (Goutte et al., 2010; Perrins, 1970).

Pre-laying corticosterone levels

We did not find a relation between baseline corticosterone levels measured in pre-laying individuals and the previous wintering stage nor with the subsequent breeding output (i.e., reproduction onset and success). Other studies have shown either negative effects (Harms et al., 2015), no effects (Bourgeon et al., 2014) or even positive effects (Pérez et al., 2016) of corticosterone levels measured in winter-grown feathers into the subsequent reproductive output. These mixed results likely reflect variations in the strength and persistence of carry-over effects in relation to conditions experienced during previous stages (Ramos et al., 2018). In our study population, the effects of the wintering behaviour did not carry into the breeding stage, and potential carry-over effects into the hormonal stress response of pre-laying birds were likely buffered as well. Moreover, kittiwakes could not be sampled immediately after their return from the wintering stage, and their blood corticosterone levels may thus reflect the foraging conditions experienced in the past weeks at the breeding colony more than those experienced on the wintering site (Kitaysky, Kitaiskaia, et al., 2001). In line with this, Goutte et al., (2014) found that corticosterone levels of pre-laying kittiwakes varied among years and were lower in years of earlier breeding onset. How corticosterone varies according to local environmental conditions and foraging activity of pre-laying individuals remains unclear and would require further investigation. Measuring the corticosteroid binding globulin (CBG), rather than the total plasma concentration, would improve understanding of changes in the circulating, active proportion of corticosterone in relation to environmental conditions experienced (Desantis et al., 2013).

CONCLUSION

Overall, variations in individual quality associated to breeding performances and repeatability in behaviour were dominant in determining seasonal interactions in behaviour and performance of the study population. We found that individuals with better breeding performance (successful breeders) were also performing better in winter (lower energy expenditure), leading to positive correlations across seasons between current reproduction, winter distribution and future reproduction. It is only after controlling experimentally for consistency in breeding performance (individual quality) that we could conclude these correlations were attributed to differences in individual quality, and also reveal underlying carry-over effects that were otherwise masked by quality. Because variations in costs and in quality are likely both present in a population, it is not possible to predict the sign of the covariance between traits (Wilson & Nussey, 2010). Moreover, it is not possible to assess the strength of carry-over effects if the covariance is negative, nor to conclude that underlying costs are absent if the covariance is positive (Wilson & Nussey, 2010). An experimental approach is required to separate costs and quality effects as they can both have important, but different, evolutionary and demographic consequences on animal populations (Harrison et al., 2011).

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STATEMENTS

Conflict of interest

The authors declare that they have no competing or conflict of interests.

Author contributions

D.-J. Léandri-Breton, K. Elliott, O. Chastel and P. Legagneux conceived the ideas and designed methodology; D.-J. Léandri-Breton, W. Jouanneau, F. Amélineau, F. Angelier, P. Blévin, A. Goutte, S. Tartu collected the data; A. Tarroux, P. Fauchald, V.S. Bråthen and B. Moe carried out geolocation preliminary analyses and data management; C. Parenteau and W. Jouanneau conducted hormone radioimmunoassay; G.W. Gabrielsen provided expert advice; D.-J. Léandri-Breton led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data supporting this study will be deposited in a public repository (Dryad) upon acceptance.

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CHAPTER 6 – GENERAL DISCUSSION

DISCUSSION

Everyone who visited a seabird colony undoubtedly recalls the noise, the smell and the cacophony of birds fighting, squabbling, mating and flying everywhere. In larger colonies, the multitude of birds can be almost overwhelming, but for ecologists, these present fantastic research opportunities. The density of their nests, their philopatry to the nesting site and their relative ease of capture render breeding colonial seabirds exceptional models to investigate a vast array of research questions. However, at the conclusion of the breeding season, seabirds leave their colony for the open ocean, often not returning to land until the onset of the next breeding season. While they are readily monitored during the few months they remain attached to their breeding sites, most seabirds become remarkably inconspicuous and challenging to study outside of the breeding season. Many of them even spend the majority of the year in the 'high sea', beyond any national borders and out of reach for scientists (Beal et al. 2021). Consequently, there is a clear bias in the literature toward the breeding stage, with a notable knowledge gap concerning the non-breeding ecology of seabirds, and migratory species in general. This thesis connects the non-breeding stage with the breeding stage with the aim to investigate the factors underpinning year-round seasonal interactions. Throughout, I place a significant emphasis on the movements and ecology of individuals during the non-breeding stage, as this period remains the least known in migratory species' annual life-cycle.

To achieve this objective, I adopt an integrative approach, combining movement ecology, phenology, endocrinology, ecotoxicology, ecophysiology, long-term population monitoring, and experimental methods. I concentrate on a single system, providing one of the lengthiest available datasets on avian non-breeding movements, spanning 13 years of tracking and population monitoring. While the trend in research now favours large, multi-site studies (Reichman et al. 2011, Davidson et al. 2020, Nathan et al. 2022), focusing on a single system permits a comprehensive exploration of inter- and intra-individual differences that may be obscured by variations among sites when employing "Big Data" approaches. Although the results may sometimes be site-specific, they can offer illustrative examples and reveal clues that can subsequently be generalized through meta-analyses.

Space

Fidelity in space utilization is a common form of repeatability widespread in animals and associated to predictability in resources (Switzer 1993, Börger et al. 2008, Piper 2011). I present evidence that even among highly pelagic species, spatial repeatability is observable, and this consistency can be largely attributed to individual quality. I demonstrate that kittiwakes are consistent in their non-breeding movements (Chapter 2, Chapter 5), with individuals showing spatial consistency across their overall routes among years (Chapter 2) and in the position of their distribution’s centre (Chapter 5). This site fidelity affected the energy expenditure (Chapter 2, Chapter 5) and exposure to poly- and per-fluoroalkyl substances (Chapter 4), indicating that migratory strategy can lead to differential costs among individuals. Furthermore, I demonstrated experimentally that site fidelity is related to individual quality. Indeed, throughout their annual cycle, individuals displayed cross-seasonal consistency in their performance: those with better breeding performance (i.e., successful breeders) also exhibited better performance during the winter (lower energy expenditure, Chapter 5). Such positive correlations across seasons between current reproduction, winter distribution and future reproduction suggest that disparities in individual quality rather than carry-over effects drive seasonal interactions. In the context of carry-over effects, assessing repeatability thus helps to differentiate between quality and costs since both are likely present in populations.

Repeatability

Evaluating the repeatability of traits is also essential for understanding a population's susceptibility to environmental changes (Phillips et al. 2017). Populations with high repeatability may be more vulnerable to alterations in resource and environmental conditions (Pulido 2007, Charmantier et al. 2009). Carry-over effects resulting from these factors are therefore more likely to impact a larger proportion of the population simultaneously. Similarly, populations displaying high intra-individual repeatability may be less resilient to rapid environmental changes, as individuals with low plasticity may struggle to adapt quickly (Canale and Henry 2010).

In light of this, does the spatial specialization in winter observed in kittiwakes indicate vulnerability to environmental changes? Since site fidelity is closely linked to resource quality and predictability over space and time (Switzer 1993), the repeatability of individual space use might imply that individuals were consistently able to locate predictable resources over the years of the study, rather than suggesting low plasticity. Additionally, some individuals exhibited more flexibility in their movements, visiting distant oceanic areas during the same winter, potentially "sampling" different conditions in the process (Chapter 2, and see Merkel et al., MEPS, 2021). Kittiwakes are indeed considered generalist predators capable of feeding on a wide variety of prey (Erikstad 1990, Reiertsen et al. 2014). However, they can also exhibit sensitivity to changes in environmental conditions and prey availability. For example, a massive marine heatwave in the Northwest Pacific in 2015-2016 resulted in significant breeding failures in kittiwakes and other seabirds (Osborne et al. 2020, Piatt et al. 2020). Warm water temperatures in this region are negatively associated with capelin abundance (Anderson and Piatt 1999), a prey species that is positively linked to kittiwake breeding success (Hatch 2013). Substantial shifts in oceanographic conditions in the Barents Sea (known as 'Atlantification') also led to a decline in the kittiwake population in the 1990s due to changes in the primary prey base (Vihtakari et al. 2018). However, the population has since rebounded, indicating that kittiwakes can exhibit plasticity (Descamps and Ramírez 2021), although plasticity alone may not be sufficient to adapt to rapid climate changes (Whelan et al. 2022).

These examples demonstrate that kittiwakes respond to changes in resource availability, at least during the breeding stage. Yet, much less is known about seabird responses to resource availability during the winter. Estimating movement consistency over the years provided insights into this, and the results did not reveal any clear shifts in individuals' wintering ranges that would be expected if changes in winter resource availability had occurred (Chapter 2). Furthermore, the winter distribution of individuals and their energy expenditure did not have a direct impact on fitness (Chapter 3, Chapter 5). Therefore, different wintering strategies appear to be profitable, with higher energy loss being compensated for by increased energy intake.

Time

The annual life cycle of migrating species is highly sequential, typically organized into well-defined life history stages, and the fitness of individuals relies on the successful integration of these stages in time (Harrison et al. 2011). Time is, therefore, a critical resource for migratory species, and running out of it can have significant consequences. For example, the timing of breeding plays a nearly universal role in determining breeding success (Verhulst and Nilsson 2008, Perrins 2008), and kittiwakes are no exception (Chapter 5).

While consistency in behaviour and performance predominates over the study period, individuals display more variation in their phenology, as indicated by the low individual repeatability in the timing of migratory and breeding events (Chapter 2, Chapter 5). Furthermore, the results presented here suggest that individuals may exhibit plasticity in their movement phenology in response to environmental conditions. Individuals show higher repeatability in space than in time, suggesting that they are likely following resource pulses that vary more in time than in space (Chapter 2). Marine systems are inherently dynamic, and the timing of climatic events (e.g., sea ice breakup, peak in primary productivity) can exhibit high interannual variations associated with fluctuations in the strength of large-scale climatic and oceanographic systems like the North Atlantic Oscillation (NAO; Visbeck et al. 2001). Notably, the geographical area and strength of the subpolar gyre in the North Atlantic vary by 10% in average among years, resulting in strong variations in the extent of the oligotropic waters, characterized by low primary productivity (surface chlorophyll activity) (Polovina et al. 2008, Foukal and Lozier 2017). Time series show an overall decline in the strength of the subpolar gyre over time (-5% per decade; Foukal and Lozier 2017), and subsequent increase in the oligotropic area (Polovina et al. 2008). Moreover, through such environmental alteration in the marine system, climate changes are significantly affecting the conditions experienced by birds at the colony and wintering areas used by the study population (Fluhr et al. 2017, Descamps et al. 2017, Strøm et al. 2021).

A substantial body of literature suggests that phenological shifts in response to environmental changes are widespread across taxa (Burrows et al. 2011, Poloczanska et al. 2013), although seabirds have been considered insensitive to phenological changes in environmental conditions by some authors (Keogan et al. 2018). The breeding phenology of kittiwakes was partly influenced by carry-over effects from previous breeding costs, providing support for the notion that breeding phenology is sensitive to conditions experienced by individuals (Chapter 5). Kittiwakes in the Pacific have been shown to respond to the timing of environmental resource availability (Shultz et al. 2009, Whelan et al. 2022), but no advancement in breeding phenology across recent decades was detected either in the Pacific or in the Atlantic (Moe et al. 2009, Whelan et al. 2022). Climate changes can also shift the phenology of the migratory movements (Gordo 2007, Van Buskirk et al. 2009). Interestingly, exploratory analyses suggest a temporal trend in migration phenology of kittiwakes over the study period, with an advancement in migration onset and arrival date in spring since 2012 (Fig. 6.1). I have not presented these results as a more comprehensive dataset combining multiple sites and offering greater statistical power would be needed for a more robust investigation. Although the sample size available for this thesis appears large, with up to 280 tracks in some chapters, this number rapidly diminishes to fewer than ten individuals in some years, providing limited statistical power to explore interannual variations.

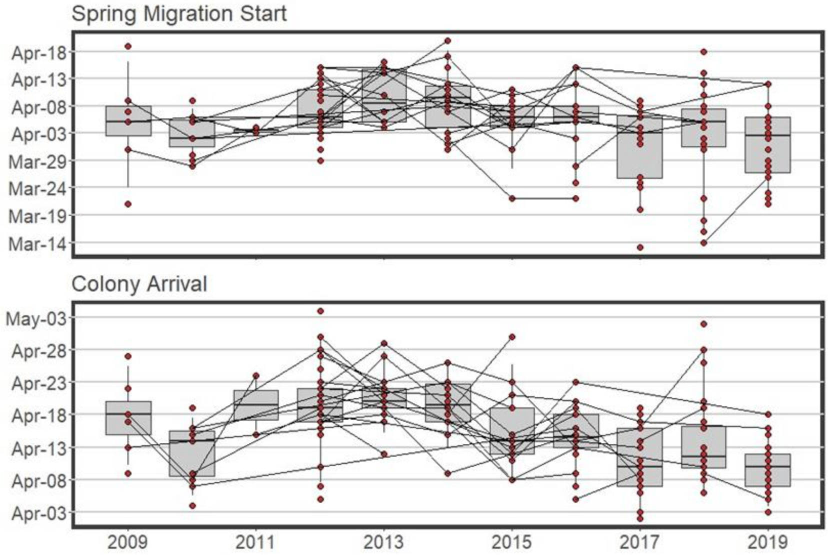


Figure 6.1: Annual variation in timing of spring migration onset and arrival in the colony area for black-legged kittiwakes (*Rissa tridactyla*) tracked with geolocators and breeding in Svalbard, Norway. These preliminary results suggest a potential advancement in the movement phenology after 2013.

Hormones

At the proximal level, the endocrine system translates information from the environment and the individual's internal state into behavioural responses, thus potentially playing a crucial role in mediating carry-over effects. Glucocorticosteroids, such as corticosterone in birds, notably regulate carbohydrates, enabling organisms to maintain stability in their energy balance throughout their life-history cycle (McEwen and Wingfield 2003b), but additional empirical evidence to support this is needed. I did not observe any relationships between baseline corticosterone levels measured in pre-laying individuals and their previous wintering stage or their subsequent breeding outcomes, including reproduction onset and success (Chapter 5). It is important to note that individuals were sampled late in the pre-breeding stage, when decisions about timing of breeding may need to be made weeks earlier as egg production takes up to 9-15 days in kittiwakes (Roudybush et al. 1979). Further research is thus necessary to explore the potential role of corticosterone and physiological mechanisms in general in mediating carry-over effects during this stage, which is notoriously challenging to study due to individuals being more elusive and less attached to their breeding site.

Nevertheless, prior research suggests that elevated corticosterone levels, required to meet increased energy demands, can create physiological conflicts with other functions, particularly reproduction. This interference may include impacts on the hypothalamic-pituitary-gonadal axis responsible for releasing reproductive hormones, potentially resulting in reduced levels of circulating testosterone (Goutte et al. 2010a, b, Deviche et al. 2012). In the context of carry-over effects, the conditions experienced during previous stages may influence the pre-breeding levels of reproductive hormones, possibly through a timing delay influenced by arrival at the colony or a diminished nutritional condition.

A logical follow-up to the current thesis would involve investigating the interaction between corticosterone levels and the reproductive preparedness of individuals in relation to the conditions experienced during the previous breeding stage. An experimental design would be necessary to test this. For instance, this could entail the manipulation of adult energy costs through food supplementation (resulting in increased net energy intake), the induction of breeding failure (resulting in reduced breeding costs), or the induction of flight impairment (leading to a reduced net energy intake due to increased flight costs). Recapturing individuals upon their return to the colony the following year would allow to assess their nutritional condition, corticosterone levels, and reproductive hormone levels (e.g., luteinizing hormone, testosterone, estradiol) throughout the pre-breeding stage. Such an experiment would help provide answers to many questions relative to the breeding phenology and condition of individuals set by carry-over effects. Are individuals responding to the perception of food availability or to their own nutritional condition to initiate reproduction? Is there a timing delay in the hormonal preparation for breeding set by the arrival at the colony? What is the importance of social information and the partner’s condition in determining the initiation of breeding?

Energy

The role of energy as a pivotal currency governing life-history trade-offs is a recurring theme throughout this thesis. I have demonstrated significant variations in the "energyscape" that can result in seabirds experiencing highly divergent energy costs during winter. Specifically, kittiwakes wintering closer to the centre of the population’s range incurred significantly higher energy expenditures compared to those wintering at the periphery (Chapter 2). This observation, coupled with the site fidelity displayed by individuals, suggests that deteriorating feeding conditions could disproportionately impact individuals at the range centre, potentially having dire consequences for population demography, as this region exhibits the highest population density (Chapter 2 and Frederiksen et al. 2012).

Maintaining energy balance is particularly challenging for animals wintering in cold climates, and in the case of seabirds, is linked to mass mortality events referred to as "winter wrecks" (Gaston 2004, Fort et al. 2009, Clairbaux et al. 2021). However, energy expenditure did not have direct carry-over effects on reproductive success (Chapter 5), implying that higher energy loss might have been compensated by increased energy intake (Chapter 3). Nonetheless, it remains necessary to verify this assumption, as estimating energy gain and foraging success during the non-breeding stage remain highly challenging and such data were not available for the dataset analyzed here. Existing techniques to accomplish this have limitations in terms of invasiveness when requiring surgery (oesophagus implants, (Hanuise et al. 2010) or harness attachment impairing movements (accelerometers), and in terms of battery or storage life duration (e.g., micro-camera). Non-invasive techniques like accelerometers and beak-opening sensors are particularly promising (Brisson-Curadeau et al. 2021), although the attachment methods need to be refined and tested for long deployments on flying species. Such data loggers would certainly provide needed insights into the ability of non-breeding animals to maintain their energy balance during the non-breeding stage and navigate the ‘energyscape’, and in the role of energy in mediating carry-over effects.

I found no robust support for the notion that winter energy costs can lead to carry-over effects within this population (Chapter 3, Chapter 5). Controlling for individual quality by inducing reproductive failure, however, revealed underlying carry-over effects stemming from breeding costs (Chapter 5). These costs were paid in terms of delayed onset of breeding in the subsequent season (Chapter 5). Moreover, individuals with lower reproductive costs (failed breeders) experienced reduced energy expenditure on the wintering site compared to control individuals

(Chapter 5). This difference in energy expenditure suggests that individuals with higher reproductive costs (control individuals) increased their activity to regain condition following their higher breeding investment, while experimental individuals were able to ‘take it easy’ the winter following the manipulation.

Reproduction represents an especially demanding life-history stage, necessitating energy and other resources that cannot be reallocated to other functions such as self-maintenance (Harshman and Zera 2007). Such trade-offs can lead to conflicts between the investment in current reproduction, survival and future reproduction (Williams 1966, Reznick et al. 2000). Nevertheless, as demonstrated in this thesis, individuals frequently exhibit positive correlations among their breeding attempts, revealing substantial differences in individual quality (Chapter 5). Most carry-over studies, however, are correlative and fail to account for differences in quality, which can lead to erroneous conclusions regarding the presence or strength of carry-over effects.

Overall, these results illustrate that apparent interactions among life stages were dominated by individual quality and specialization. Thus, although the colony may appear as a superorganism when sitting in it, individual processes are crucial in driving population ecology and dynamics. By looking at the colony as individuals, not just as a colony, I was able to investigate implications of individual variations which might have been otherwise overlooked.

FINAL CONCLUSION

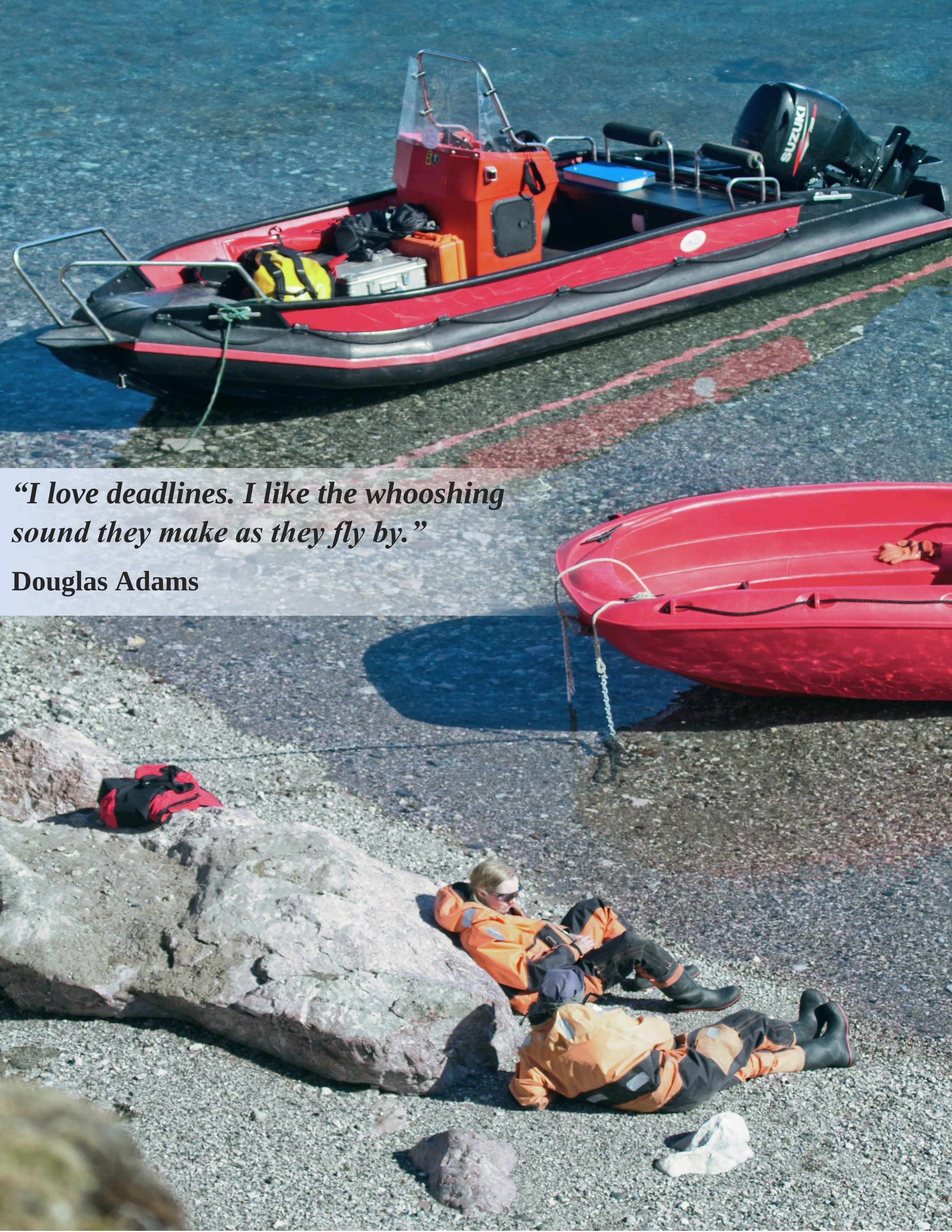
The field of migration research is currently experiencing a new surge, facilitated by recent advancements in biologging technology, progressively revealing the extent and complexity of this phenomenon. Migrants connect ecosystems as they transport energy, nutrients, and contaminants between separate locations, thereby altering trophic interactions and energy flow within resident communities through their pulsed and predictable movements between breeding and non-breeding grounds. In this thesis, I bridge these two worlds by examining migration as a whole, with the objective of understanding some of the mechanisms behind seasonal interactions.

First, I investigated movement consistency over the non-breeding stage. Individuals displayed site fidelity even over deep-water areas, and their movement consistency was stronger in space than in time, suggesting that it was driven by consistent resource pulses that may vary more over time than in space. Next, I explored the energetic consequences of this fidelity to wintering areas. I demonstrated that different migratory decisions can lead to significant interindividual variations in energy expenditure during winter. Individuals wintering at the centre of the population's wintering range experienced significantly higher energetic costs than those wintering towards the range's periphery. However, these higher costs did not carry over into the following reproductive success.

I also investigated whether winter site fidelity leads to interindividual differences in exposure to anthropogenic pollutants that can carry over to the following breeding stage. I showed that the per- and polyfluoroalkyl (PFAS) burden of breeding kittiwakes can be obtained in the wintering areas thousands of kilometres away and brought to the Arctic. The PFAS concentrations varied with the wintering latitude and were related to the carbon chain length of the compound tested, with individuals wintering further south carrying a higher burden of longer carbon chains considered more toxic to wildlife.

Finally, I integrated the information acquired on movement, phenology, and energetics to investigate the interactions across the full annual life cycle and their mechanisms. Variations in individual quality associated with breeding performance and repeatability in behaviour were dominant in determining seasonal interactions. Experimentally controlling for consistency in breeding performance (individual quality) revealed underlying carry-over effects that were otherwise masked by quality.

Overall, I demonstrated that seasonal interactions in migratory animals are determined by a complex interplay between the costs of decisions made by individuals at each stage of their annual cycle and their intrinsic quality, which influences their ability to cope with these costs. This thesis provides a unique perspective on the full annual cycle of migrants and the importance of individual processes in linking its different parts through spatial, phenological, energetic, physiological, and ecotoxicological processes. These results contribute to unravelling the multifaceted constraints that migrants face, which is an essential step towards understanding the role of migration in connecting geographically distant ecosystems.



> *“I love deadlines. I like the whooshing sound they make as they fly by.”*
>
> **Douglas Adams**

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SUPPLEMENTARY MATERIALS

SUPPLEMENTARY MATERIALS FOR CHAPTER 2

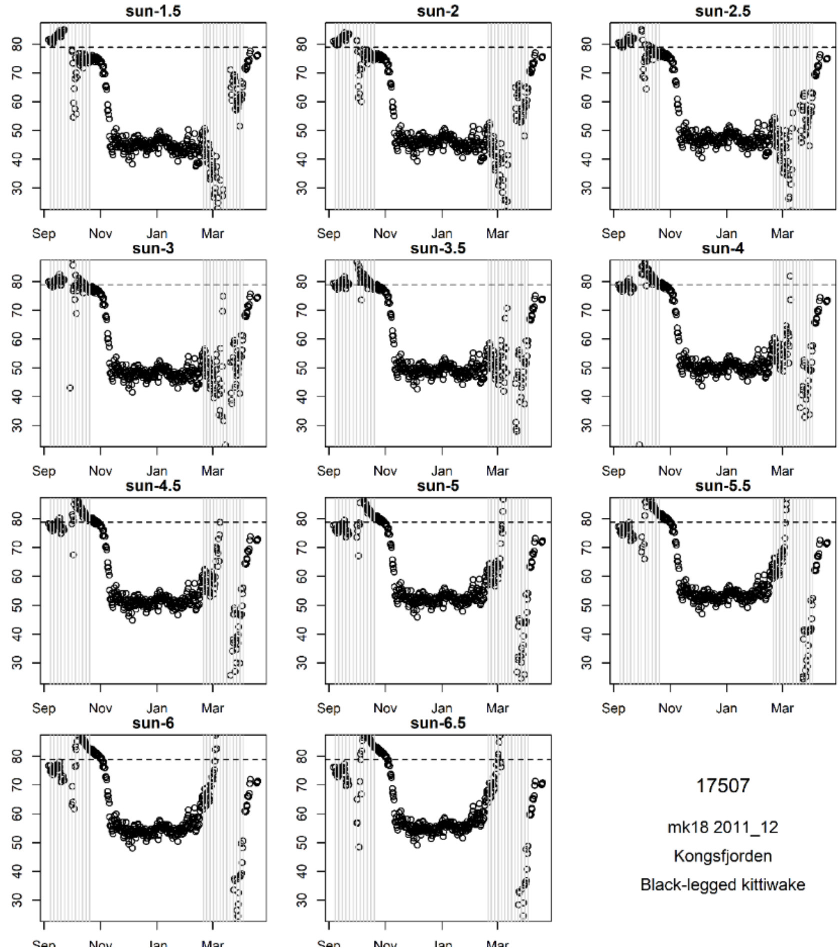


Figure S2.1: Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (June 2011 to June 2012). For each annual track, latitude versus time is plotted for different sun elevation angles and the sun elevation angle selected 1) minimized the amplification of the latitudinal error close to the equinoxes, 2) resulted in matching latitudes at both sides of the equinox and 3) resulted in positions that fitted the latitude of the colony (Kongsfjorden, Svalbard; 78°5′N) at the beginning and the end of the track. In this example, we selected -3.0° as the appropriate sun elevation angle mainly from criteria 1) and 3) since the bird moved north during the spring equinox period, making criteria 2) less useful here. The horizontal dotted line shows the latitude of the colony, and the vertical grey lines indicate the periods around autumn and spring equinoxes.

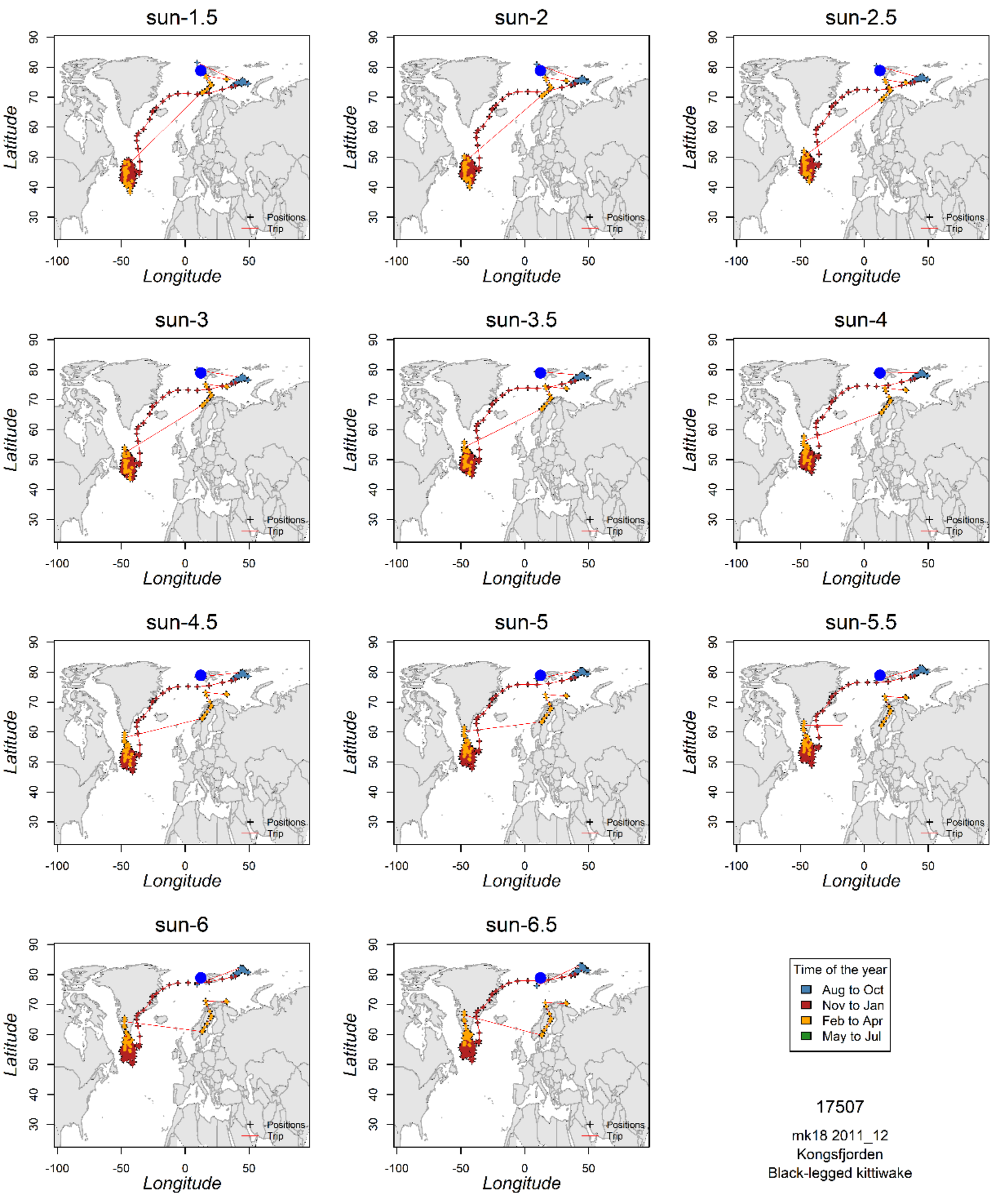


Figure S2.2: Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (same track as in Figure S1). Smoothed and filtered positions calculated with different sun elevation angles. In combination with the steps illustrated in Figure S1, these maps supported the selection of -3.0° as sun elevation angle as it resulted in a track that best fitted the shape and position of the oceans and continents. The location of the colony (Kongsfjorden, Svalbard; 78°N, 12°E) is marked with a filled blue symbol, and positions are coloured by month. Positions from the equinox periods have been excluded from the map.

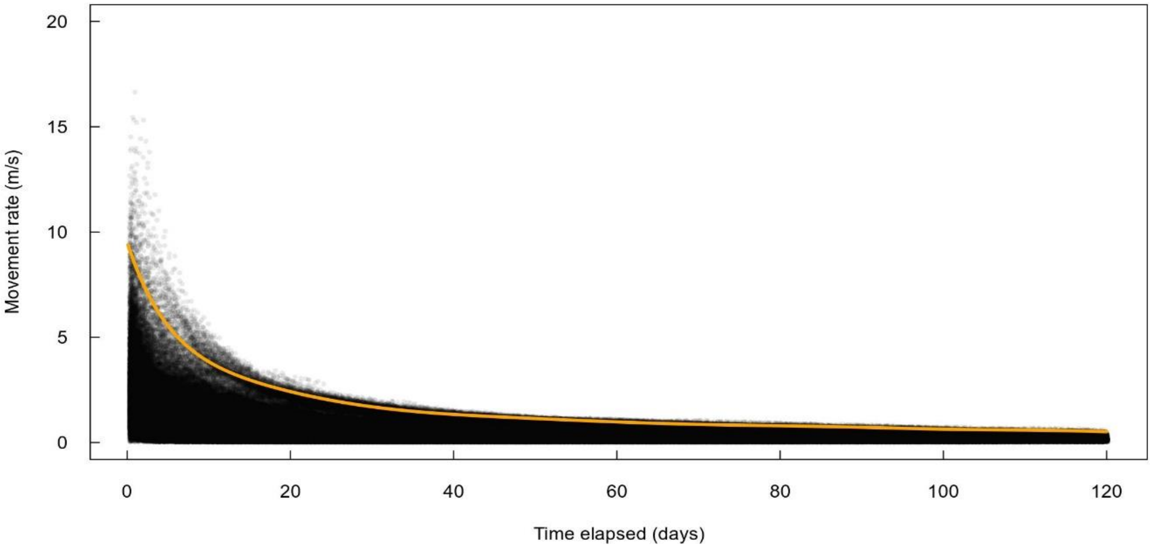


Figure S2.3: Movement rate plotted against time elapsed between two locations, for black-legged kittiwakes. The orange curve represents the 99th percentile predicted from a quantile regression model.

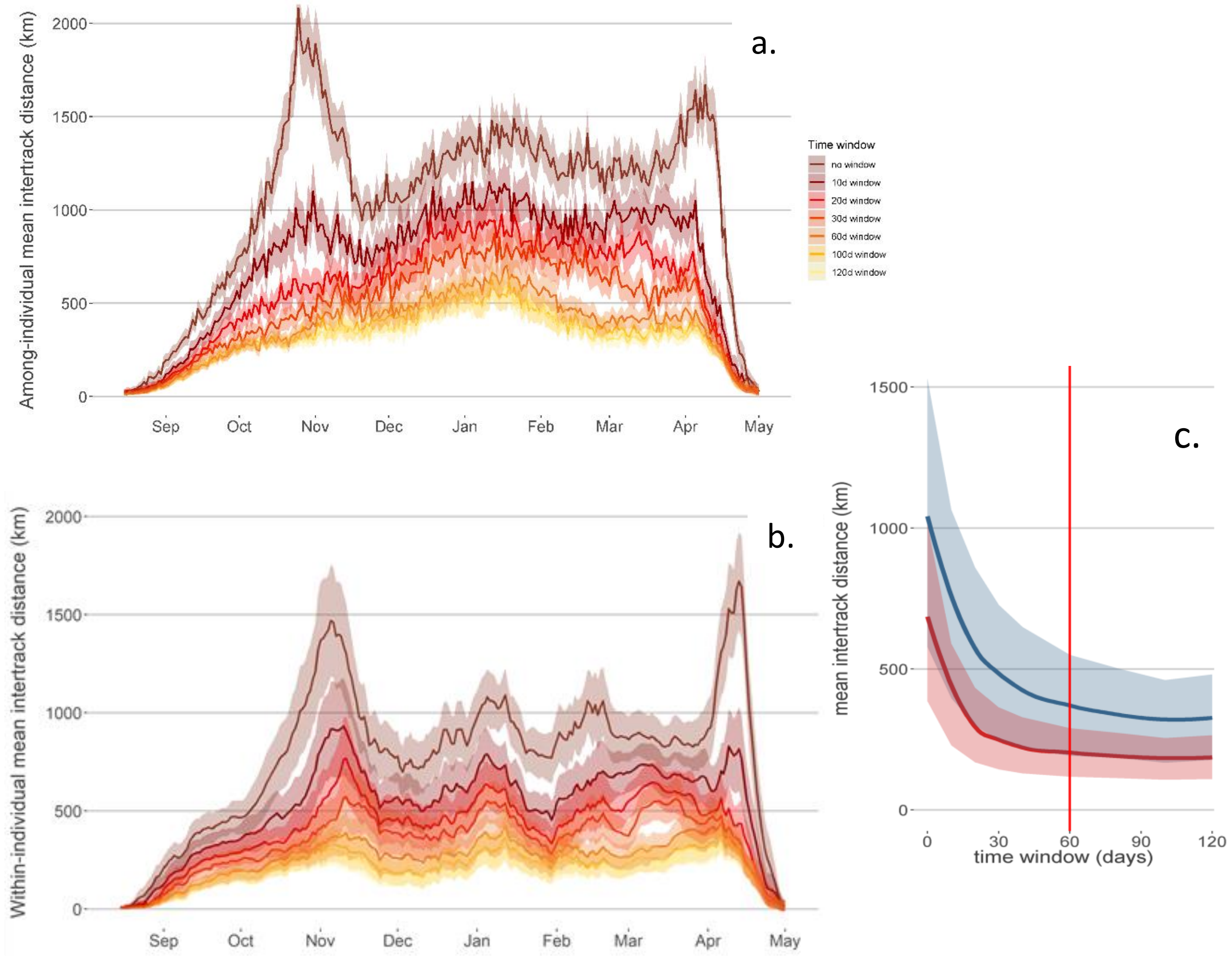


Figure S2.4: Comparison of variation among individuals (a. and blue line in c.) and within individual (b. and red line in c.) in mean intertrack distances estimated using different time windows. The increase in the time-window duration results in a gradual fading of timing effects which is otherwise particularly strong during migration periods (Oct-Nov and Apr). The 60-day time window selected allows for comparison of tracks where dissimilarities mostly originate from spatial differences.

Table S2.1: Global location sensors (GLS) deployed and retrieved at the black-legged kittiwake colony in Kongsfjorden (Svalbard) between 2008 and 2019 and the number of complete annual tracks acquired and used in the analyses. The complete tracks were obtained after filtering for partial tracks caused by GLS failure or battery discharge. The GLS can be retrieved two or three years after deployment and can then record up to two complete annual tracks before battery discharge.

Year of deployment	**Number of GLS deployed**	**Number of GLS retrieved**	**Complete tracks recovered**
2008	10	NA	NA
2009	11	8	8
2010	12	11	11
2011	56	12	2
2012	19	50	45
2013	20	13	15
2014	18	17	14
2015	25	13	13
2016	43	18	18
2017	21	39	21
2018	41	16	24
2019	NA	31	29
Total	276	228	200

Table S2.2: Mean difference in number of days (and SD) in the observed timing variation of phenological events estimated at the population level (i.e., variation among individuals) and at the intra-individual level (i.e., variation among years for individuals tracked multiple years).

Phenological parameter	**Stage**	**Population level**		**Intra-individual level**	
		mean	**SD**	**mean**	**SD**
Colony Departure (n days)	Fall migration	18.4	9.5	12.5	9.8
Start of migratory movement (n days)	Fall migration	24.1	17.3	10.3	11.2
Crossing of the Arctic Circle (n days)	Fall migration	20.1	13.1	9.9	8.3
Start of migratory movement (n days)	Spring migration	8.4	9.4	6.1	3.7
Colony Arrival (n days)	Spring migration	10.7	11.0	7.9	9.9

Table S2.3: individual repeatability (*r*) in timing of phenological events of fall and spring migrations of black-legged kittiwakes (*Rissa tridactyla*) breeding in Svalbard and associated standard error, confidence intervals and *p* value, where 0 corresponds to low repeatability and 1 to high repeatability. Only individuals tracked multiple years were included (n = 104 repeated tracks from 33 individuals).

Phenological parameter	**Stage**	***r***	**SE**	**CI**	***p***
*Colony Departure**	Fall migration	0.203	0.096	0.020 – 0.390	< 0.001
Start of migratory movement	Fall migration	0.796	0.058	0.653 – 0.880	< 0.0001
Crossing of the Arctic Circle	Fall migration	0.542	0.096	0.328 – 0.691	< 0.0001
Start of migratory movement	Spring migration	0.363	0.112	0.122 – 0.553	< 0.01
Colony Arrival	Spring migration	0.277	0.115	0.038 – 0.494	0.016

* ‘year’ included as a random factor to account for interannual variation in this parameter

Table S2.4: Frequency of step length and turning angle for each state used in four-state, three-state and two-state Hidden Markov Models. The final values of these parameters were defined after running iterations with varying initial values to ensure numerical maximization of the likelihood. We used *gamma* distribution to describe the step length frequency and *Von Mises* distribution to describe the turning angle frequency. The four-state model was selected after examination of the pseudo-residuals and because it better fitted the GLS data than the two- or three-state models based on AICs and initial inspection of distribution of movement parameters.

Models	Parameters		State 1	State 2	State 3	State 4	AIC
Four-state	*Step length (km)*	*Mean ± SD*	40.9 ± 29.3	84.5 ± 50.6	151.1 ± 102.6	218.9 ± 105.5	1244778
	Turning angle	*Mean*	0.16	0.03	3.10	0.01	
		Concentration	0.04	1.06	0.55	6.91	
Three-state	*Step length (km)*	*Mean ± SD*	42.7 ± 30.4	107.4 ± 71.3	215.8 ± 118.3	NA	1252182
	Turning angle	*Mean*	0.04	0.04	0.01	NA	
		Concentration	0.11	0.75	11.26	NA	
Two-state	*Step length (km)*	*Mean ± SD*	44.4 ± 31.5	139.4 ± 94.5	NA	NA	1261858
	Turning angle	*Mean*	0.01	0.03	NA	NA	
		Concentration	0.15	1.21	NA	NA	

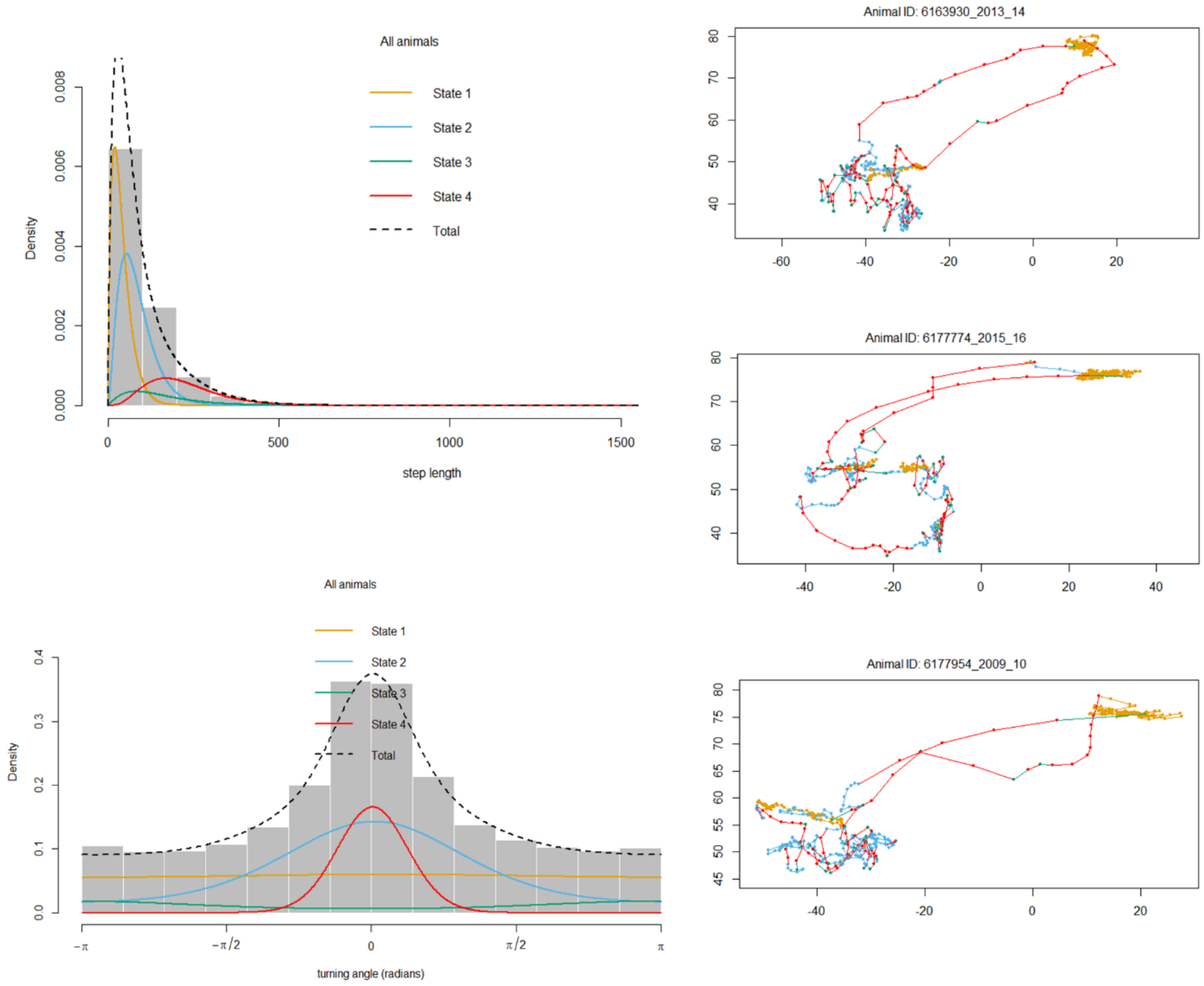


Figure S2.5: Distribution of step length (top left panel) and turning angle (bottom left panel) used in the final four-state Hidden Markov model selected to identify the sequence of behavioural states along the non-breeding tracks of individuals with three tracks as examples. The states 1 (orange) and 2 (blue) were defined by short steps (< 85 km on average) with either frequent shifts in direction (state 1) or moderately directional movement (state 2) and attributed to periods of staging in more intensively utilized areas while the states 3 (green) and 4 (red) were defined by long steps (>150 km on average) with moderate shifts in direction (state 3) or highly directional movement (state 4) that characterized transient and commuting behaviours during travelling periods.

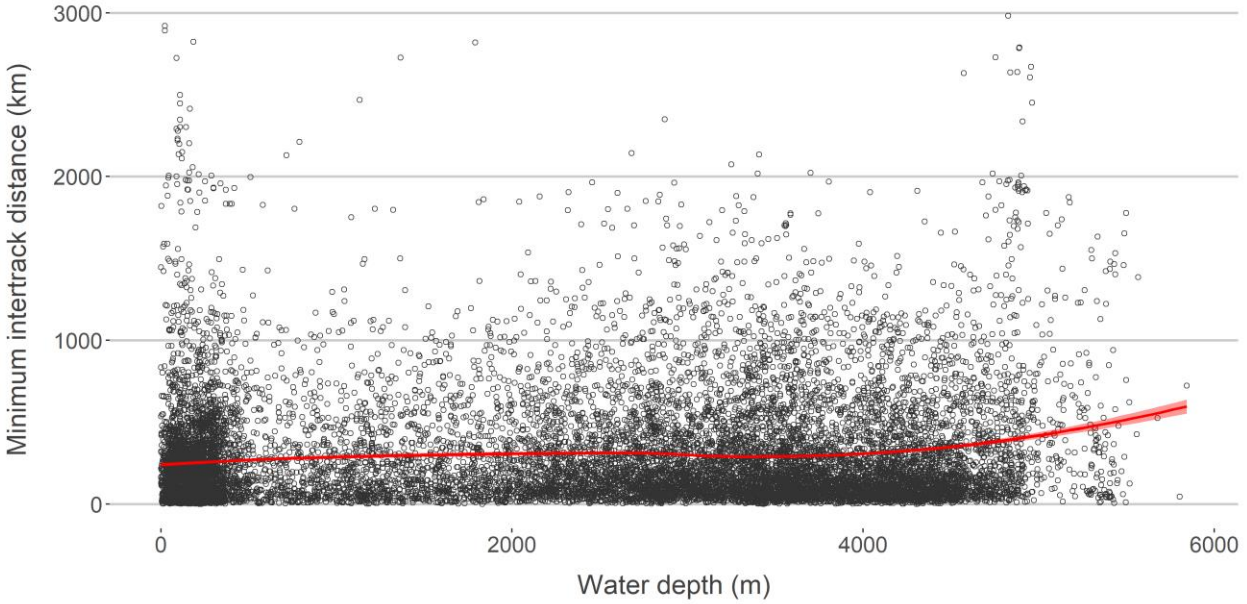


Figure S2.6: Within-individual spatial consistency over the ocean water depth. The red line is the moving average (using 'loess' smoother) of the intertrack minimum distances (± SE) and indicates that the individual site fidelity remains high over deep-water areas (depth > 500 m). The curve is plotted over the raw minimum intertrack distance data (black dots) estimated through the nearest neighbour distance analysis using a 60-day time window.

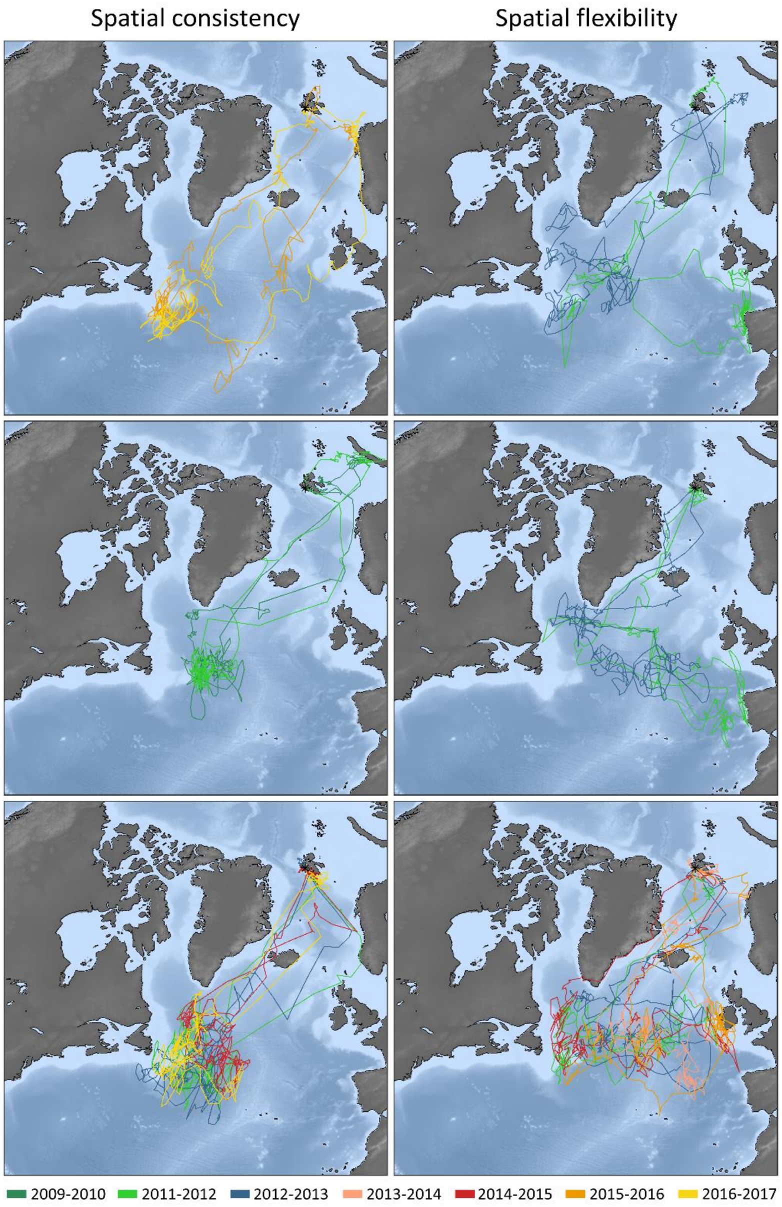


Figure S2.7: Examples of non-breeding tracks from six individuals tracked multiple years (from 2 to 5 years). The left panels show individuals displaying high interannual spatial consistency (mean nearest neighbour distance < 200 km) and the right panels show individuals displaying more flexibility in their non-breeding movement (mean nearest neighbour distance > 400 km), with shifting and itinerancy behaviours. Each colour represents one year of tracking (from the colony departure in fall to the colony arrival in spring). The black asterisk indicates the colony location.

SUPPLEMENTARY MATERIALS FOR CHAPTER 3

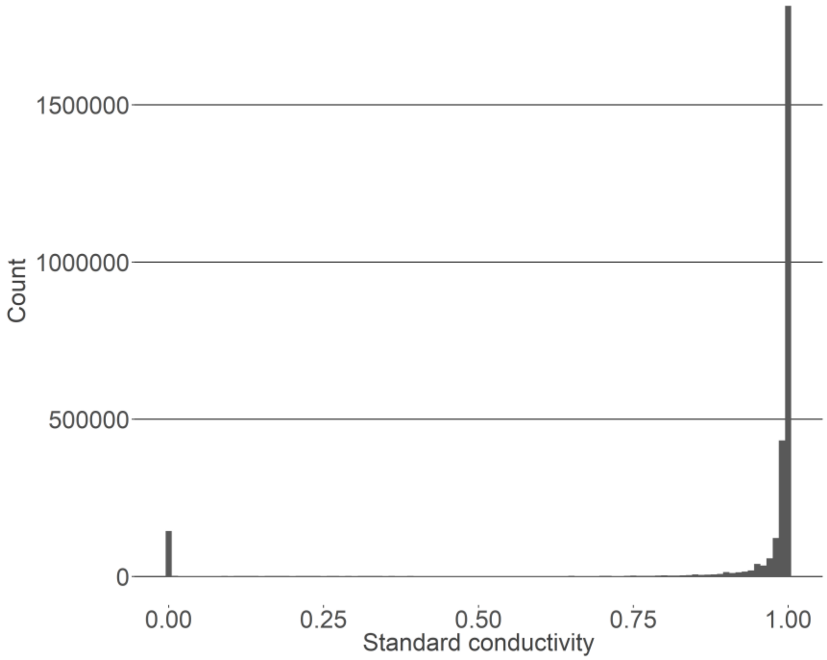


Figure S3.1: Distribution of standard conductivity counts during nighttime showing very high standard saltwater immersions associated to resting behaviour on water. To take this into account and avoid a bias towards foraging at night, a threshold of 0 < standard conductivity <0.98 was defined to identify the foraging activity periods. Nighttime periods were estimated after excluding the nautical twilights (6° and 12° below the horizon).

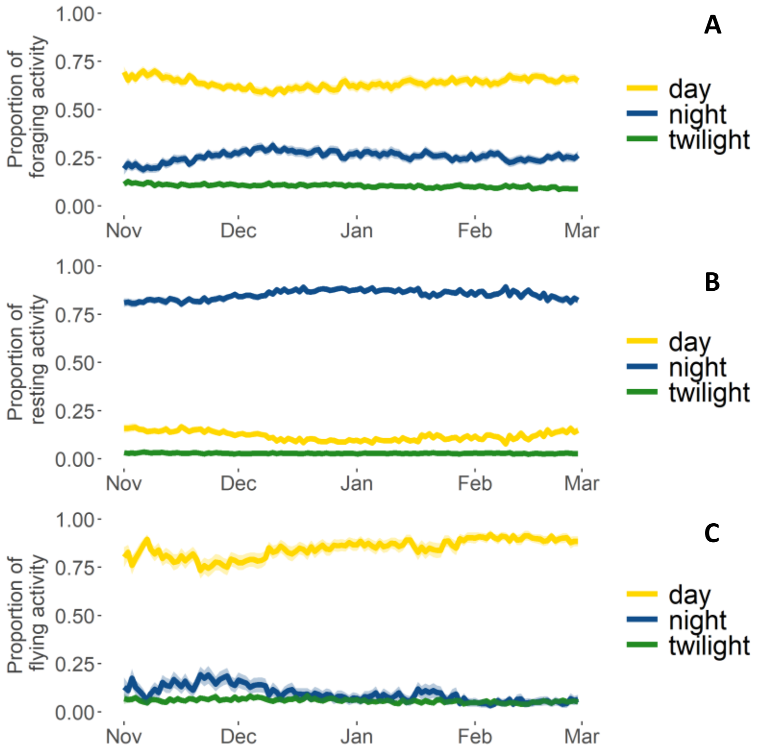


Figure S3.2: Proportion of time spent daily (A) foraging, (B) resting and (C) flying during the daytime, night-time and twilight time over the non-breeding period. These periods were determined based on the nautical twilights (6° and 12° below the horizon).

Table S3.1: Results from beta regression models for each behavioural response, i.e. the proportions of time flying, foraging and resting in averaged over a 24-hr period. The coefficients of the predictors are reported, along with the standard error, the *p*-value and the 95% confidence intervals. Statistically significant interactions are reported in bold. In all three models, the individual identification and the year were included as random factors.

Response	**Predictors**	**Coef**	**SE**	***p*-value**	**95% CI**
Flying time (daily proportion)	**Distance to range centre (km)**	**-0.0002**	**0.00003**	**<0.0001**	**[-0.0002, -0.0001]**
	Mean daylength (scaled)	-0.0087	0.0174	0.6	[-0.04, 0.03]
	Sex (male vs female)	-0.0277	0.0321	0.4	[-0.09, 0.04]
Foraging time (daily proportion)	**Distance to range centre (km)**	**0.0001**	**0.00004**	**0.008**	**[0.00003, 0.00020]**
	Mean daylength (scaled)	**0.1308**	**0.0171**	**<0.0001**	**[0.10, 0.16]**
	Sex (male vs female)	**-0.0779**	**0.0315**	**0.01**	**[-0.14, -0.02]**
Resting time (daily proportion)	Distance to range centre (km)	0.00001	0.00002	0.7	[-0.00003, 0.00004]
	Mean daylength (scaled)	**-0.0943**	**0.0130**	**<0.0001**	**[-0.12, -0.07]**
	Sex (male vs female)	**0.0828**	**0.0244**	**<0.001**	**[0.03, 0.12]**

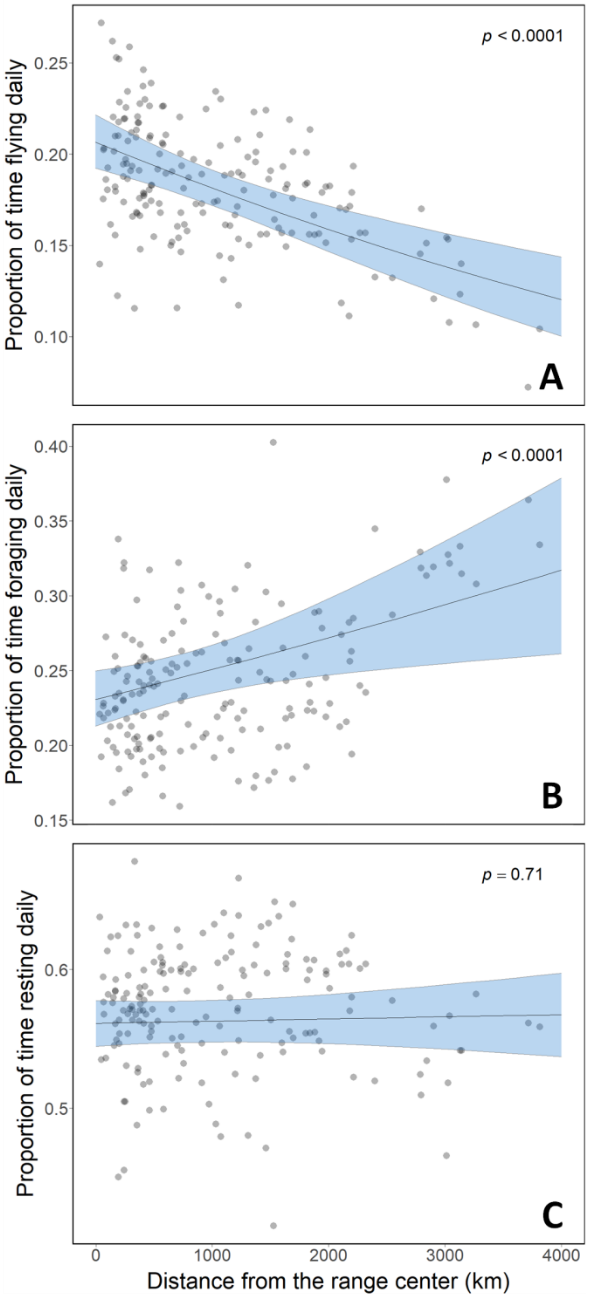


Figure S3.3: Proportion of time spent A) flying, B) foraging and C) resting over a 24-hr period over the distance from the centre of the population's wintering range. Plots show the predictions from beta regression models with their 95% confidence intervals, over the jittered raw data. In all three models, the individual identification and the year were included as random factors.

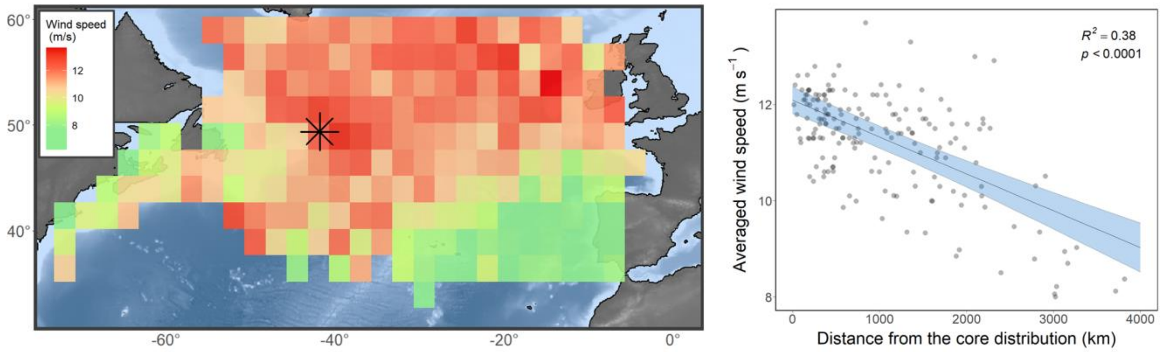


Figure S3.4: Heat maps illustrating the spatial heterogeneity in wind intensity (m s^{-1}) experienced by individuals during winter, with the corresponding model predictions over the distance from the centroid of the population's winter distribution. Darker grid cells (2.5° latitude × 2.5° longitude) indicate areas of higher values. The black star (✳) shows the centroid of the population's distribution (n = 20 357 positions).

SUPPLEMENTARY MATERIALS FOR CHAPTER 4

Table S4.1: PFAS screened in black-legged kittiwake (*Rissa tridactyla*) blood samples, with their respective limit of detection (LOD) and the detection rate above the LOD. Nine compounds (in bold) with ≥ 70% of measurements above the LOD were selected for further analysis.

Group	PFAS compound	Abbreviation	LOD (ng g^{-1} ww)	Detection rate (%) above the LOD
	Perfluorooctane sulfonamide	FOSA	0.100	0.0
Perfluoroalkane sulfonic acids	Perfluorobutanesulfonic acid	PFBS	0.10	1.8
	Perfluoropentanesulfonic acid	PFPS	0.10	0.0
	Perfluorohexanesulfonic acid	**PFHxS**	**0.10**	**81.1**
	Perfluoroheptanesulfonic acid	PFHpS	0.100	16.2
	Branched perfluorooctanesulfonic acid	**brPFOS**	**0.250**	**88.3**
	Linear perfluorooctanesulfonic acid	**linPFOS**	**0.100**	**100.0**
	Perfluorononanesulfonic acid	PFNS	0.200	9.9
	Perfluorodecanesulfonic acid	PFDcS	0.3	6.3
Perfluoroalkyl carboxylic acids	Perfluorobutanoic acid	PFBA	0.400	0.0
	Perfluoropentanoic acid	PFPA	0.200	0.9
	Perfluorohexanoic acid	PFHxA	0.200	0.0
	Perfluoroheptanoic acid	PFHpA	0.050	0.0
	Perfluorooctanoic acid	PFOA	0.080	60.4
	Perfluorononanoic acid	**PFNA**	**0.100**	**100.0**
	Perfluorodecanoic acid	**PFDcA**	**0.100**	**100.0**
	Perfluoroundecanoic acid	**PFUnA**	**0.100**	**100.0**
	Perfluorododecanoic acid	**PFDoA**	**0.100**	**100.0**
	Perfluorotridecanoic acid	**PFTriA**	**0.100**	**100.0**
	Perfluorotetradecanoic acid	**PFTeA**	**0.10**	**100.0**
	Perfluorohexadecanoic acid	PFHxDA	0.15	27.0

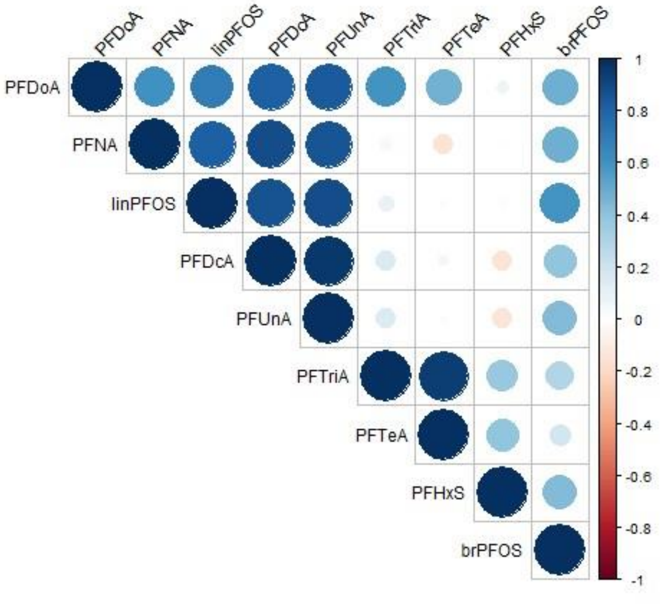


Figure S4.1: Correlation matrix among PFAS compounds included in the principal component analysis (PCA).

Table S4.2: Principal component analysis output (loadings, eigen values and cumulative variance) for each PFAS compounds on the first four components (PCs). Larger loadings indicate stronger correlations with the PC and the sign illustrate the direction of the relationship. Strong correlations above the cut-off are illustrated in bold (0.33, calculated as $\sqrt{\frac{1}{x}}$ where x is the number of PFAS compounds included in the PCA).

PFAS compounds	**PC$_1$**	**PC$_2$**	**PC$_3$**	**PC$_4$**
linPFOS	**0.417**	-0.159	0.110	-0.161
PFNA	**0.395**	-0.226	0.172	**0.338**
PFDcA	**0.433**	-0.156	-0.164	0.181
PFUnA	**0.437**	-0.158	-0.129	0.092
PFDoA	**0.412**	0.170	-0.247	-0.010
PFTriA	0.167	**0.566**	-0.246	-0.090
PFTeA	0.115	**0.583**	-0.259	0.029
PFHxS	0.039	**0.400**	**0.636**	**0.589**
brPFOS	0.282	0.157	**0.571**	**-0.680**
Eigenvalue	4.646	2.410	1.137	0.404
Cumulative variance explained	51.624	78.401	91.031	95.525

Table S4.3: Contribution of each PFAS compound to the first four principal components (PCs).

PFAS compounds	PC_1	PC_2	PC_3	PC_4
linPFOS	17.42	2.52	1.22	2.58
PFNA	15.59	5.11	2.96	11.40
PFDcA	18.72	2.42	2.68	3.28
PFUnA	19.06	2.48	1.67	0.84
PFDoA	16.99	2.89	6.12	0.01
PFTriA	2.77	32.06	6.02	0.81
PFTeA	1.33	34.04	6.72	0.09
PFHxS	0.16	16.00	40.01	34.71
brPFOS	7.96	2.47	32.61	48.29

Table S4.4: Quality of representation of each PFAS compound in the first four principal components (PCs).

PFAS compounds	PC_1	PC_2	PC_3	PC_4
linPFOS	0.810	0.061	0.014	0.010
PFNA	0.724	0.123	0.034	0.046
PFDcA	0.870	0.058	0.030	0.013
PFUnA	0.886	0.060	0.019	0.003
PFDoA	0.789	0.070	0.070	0.000
PFTriA	0.129	0.773	0.068	0.003
PFTeA	0.062	0.820	0.076	0.000
PFHxS	0.007	0.386	0.455	0.140
brPFOS	0.370	0.059	0.371	0.187

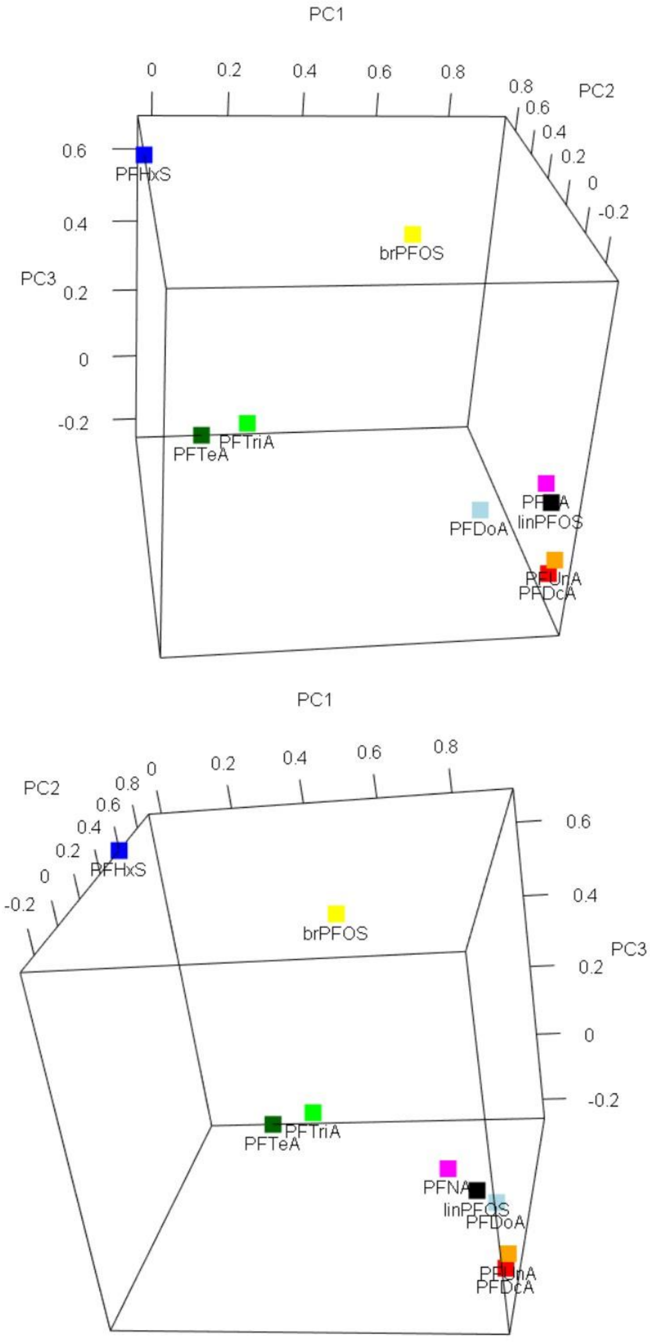


Figure S4.2: Visualization of the distribution of the PFAS variables over the three first components. Left and right panels show the same 3D plot but with different angle.

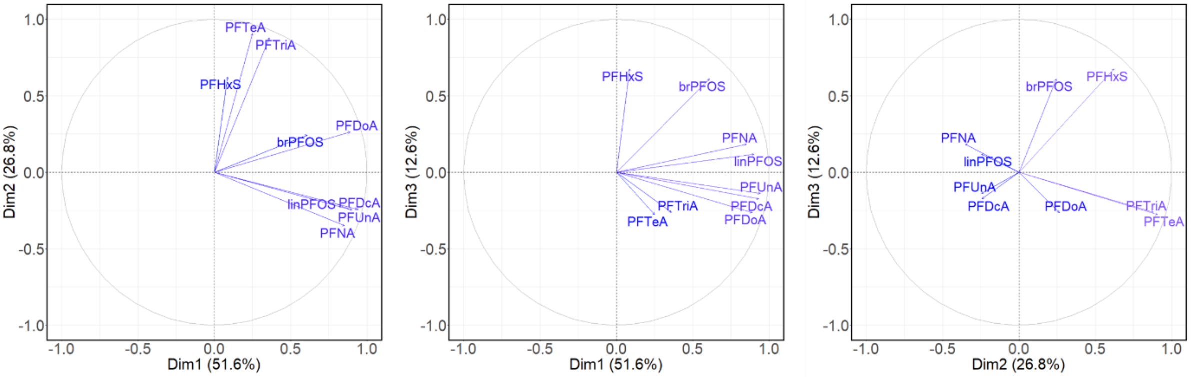


Figure S4.3: Visualization of the distribution of the PFAS variables over the three first components (2D representations).

SUPPLEMENTARY MATERIALS FOR CHAPTER 5

Geolocation light data processing – detailed methods from Léandri-Breton et al.(2021)

To infer geographic positions, geolocator data were processed according to the procedure developed for the SEATRACK project (Bråthen et al. 2021) and based on the threshold method calculating positions from twilight events (‘coord’ function from *GeoLight* package; Hill & Braun, 2001; Lisovski et al., 2020; Lisovski & Hahn, 2012). The procedure automatically identifies twilight events from raw light data (‘twilightCalc’ function from *GeoLight* package; Lisovski & Hahn, 2012) and applies a set of filters to twilight events (removing or moving events from false day/night detections or noise) and positions (speed, distribution limits, angle filter). Thus, all the geolocator data were processed automatically and consistently for all years of the study. Because light sensors from different geolocator models may differ, each track was calibrated individually. As such, the calibration method avoided systematic bias in latitude related to potential differences in light sensors among geolocator models or years of production. Based on the approach by Hanssen et al. (2016) and van Bemmelen et al., (2019), the calibration method used a set of criteria that allowed calibration of tracks from kittiwakes breeding in the Arctic (79° N), where constant daylight prevents calibration at the time of deployment and recapture. By plotting the latitude against time for a range of sun elevation angles and for each track (Fig. S5.1), the sun elevation angle that was manually selected (1) minimized the amplification of the latitudinal error close to the equinoxes, (2) resulted in matching latitudes at both sides of the equinox, (3) resulted in positions that fitted the latitude of the colony at the beginning and the end of the track and (4) fitted the shape and position of the oceans and continents when plotting the positions on a map (Fig. S5.2). The method also included rooftop calibration of geolocator models, with the purpose to select model specific thresholds that would result in approximately the same sun elevation angles among geolocator models. The mk-series geolocators from the British Antarctic Survey and Biotrack were as signed a threshold of 1 unit, while Intigeo geolocators from Migrate Technology were assigned a threshold of 11 units.

Although longitudes can still be determined reliably around the equinoxes, estimation of latitudes is inherently imprecise during this period, because day length is similar around the globe (Lisovski et al. 2012). Therefore, locations around equinoxes were excluded (8 Sep−20 Oct, 20 Feb−3 Apr; Bråthen et al., 2021). Additionally, continuous daylight during the polar summer (or continuous night during polar winter) does not allow geolocation-based tracking using light-level sensors. To fill these gaps and reduce biases along the trajectories, missing locations were re-estimated by interpolation between known locations using an algorithm that was specifically developed for SEATRACK (Fauchald et al., 2019;see Fig. S5.3), based on a method originally proposed by Technitis et al., (2015). In short, this algorithm is based on the determination of so-called space-time prisms, which are 3- dimensional volumes defined by the coordinates *(x,y)* and time *(z)*. The space-time prism delineates all the potential paths that can be followed by an individual moving from point A to point B, given 3 parameters: the distance from A to B, the time budget available, and the maximum rate of movement (Miller 1991). When projected onto a 2-dimensional plane, the space-time prism becomes the potential point area (hereafter *Ppa*; Technitis et al., 2015). Although the 3-dimensional representation of the space-time prism is useful to understand its concept (Neutens et al. 2007), it is naturally more convenient to work with only 2 dimensions when dealing with discrete time steps, as is the case in tracking studies, where locations are obtained at specific time intervals. Computing the *Ppa* in this context is straightforward (Technitis et al. 2015), given that the 3 above-mentioned parameters are known. Let us consider a startpoint (A) and start time *(ti*−1), and an endpoint (B) and end time *(ti*+1). Knowing the maximum rate of movement and the time *ti* at which a new location *(Ni)* is to be created, one can determine the circle defining the maximum range *(rgi*−1) from point A to the new location and the circle defining the maximum range *(rgi*+1) to point B, centred on B. The *Ppa* corresponds to the area of overlap between those 2 circles of maximum range, i.e. the area delimiting all locations that are reachable from both A and B, given the time budget and maximum movement rate. This process can be repeated any number of times, depending on the number of new locations that need to be generated. The new locations are generated in a random order (i.e. not chronological), thus creating a sort of correlated random walk respecting the constraints set by the relative position of A and B, the time budget, and the maximum movement rate. Here, we used a dynamic value for the maximum movement rate parameter, based on the distribution of observed movement rates as a function of time elapsed between 2 locations from the dataset. To do so we calculated, based on each individual track, the movement rates for random combinations of known locations separated by varying time-intervals. We used the 75th percentile from that distribution as the maximum movement rate (Fig. S5.4). The 75th percentile was computed by quantile regression, using the function 'rq' from package *quantreg* (Koenker 2020). Finally, the algorithm uses additional information to constrain the new positions obtained: (1) immersion data to determine attendance at the colony and force a new location to remain close to the colony during the breeding season, (2) land masks (land filters) to constrain positions over the ocean, (3) longitudes (obtained from the geolocator data, as longitude can still be estimated during the equinoxes), and (4) light levels to determine whether the new position was north of the latitudinal limit of the polar day in summer or night in winter (i.e. continuous day/night recorded by the loggers).

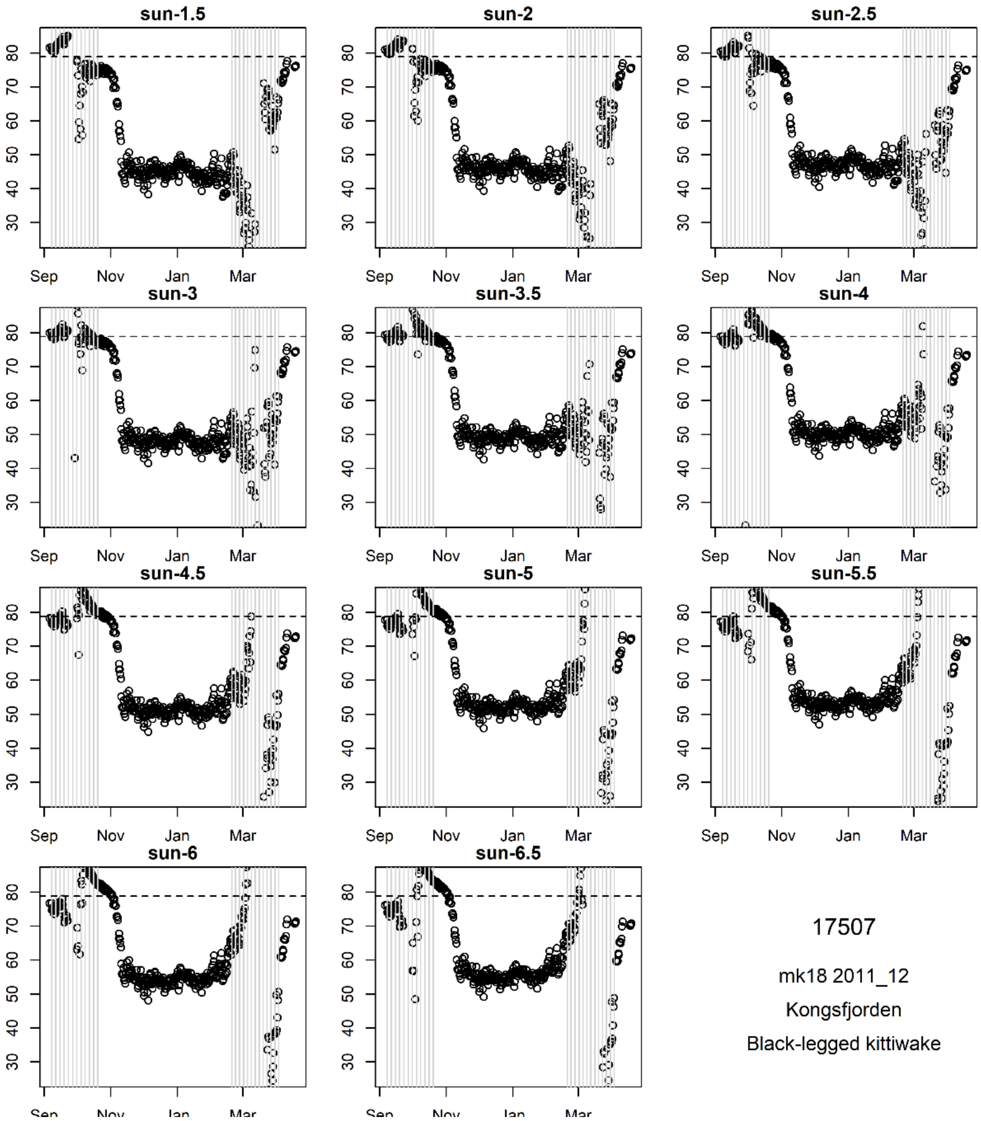


Figure S5.1: Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (June 2011 to June 2012). For each annual track, latitude versus time is plotted for different sun elevation angles and the sun elevation angle selected 1) minimized the amplification of the latitudinal error close to the equinoxes, 2) resulted in matching latitudes at both sides of the equinox and 3) resulted in positions that fitted the latitude of the colony (Kongsfjorden, Svalbard; 78°5′N) at the beginning and the end of the track. In this example, we selected -3.0° as the appropriate sun elevation angle mainly from criteria 1) and 3) since the bird moved north during the spring equinox period, making criteria 2) less useful here. The horizontal dotted line shows the latitude of the colony, and the vertical grey lines indicate the periods around autumn and spring equinoxes.

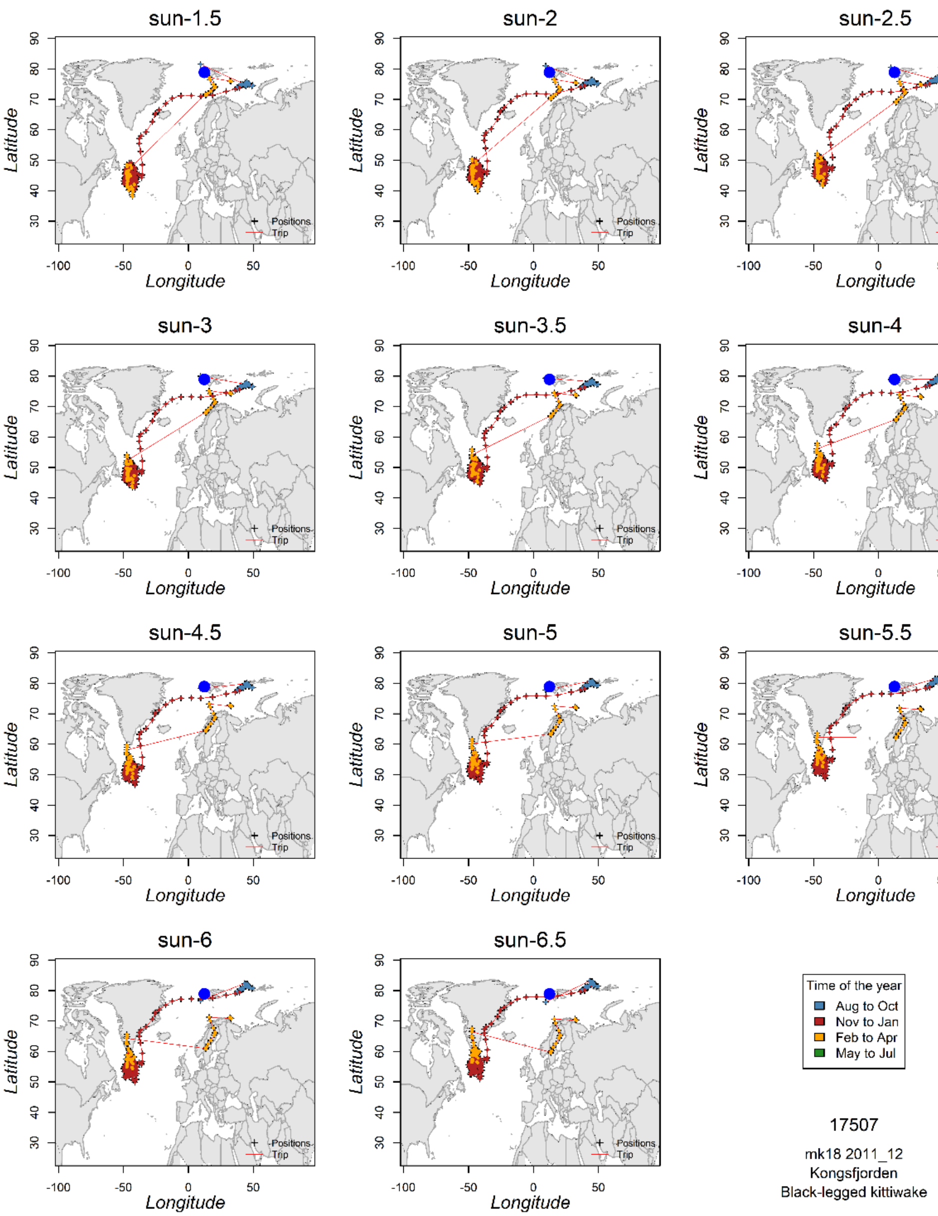


Figure S5.2: Example of sun elevation angle selection from Bråthen et al. (2021) for a black-legged kittiwake track (same track as in Figure S1). Smoothed and filtered positions calculated with different sun elevation angles. In combination with the steps illustrated in Figure S1, these maps supported the selection of -3.0° as sun elevation angle as it resulted in a track that best fitted the shape and position of the oceans and continents. The location of the colony (Kongsfjorden, Svalbard; 78°N, 12°E) is marked with a filled blue symbol, and positions are coloured by month. Positions from the equinox periods have been excluded from the map.

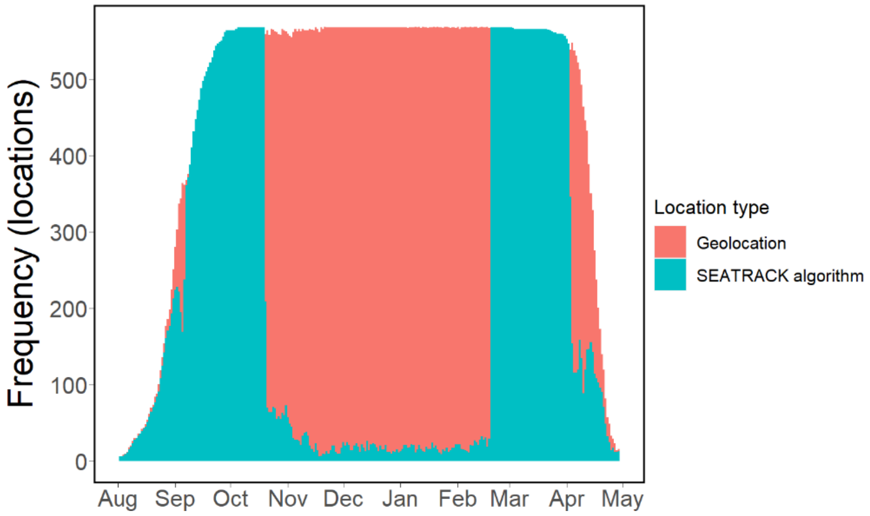


Figure S5.3: Frequency distribution of daily locations of black-legged kittiwakes estimated from the geolocation data only and those re-estimated with the algorithm IRMA developed for the SEATRACK program, over the tracking period.

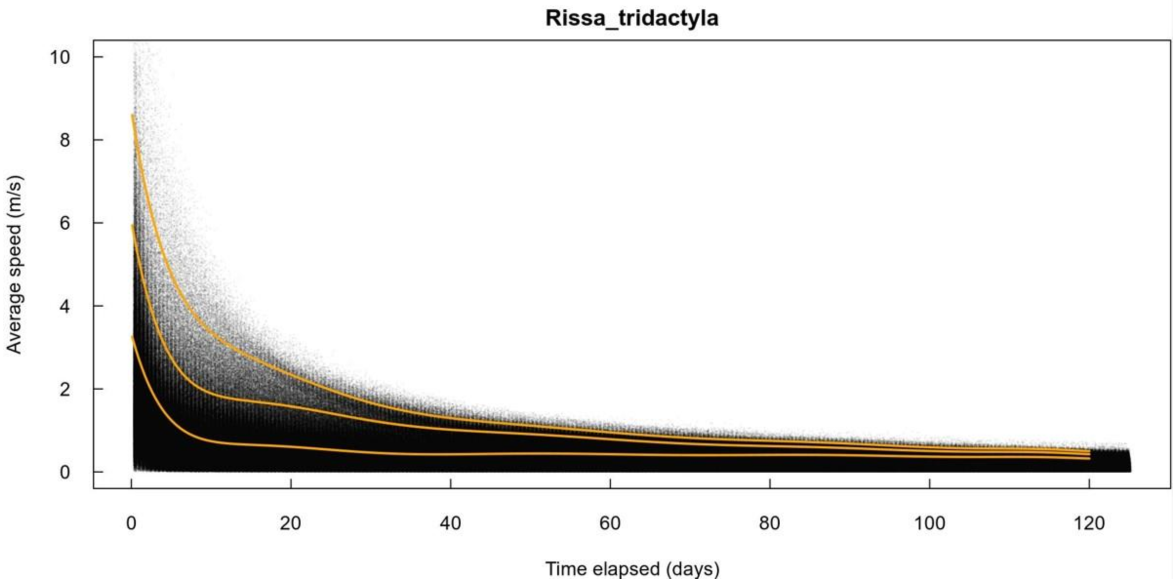


Figure S5.4: Movement rate plotted against time elapsed between two locations, for black-legged kittiwakes. The orange curves represent the 99th, 95th, and 75th percentiles predicted from a quantile regression model. The more conservative 75th percentile (lower regression curve) was selected for further analyses.

Colony departure and arrival – detailed methods from Léandri-Breton et al. (2021)

Departure from the colony and return to the colony were identified using Lavielle partitioning algorithm (‘ts.LaviellePart*’* function from R package adehabitatLT; (Calenge 2006, Barraquand and Benhamou 2008) over a 5 d running maximum of the saltwater immersion data indicating a transition between land use (mostly dry) and continuous pelagic behaviour (mostly wet). The function partition the time series to find the segmentation which minimize the contrast between the actual series and the segmented series (Calenge 2006). Departure and arrival dates were adjusted according to visual inspection of the individual’s locations right after the behavioural transition from land use to pelagic in fall, and right before the transition from pelagic to land use in spring. In spring, foraging trips after the first visit to the colony area were excluded, as individuals start to display a central place foraging behaviour, including long pre-laying trips as far as Iceland (Bogdanova et al. 2011).

Daily Energy Expenditure (DEE) in winter – Detailed Methods

Saltwater immersion data were used to build a time-activity budget based on the identification of three behaviours (see similar methods in (McKnight et al. 2011, Fayet et al. 2016, Dunn et al. 2020): 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 $x_{st} = x/x_{max}$, 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 ≥ 98%) and active foraging (0% < 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% < SSI < 100%, see Fig. S5.4).

To calculate the daily energy expenditure, we combined the time-activity budget with the population-specific resting metabolic rate (i.e., 1.64 mL O_2 g^{-1} h^{-1}, (Gabrielsen et al. 1988, Blévin et al. 2017a) and the activity-specific field metabolic rates. 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 (0.1000 mL O_2 g^{-1} h^{-1} $°C^{-1}$) 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 equation (1) when the SST was below the species' thermoneutral zone (<4.5°C) and equation (2) when above it:

$$\textbf{(1)}\ \ DEE\ = 7.3\,RMR\ \cdot\ T_{fly} + 4.05\,RMR\ \cdot\ T_{for} + (\beta - TC\ \cdot\ SST)T_{rest}$$

$$\textbf{(2)}\ \ DEE = 7.3\,RMR\ \cdot T_{fly} +\ 4.05\,RMR\ \cdot T_{for} +\ RMR\ \cdot T_{rest}$$

Where RMR is the resting metabolic rate (in mL O_2 g^{-1} h^{-1}), β is the intercept of the RMR at 0°C, TC is the thermal conductance in water (O_2 g^{-1} h^{-1} $C^{°-1}$), 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 $O_2 g^{-1}$ 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 O_2 (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 murres (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 hrs 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. The results from the daily time-activity budget were bootstrapped 10 000 times to calculate the averaged DEE.

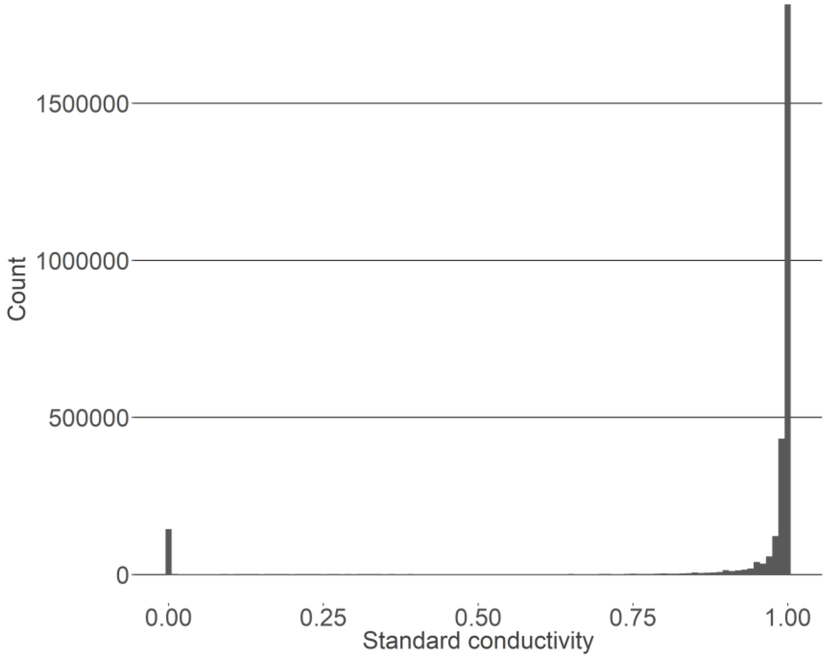


Figure S5.5: Distribution of standard conductivity counts during nighttime showing very high standard saltwater immersions associated to resting behaviour on water. To take this into account and avoid a bias towards foraging at night, a threshold of 0 < standard conductivity <0.98 was defined to identify the foraging activity periods. Nighttime periods were estimated after excluding the nautical twilights (6° and 12° below the horizon).

Blood sampling and corticosterone levels

From 2019 to 2021, kittiwakes previously equipped with a geolocator were recaptured during the pre-laying stage and sampled within 3 min (n = 92, average sampling time: 129±29 sec, range: 72-180 sec) for 2 mL of blood from the brachial vein. We tested whether the time between the bird capture and the blood sampling (i.e., sampling time) affected the corticosterone levels. Since the sampling time is bounded 0-3 minutes duration, we performed a beta regression using package *glmmTMB* (function 'glmmTMB', Brooks et al., 2017). There was no effect of time before bleeding on the corticosterone levels for samples collected within 3 minutes (*coef*=0.044, *SE*=0.053, *df*=55, *p*=0.41, Fig. S5.5).

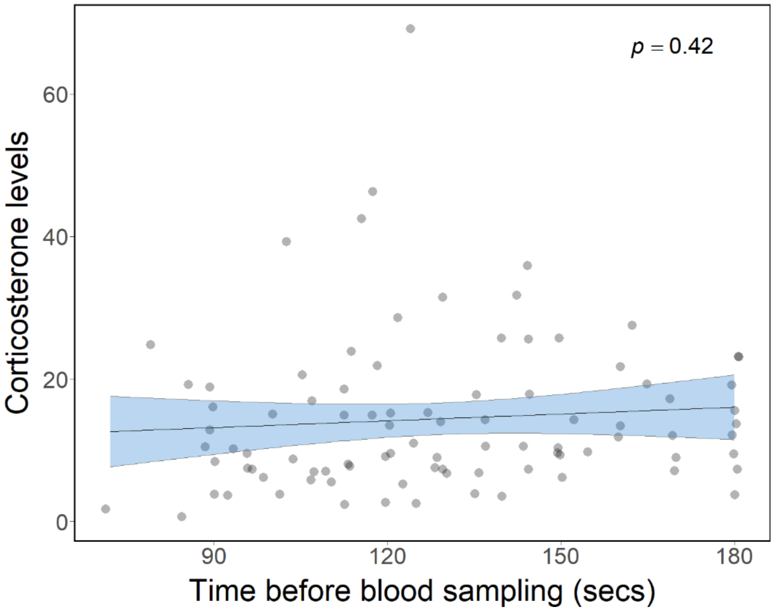


Figure S6: Levels of corticosterone in plasma of black-legged kittiwakes (*Rissa tridactyla*) over the time before blood sampling (in seconds). Plots show the predictions from beta regression models with their 95% confidence intervals, over the jittered raw data.

Table S5.1: Number of non-breeding tracks per year of tracking and per sex determined by molecular sexing (following Fridolfsson & Ellegren, 1999) or through behaviour when paired with a known-sex partner.

Year of tracking	Non-breeding tracks	sex		
		female	male	undetermined
2008-2009	6	3	3	0
2009-2010	11	5	6	0
2010-2011	2	0	2	0
2011-2012	44	23	20	1
2012-2013	15	6	9	0
2013-2014	13	9	4	0
2014-2015	12	9	3	0
2015-2016	18	11	7	0
2016-2017	21	10	9	2
2017-2018	24	9	12	3
2018-2019	32	4	15	13
2019-2020	10	3	4	3
2020-2021	69	18	20	31
TOTAL	277	110	124	43

Table S5.2: Pathways included in each three piecewise structural equation models (PSEM) fitted to test direct and indirect causal effects between consecutive breeding stages of the annual life cycle of black-legged kittiwakes (*Rissa tridactyla*). The coefficients (original scale and standardized) of each pathway are reported along with their standard error, 95% confidence intervals, degree of freedom and *p*-value. Statistically significant pathways are reported in bold. The sampling years and sample for each PSEM are also reported.

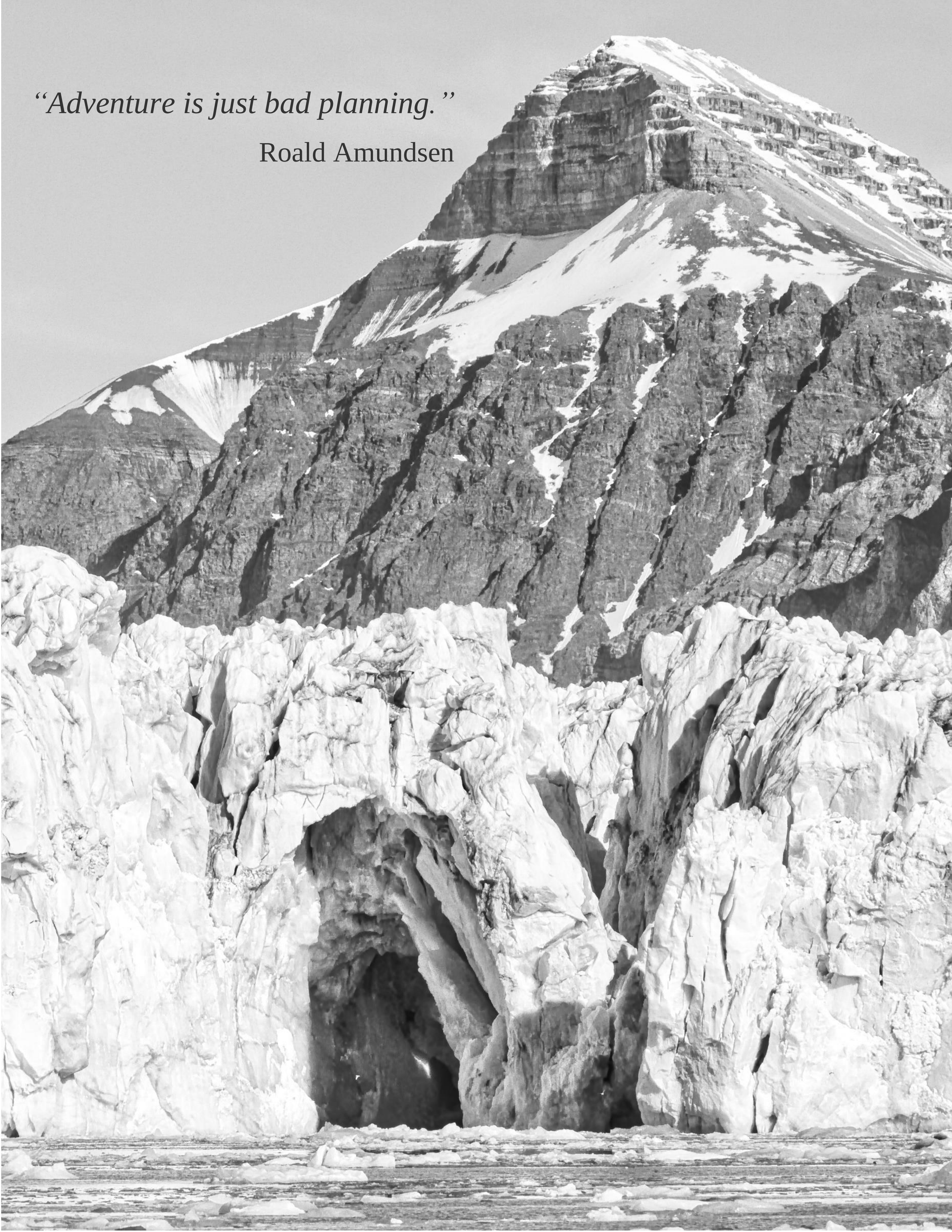
Model	Sample size	Response	Predictor	Coef	SE	95% CI	DF	*p*	Std coef
PSEM1 **(2008-2021)**	**141 tracks** (104 individuals)	**Colony departure (year *x*)**	**Breeding success (year *x*)**	**7.723**	**2.2887**	**[2.756, 11.747]**	**133**	**<0.01**	**0.219**
		Distance to range centre (log)	**Breeding success (year *x*)**	**0.907**	**0.2064**	**[0.498, 1.310]**	**134**	**<0.0001**	**0.314**
		Distance to range centre (log)	Colony departure (year *x*)	-0.009	0.0069	[-0.023, 0.004]	99	0.18	-0.108
		Winter DEE	**Distance to range centre (log)**	**-17.147**	**5.0175**	**[-27.100, -7.348]**	**139**	**<0.001**	**-0.285**
		Colony arrival (year *x* + 1)	Winter DEE	0.008	0.0072	[-0.006, 0.022]	118	0.29	0.069
		Laying date (year *x* + 1)	**Breeding success (year *x*)**	**-4.021**	**1.0053**	**[-6.054, -1.981]**	**125**	**<0.0001**	**-0.189**
		Laying date (year *x* + 1)	Colony arrival (year *x* + 1)	-0.026	0.0703	[-0.164, 0.113]	130	0.71	-0.024
		Breeding success (year *x* + 1)	**Breeding success (year *x*)**	**0.196**	**0.0822**	**[0.035, 0.352]**	**134**	**0.02**	**0.153**
		Breeding success (year *x* + 1)	Colony departure (year *x*)	-0.005	0.0027	[-0.011, 0.0003]	123	0.06	-0.139
		Breeding success (year *x* + 1)	Winter DEE	0.001	0.0005	[-0.00003, 0.002]	132	0.07	0.116
		Breeding success (year *x* + 1)	**Laying date (year *x* + 1)**	**-0.042**	**0.0051**	**[-0.052, -0.032]**	**43**	**<0.0001**	**-0.701**
PSEM2 **(2019-2021)**	**54 individuals**	Colony arrival (year *x* + 1)	Distance to range centre (log)	-0.452	0.862	[-2.182, 1.278]	51	0.60	-0.075
		Colony arrival (year *x* + 1)	Winter DEE	0.004	0.011	[-0.017, 0.025]	51	0.68	0.059
		Winter DEE	Distance to range centre (log)	-17.527	10.950	[-39.500, 4.446]	52	0.12	-0.217
		Corticosterone (year *x* + 1)	Winter DEE	-0.037	0.026	[-0.089, 0.015]	51	0.16	-0.195
		Corticosterone (year *x* + 1)	Colony arrival (year *x* + 1)	0.216	0.349	[-0.485, 0.916]	51	0.54	0.085
		Laying date (year *x* + 1)	Colony arrival (year *x* + 1)	-0.177	0.301	[-0.739, 0.386]	51	0.53	-0.088
		Laying date (year *x* + 1)	Corticosterone (year *x* + 1)	-0.077	0.119	[-0.298, 0.145]	51	>0.5	-0.097
		Breeding success (year *x* + 1)	**Laying date (year *x* + 1)**	**-0.468**	**0.062**	**[-0.835, -0.247]**	**52**	**<0.001**	**-0.927**
PSEM3 **(2019-2021)**	**70 individuals** 44 control + 26 experimental individuals	Colony departure (year *x*)	Treatment	-1.140	2.820	[-6.653, 4.384]	39	0.69	-0.058
		Distance to range centre (log)	Treatment	0.434	0.225	[-0.004, 0.880]	46	0.06	0.246
		Distance to range centre (log)	Colony departure (year *x*)	-0.0027	0.010	[-0.022, 0.016]	67	0.78	-0.034
		Winter DEE	**Treatment**	**45.783**	**15.281**	**[16.151, 75.812]**	**37**	**<0.01**	**0.365**
		Winter DEE	**Distance to range centre (log)**	**-21.275**	**8.173**	**[-37.142, -5.385]**	**67**	**0.01**	**-0.300**
		Colony arrival (year *x* + 1)	Winter DEE	0.008	0.012	[-0.016, 0.032]	62	0.53	0.073
		Laying date (year *x* + 1)	**Treatment**	**2.700**	**1.122**	**[0.518, 4.881]**	**67**	**0.02**	**0.282**
		Laying date (year *x* + 1)	Colony arrival (year *x* + 1)	-0.008	0.085	[-0.174, 0.157]	67	0.92	-0.011

Table S5.3: Distribution of individuals per number of years of non-breeding movement tracking and over the time interval between first and last year of tracking, as well as the total numbers of individuals included in path analyses (n=181 individuals tracked) and in repeatability estimates of non-breeding behavioural parameters (n=58 individuals tracked multiple years).

	1 yr	**2 yrs**	**3 yrs**	**4 yrs**	**5 yrs**	**6 yrs**	**7 yrs**	**8 yrs**	**9 yrs**	**Total**
Individuals per number of years of tracking	123	37	13	3	2	2	1	-	-	181
Individuals per interval between first and last year of tracking	-	17	24	4	5	4	1	2	1	58

Table S5.4: Pathways of an additional piecewise structural equation model (PSEM) fitted to test the role of body condition index during pre-laying (instead of corticosterone level) as a potential mediator of carry-over effects (n = 54) in black-legged kittiwakes (*Rissa tridactyla*). The coefficients (original scale and standardized) of each pathway are reported along with their standard error, degree of freedom and *p*-value. Statistically significant pathways are reported in bold. Body condition index was calculated as the residuals of the linear correlation between the skull length and the body mass.

Response	**Predictor**	**Coef**	**SE**	**DF**	**p**	**Std coef**
Colony arrival (year *x* + 1)	Distance to range centre (log)	-0.452	0.862	51	0.60	-0.075
Colony arrival (year *x* + 1)	Winter DEE	0.004	0.011	51	0.68	0.059
Winter DEE	Distance to range centre (log)	-17.527	10.95	52	0.12	-0.217
Body condition (year *x* + 1)	Winter DEE	-0.094	0.062	51	0.13	-0.208
Body condition (year *x* + 1)	Colony arrival (year *x* + 1)	0.700	0.825	51	0.40	0.115
Laying date (year *x* + 1)	Colony arrival (year *x* + 1)	-0.163	0.280	51	0.56	-0.081
Laying date (year *x* + 1)	Body condition (year *x* + 1)	-0.045	0.046	51	0.34	-0.134
Breeding success (year x + 1)	Body condition (year *x* + 1)	-0.012	0.016	51	0.48	-0.067
Breeding success (year *x* + 1)	**Laying date (year *x* + 1)**	**-0.482**	**0.148**	**52**	**<0.001**	**-0.937**



"Adventure is just bad planning."

Roald Amundsen