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Consequences of diverse migration strategies in a generalist seabird

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Gull over-travels?

Consequences of diverse migration strategies in a generalist seabird

Morgan Brown
Gull over-travels? Consequences of diverse migration strategies in a generalist seabird. PhD thesis, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands

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CHAPTER 1

General introduction

J. Morgan Brown
Each year billions of animals undertake migratory journeys across the globe, a phenomenon that cannot escape the notice of even the most casual observer of nature. Migrating animals fill the skies, cross mountains and plains, and navigate freshwater streams and ocean currents. Ideas regarding how and why animals migrate date back thousands of years (Aristotle 350 BC), and current research on animal migrations span the fields of ecology, evolution, behaviour, genetics, neuro and sensory science, physiology, and conservation, among others (Bowlin et al. 2010, Lohmann 2018).

Migrants move between and inhabit two (or more) distant locations, forming connections between otherwise disparate parts of our planet. Behaviour of the individual, such as where and when to migrate, can influence both the survival and reproductive success of individuals and thus population dynamics. The seasonal arrival and disappearance of migratory species influences the communities with which they interact, and migrants impact ecosystem processes by connecting otherwise separated areas through the transportation of nutrients, energy, and other organisms (Bauer and Hoye 2014). As such, the study of migration has relevance across ecological scales.

The consequences of migration

To understand why animals migrate, we need an understanding of the costs, benefits and challenges (i.e. ‘consequences’) of migration. I briefly review some of these consequences below. First though, we must distinguish between the process of migrating, in other words, the period of the year when animals are actually moving between locations, and migration as a life-history strategy, which recognises that migratory decisions influence the subsequent conditions experienced on wintering and breeding grounds and thus influences the entire annual cycle (hereafter, ‘migration strategy’). Here I focus on migration as a strategy, where although many of the costs discussed may arise from the process of migrating, I also aim to present how migration may influence other stages in an animals annual cycle.

Migration is typically regarded as an adaptation to exploit seasonally fluctuating resource booms and subsequently avoid deteriorating conditions (Alerstam et al. 2003). In an idealized context, the movements of the migrating animal should coincide exactly with seasonal resource waves (Armstrong et al. 2016). In this way, the individual is always in the optimal location given current environmental conditions, which may increase their survival probability throughout the year and carry-over to enhance their reproductive success. In practice, moving in synchrony with the environment has clear challenges, since animals do not have comprehensive knowledge of the state of resources around the globe nor how these will change in the future. The benefits of migration are therefore
not only determined by the degree of improvement in environmental conditions obtained through migrating versus remaining stationary, but also by how well animals can track these changes.

In addition to the complex issue of where and when to move, there are potentially extra costs associated with migrating. Perhaps the most apparent cost is the energy required to complete a migratory journey. Locomotion is among the most energetically costly behaviours performed by animals per unit time (Tatner and Bryant 1986, Boisclair and Leggett 1989, Karasov 1992). Of equal relevance to the instantaneous cost of locomoting is the resulting speed at which an animal is travelling, which when combined determine the energy required to traverse a given distance. Flapping flight and swimming are generally the most efficient forms of self-powered locomotion to travel over long distances, with the former being relatively fast, and the latter requiring relatively low metabolic rates to sustain (Alexander 2002). Coinciding with this, birds, insects, and marine fauna far exceed terrestrial species in their maximal migration distances (Alerstam and Bäckman 2018). The energetic cost of transport can also be greatly offset by using passive forms of locomotion, such as drifting in water or air currents (Luschi et al. 2003), soaring on rising air (Nourani and Yamaguchi 2017), or riding on another moving body (Binns 1982). While the process of migrating may be energetically demanding, residency can also lead to elevated energy expenditure for homothermic animals if they have to increase their resting metabolism to maintain a constant body temperature as weather conditions deteriorate during the winter. Therefore, migrants must account for the potential energetic benefits of migrating, such as energy gains resulting from more abundant food resources and reduced thermoregulatory costs, with the energetic costs of tracking those conditions, which may drive the decision of where to migrate (Somveille et al. 2019).

The process of migrating can also occupy a substantial amount of time (Alerstam and Lindström 1990). Dedicating time towards one life-history stage (e.g. migration) takes away time available for other stages (e.g. breeding, periods of self-care; Wingfield 2008). The time spent migrating extends beyond the time spent moving between locations. Many animals must forage to acquire sufficient energy to fuel each leg of their journey, which often occupies more time than the migratory movements themselves (Hedenström and Alerstam 1997, Wikelski et al. 2003). Finally, migrants typically go through morphological and physiological changes to prepare for migration, and these transition periods can likewise conflict with other annual cycle stages (Ramenofsky and Wingfield 2006).

Migratory journeys may also pose a survival risk. Migrants must traverse unfamiliar habitat where it may be challenging to find appropriate food, or food may become depleted as the migration season progresses (Moore and Yong 1991, Nolet and Drent 1998). Large numbers of moving animals can attract predators (Gangoso et al. 2013, Deacy et al. 2016).
Mortality during migration is particularly high when animals must cross barriers, either natural or man-made. For migratory birds, natural barriers are stretches of landscape where they cannot land or forage, providing no safe haven if they encounter extreme weather or run out of fuel, which sometimes cause mass mortality events (Newton 2007). For terrestrial and aquatic migrants, crossing anthropogenic barriers such as roadways or dams pose serious mortality risks (Beebee 2013, Buysse et al. 2014). As with energy, the risk of migrating may be offset by improved survival through the winter and/or increased reproductive success during the breeding season.

Finally, the choice to migrate necessitates abandoning one’s home range or territory. The ability to acquire and maintain a good territory typically increases reproductive success (Wang et al. 1990, Aebischer et al. 1996, Kokko 1999). In many species, there is a ‘prior-residence effect’ where the individual first occupying an area has an advantage over potential competitors (Kokko et al. 2006), and migrating requires abandoning this advantage. The consequence of this may effect individuals in the population differently, for example, in many species males acquire and defend territories to attract females (Morbey and Ydenberg 2001). Consequently, individuals that remain residential within breeding territories, or that return earlier from migration, are expected to have a reproductive advantage (Kokko 1999).

Aim and approach

The aim of this thesis is to understand how the costs, benefits and challenges of migrating change with and trade off among migration strategies. As a life-history strategy that evolved as an adaptation to cope with fluctuating environmental conditions, it seems logical that the consequences of different migration strategies should be studied in the context of the natural environment. To do so, we can adopt a comparative approach, using natural variation in migration strategies as a natural experiment.

Comparisons of the cost and benefits of migration strategies among species and populations can be confounded by differences in their ecology and environment. Therefore, trade-offs between migration strategies are best compared within a single population (Newton 2008). Inter-individual variation in migration strategies is widespread (Chapman et al. 2011). However, the vast movements of animals between different regions of the world which is inherent to the migratory process simultaneously makes migration challenging to study empirically, as it requires following individuals year-round and across a wide geographic area for multiple years. One species that has high inter-individual variation in migration strategies and for which we have such data is the lesser black-backed gull (*Larus fuscus*, Linneaus 1758).
Chapter 1 - General introduction

Lesser black-backed gulls: the study system

Lesser black-backed gulls are a relatively large gull species which breeds along the North-West coastal regions of Europe. Like many gull species, lesser black-backed gulls are omnivorous, though marine fish make up a greater proportion of their diet than other closely related, sympatrically breeding *Larus* species (Kubetzki and Garthe 2003, Camphuysen 2013). Over the past century, lesser black-backed gulls have learned to use anthropogenic environments for food, exploiting fishery discards, refuse, livestock feeding areas and other agricultural practices (Camphuysen 1995, Camphuysen et al. 2015, Spelt et al. 2021), as well as beginning to breed within cities (Spelt et al. 2019). Coinciding with the increased prevalence of anthropogenic food sources, lesser black-backed gull populations in Western Europe have increased rapidly since the 1940s (Spaans 1998, Ross-Smith 2020), with most populations now stabilising or beginning to decline (Ross-Smith 2020).

Lesser black-backed gulls are migratory throughout most of their range. The migratory habits of lesser black-backed gulls may relate to their traditional reliance on surface feeding fish as a primary food resource. During winter at high latitudes, the phytoplankton on which fish feed ceases to grow and sinks deeper into the ocean, and the fish follow, too deep to be reached by surface diving. Many surface-feeding birds thus migrate to more tropical regions (Alerstam 1990), which at the beginning of the past century, included most lesser black-backed gulls. However, anthropogenic activity now provides food sources at high latitude year-round. Correspondingly, increasing numbers of lesser black-backed gulls remain within Western Europe year-round (Lack 1968, Baker 1980), with their contemporary wintering range extending from the UK south to West Africa, a one-way difference of over 4500 km (Klaassen et al. 2012, Shamoun-Baranes et al. 2017).

During the breeding season, lesser black-backed gulls breed in single or mixed-species colonies. They nest on the ground in relatively open habitat, with a modal clutch of three eggs. Lesser black-backed gulls are considered monogamous, and both sexes contribute equally to parental care (Kavelaars et al. 2021). While the sexes look similar, males are on average larger than females. Their wing morphology enables gulls to fly using both flapping and soaring flight (Shamoun-Baranes et al. 2016), providing them the opportunity to reduce the energetic costs of flight under certain environmental conditions.

The studies in this thesis make use of an immense dataset from several ongoing research and monitoring projects on lesser black-backed gulls breeding in the Netherlands, Belgium, and the UK. Solar-powered UvA-BiTS trackers (Bouten et al. 2013) have been deployed on over 150 lesser black-backed gulls since 2008. These trackers measure location via GPS every 5 minutes to an hour, year-round. Tri-axial acceleration is recorded along with each
GPS fix, which can be used to classify the behaviour an individual is exhibiting (for example flight style; Shamoun-Baranes et al. 2016), as well as potentially providing an estimate of activity-related energy expenditure (Gleiss et al. 2011). Concurrently, lesser black-backed gulls have been marked with uniquely coded colour rings in two Dutch colonies, with targeted resighting effort being carried out in both colonies during the breeding season, while citizen scientists have reported resightings throughout their winter range during the nonbreeding season. Finally, an intensive monitoring program on the reproductive efforts and success of gulls has been carried on in a large breeding colony on Texel Is., NL (Camphuysen 2013). Adding to this, we pilot the use of implantable heart rate loggers in free-ranging gulls, which is another proxy for energy expenditure which should capture both energy allocated towards resting metabolism as well as physical activity (Green 2011).

Thesis outline

The studies in this thesis each focus on quantifying one or a few costs, benefits or challenges of migrating in lesser black-backed gulls, and examine how they correlate with migration distance or geographic wintering area. To begin, Chapter 2 focuses on the challenge of adjusting migratory behaviour to inter-annual variation in environmental conditions. Migrating animals rely on environmental cues to predict what conditions are like at their migratory destinations (Bauer et al. 2011). Some cues, such as day length, are invariant across years and can be used to move in space and time based on long-term average best conditions, resulting in consistent behaviour across years. Others, such as local weather and food conditions, can be used to predict current conditions in the greater landscape, resulting in variable behaviour across years. As migration distance increases, the reliability of cues used to predict current conditions is expected to decrease, and as such, individuals should increasingly use time-invariant cues to inform migration decisions (Bauer et al. 2020), resulting in less behavioural variation among years. To test this, we quantified inter- and intra-individual variation in both spatial and temporal migratory behaviour from lesser black-backed gulls that were GPS tracked for multiple years, to see if it is correlated with migration distance. We also quantified repeatability of gull migration strategies to determine whether we can assume individuals consistently use the same strategies among years.

Next, we focus on the energetic costs of migrating. First, we needed to determine how to best use acceleration data to estimate daily energy expenditures throughout the year. Acceleration data can be used to identify behaviour, and an average energetic cost can be attributed to each behaviour to recreate a time-energy budget. Alternatively, the
dynamic acceleration can be summed (called dynamic body acceleration, DBA), which, when calibrated, may be used to detect variation in the work performed by the animal within a given behaviour (Gleiss et al. 2011). In Chapter 3, we simultaneously deploy implantable heart rate loggers alongside our UvA-BiTS GPS-accelerometer trackers in breeding lesser black-backed gulls to see how acceleration performs as a proxy for energy expenditure. First, we estimated average costs of different behaviours, and calculated calibration relationships between DBA and heart rate within a behaviour mode. Next, we compared DBA and time-energy budget methods for estimating daily energy expenditure determined from heart rate data, finding that both acceleration methods performed similarly, though failed to measure day-to-day variation in resting metabolic rate which is captured using the heart rate method. We applied these DBA calibrations from in Chapter 4, where we explore how migration strategy influences energy expenditure and time-budgets throughout the year. To estimate daily energy expenditure throughout the year, we used year-round acceleration data in conjunction with a bioenergetics model to estimate thermoregulatory costs. Daily time-budgets were reconstructed from the accelerometer behavioural classifications to explore how individuals using different migration strategies adjusted their behaviour to accommodate different stages in their annual cycle and while regulating their energy expenditure. We examined whether migration strategy influenced average daily energy expenditure over the year, focusing on whether energy allocated towards activity and thermoregulatory costs trade-off. We also tested if migration strategy influences how evenly energy expenditure is distributed throughout the year, with the expectation that as distance to wintering area increases, energy expenditure will be concentrated into short burst, balanced by periods of below average energy expenditure, while shorter-distance migrants will have more constant energy expenditures throughout the year.

While the time and energy consequences of different migration strategies provide a mechanistic understanding of why animals migrate to certain areas, from an evolutionary perspective we would like to know the fitness consequences of different migration strategies. In Chapter 5, we examine how survival and reproductive parameters are influenced by migration distance. For this, we assigned wintering locations to individuals based on either GPS tracking data or colour-ring resightings. We examined whether migration distance influenced when the first egg of a clutch was laid, the volumes of the eggs in the clutch, and hatching success. We estimated bi-annual survival probability using mark-recapture models based on colour-ring resightings during the breeding and wintering periods. We examined where survival probability changed with migration distance or between spring and autumn migration seasons.

In Chapter 6, I synthesize the results of these studies and discuss their general implications for our understanding of the costs, benefits and challenges of migratory life-histories.
CHAPTER 2

Long-distance migrants vary migratory behaviour as much as short-distance migrants: an individual-level comparison from a seabird species with diverse migration strategies

J. Morgan Brown, E. Emiel van Loon, Willem Bouten, Kees C.J. Camphuysen, Luc Lens, Wendt Müller, Chris B. Thaxter, Judy Shamoun-Baranes

Abstract

1. As environmental conditions fluctuate across years, seasonal migrants must determine where and when to move without comprehensive knowledge of conditions beyond their current location. Animals can address this challenge by following cues in their local environment to vary behaviour in response to current conditions, or by moving based on learned or inherited experience of past conditions resulting in fixed behaviour across years.

2. It is often claimed that long-distance migrants are more fixed in their migratory behaviour, because as distance between breeding and wintering areas increases, reliability of cues to predict distant and future conditions decreases. While supported by some population-level studies, the influence of migration distance on behavioural variation is seldom examined on an individual-level.

3. Lesser black-backed gulls (*Larus fuscus*) are generalist seabirds that use a diversity of migration strategies. Using high-resolution multi-year GPS tracking data from 82 individuals from 8 colonies in Western Europe, we quantified inter- and intra-individual variation in non-breeding distributions, winter site fidelity, migration routes and timing of migration, with the objectives of determining how much variation lesser black-backed gulls have in their migratory behaviour and examining whether variation changes with migration distance.

4. We found that intra-individual variation was significantly lower than variation between individuals for non-breeding distributions, winter site fidelity, migration routes and timing of migration, resulting in consistent individual strategies for all behaviours examined. Yet, intra-individual variation ranged widely among individuals (e.g. winter site overlap: 0 – 0.91 out of 1; migration timing: 0 – 192 days), and importantly, individual differences in variation were not related to migration distance.

5. The apparent preference for maintaining a consistent strategy, present in even the shortest distance migrants, suggests that familiarity may be more advantageous than exactly tracking current environmental conditions. Yet, variation in behaviour across years was observed in many individuals and could be substantial. This suggests that individuals, irrespective of migration distance, have the capacity to adjust to current conditions within the broad confines of their individual strategies, and occasionally, even change their strategy.
Introduction

Seasonal environments offer animals predictable periods of high productivity, though also present the challenge of scarcity during the other portion of the annual cycle. Seasonal migration is a life-history strategy by which animals can exploit fluctuations in habitat suitability by moving between distant regions at predictable times throughout the year (Shaw and Couzin 2013). Animals that match their movements more precisely to coincide with environmental patterns in their landscape (e.g. food, weather) typically have higher survival and reproductive success (Both et al. 2006). Environmental conditions, however, vary unpredictably among years. This poses a challenge for migrants who must determine when and where to move without comprehensive knowledge of the environment through which they must move.

When environmental conditions are spatially and temporally autocorrelated (Koenig 1999), conditions at one location can provide information about conditions in another. Such correlations can be used as cues for migratory behaviour (Saino and Ambrosini 2008), but as the distance an animal migrates increases, the correlation of conditions between wintering and breeding areas, and thus the reliability of these cues, is expected to decrease. A lack of reliable information favours tracking of past conditions, i.e. average long-term trends), rather than responding to current conditions (Bauer et al. 2020). Due to these differences in the availability and reliability of cues for predicting remote conditions, it is commonly suggested that long-distance migrants should be more fixed in their migratory behaviour than short-distance migrants (Gwinner 1977, Hagan et al. 1991, reviewed by Knudsen et al. 2011).

Long-distance migrants are thus expected to move based on learned (Campioni et al. 2020), socially transmitted (Jesmer et al. 2018), or genetically inherited (i.e. endogenous, Åkesson et al. 2017, Berthold 1996, Gwinner 2003) information about spatiotemporal resource availability in the past. Movement based on past information is synonymous to memory-based movement (Fagan et al. 2013), and movements should coincide with average climatic conditions (Thorup et al. 2017, Abrahms et al. 2019). Using past information should result in low intra-individual variation in time and space across years, and consistent differences in behaviour between individuals. Short-distance migrants, on the other hand, are generally expected to adjust migratory behaviour based on current conditions, resulting in intra-individual variation across years. This may be done by either following current resource gradients (i.e. surfing resource waves, Armstrong et al. 2016 Van der Graaf et al. 2006) or using local environmental cues such as temperature (Deutsch et al. 2003) or vegetation (Van der Graaf et al. 2006, Balbontin et al. 2009, Merkle et al. 2016) to predict remote and future resource patterns. Explicit laboratory experiments for
differential information use by migration distances have not been performed, while support from inter-species comparisons of variation in phenology of wild populations is mixed (Knudsen et al. 2011): most report that timing of migration in long-distance migrating species is less varied than short-distance ones (Hagan et al. 1991, Butler 2003, Murphy-Klassen et al. 2005, Rainio et al. 2006, Miller-Rushing et al. 2008, Rubolini et al. 2010, La Sorte et al. 2016), while others observe no differentiation or even more advancement in long-distance migrants (Hüppop and Hüppop 2003, Jonzén et al. 2006).

Most field-based studies examining the influence of migration distance on variation in migration behaviour occur at the population level (Charmantier and Gienapp 2014), and the extent to which individual-level behavioural plasticity contributes to population-level changes in migratory behaviour remains unclear (Knudsen et al. 2011). Repeated-measures of migratory traits from individuals to measure inter- and intra-individual variance is a commonly used method to assess plasticity in migratory behaviour (Conklin et al. 2013, Fraser et al. 2019). Consistent individual differences, or repeatability, may be indicative of inherited or learned preferences based on past conditions, while the residual within-individual behavioural variability reflect the combination of plastic responses to the environment (i.e. adjustment to current conditions) and flexibility (i.e. variation independent of the environment; Hertel et al. 2020, Nakagawa and Schielzeth 2010, Noordwijk et al. 2006). While repeatability of migratory behaviour has been calculated previously for many avian species (reviewed by Both et al. 2016 and Phillips et al. 2017), typically the spatial accuracy of these studies are low due to the tracking technology used, and comparisons among individuals or populations using different strategies are seldom carried out. It is therefore challenging to compare results across these studies to understand the ultimate ecological cause for differences in behavioural variation across taxa (Charmantier and Gienapp 2014). Species containing individuals with different migratory strategies are interesting systems for examining whether migration distance influences individual variation in migratory behaviour.

Lesser black-backed gulls (Larus fuscus) are medium-sized, long-lived seabirds that migrate to diverse wintering regions. A single colony typically contains individuals ranging from short-distance migrants that remain local and only move to winter roosting sites 50 km away, up to intercontinental long-distance migrants travelling thousands of kilometres (Stienen et al. 2016, Shamoun-Baranes et al. 2017, Thaxter et al. 2019). An individual's wintering region is thought to be consistent across years and is not related to either sex or size (Baert et al. 2018). Lesser black-backed gulls are capable of using a range of resource types, including marine, terrestrial and urban (Camphuysen et al. 2015, Baert et al. 2018), though within a given period, many individuals tend to specialize on a particular foraging strategy (Camphuysen et al. 2015, Isaksson et al. 2016). Having the capacity to forage
in a broad range of habitats and survive in a range of climatic conditions provides many potential options with regards to how, when, and where they migrate.

Using a long-term, high resolution GPS-tracking dataset of lesser black-backed gulls breeding in colonies in Belgium, the UK and the Netherlands, with individuals that have been tracked for multiple years, we measured variation in the following migratory behaviours: non-breeding distribution, fine-scale wintering site fidelity, migratory routes, and date of arrival and departure from breeding and wintering areas. One of the advantages of our study system is the high spatio-temporal resolution of our data across all colonies (hourly at ± 3m spatial resolution) which enables us to accurately quantify at a fine spatio-temporal scale each of the migratory behaviours we studied. Our first objective is to quantify inter- and intra-individual variation of these migratory behaviours in lesser black-backed gulls and determine whether individuals use consistent strategies. While a range of behavioural options may be available to an individual, there are benefits to behaving consistently in space and time (Gunnarsson et al. 2004, Piper 2011). Thus, we hypothesize that individuals will generally be consistent in their migratory behaviour, with population variation being largely a result of inter-individual differences. Our second objective is to determine whether individual variation in migratory behaviour changes with migration distance. Studying variation in migration behaviour at the individual-level, a high spatio-temporal resolution and along such a broad range migration distances has rarely been possible, allowing us to address this question from a new ecological perspective.

**Methods**

**Tracking and data processing**

We used GPS tracking data from adult lesser black-backed gulls tracked for two or more years from 8 colonies in the Netherlands, Belgium, and the UK (Table 2.1, Fig. 2.1). Gulls were captured during the breeding season using walk-in traps set over the nest during incubation. Subsequent movements were recorded using solar-powered GPS-trackers (UvA-BiTS; Bouten et al. 2013), attached with a Teflon wing harness (Thaxter et al. 2014). Total mass of tracker and harness were less than 3% of total body mass.

The breeding season was defined as the period of the year during which an individual occurs in the breeding colony, regardless of their breeding status. The non-breeding season therefore starts with date of colony departure (last detection within 10 km of the breeding colony following the breeding season) and continues until date of colony arrival (first detection within 10 km of the colony prior to the breeding season). To quantify time spent in different areas throughout the non-breeding season (non-breeding distribution),
we calculated a utilization distribution (UD) from the 95% kernel density estimates of GPS locations taken during the non-breeding season. Tracking data were subsampled to a 12-hour interval to reduce autocorrelation and help distribute data equally through time (in the case of multi-day data gaps) and were projected onto a Lambert equal-area projection (EPSG 3035). UDs were created using the R package “adehabitatHR” (Calenge 2006) with a bivariate normal kernel on a grid with a 10 km resolution, using a fixed bandwidth (h) of 100 km.

Gulls can use several distinct core areas over the course of a non-breeding season. These core areas were identified by polygons of the 50% contour from the non-breeding distribution UD (see Fig. S2.1 in the supplementary material for examples). Core areas identify coarse-scale regions (hundreds of kilometres in diameter) where birds either wintered or stopped-over for prolonged periods.

Many non-breeding seasons contained multi-day gaps caused by low battery or device malfunction which can influence the UD. Any non-breeding season with a consecutive gap longer than 21 days (the minimum time spent in a core area from gap-free seasons) was removed. If these removals resulted in an individual with only one remaining season, this individual was removed from the study. One individual who remained within 10 km of its colony year-round was also removed.

The core area in which an individual spent the most amount of time between December and March was considered the wintering area, and apart from one individual, was the furthest core area from the colony. Date of arrival to wintering area and date of departure from wintering area were the date of the first and last GPS detection within this polygon, respectively. The remaining core areas are considered to represent stopover areas. Time spent in these stopover areas sometimes exceeds time spent in the wintering area, and these areas are typically occupied in summer and autumn months (Klaassen et al. 2012). Migration distance, representing the migration strategy of an individual (i.e. direct rather than cumulative distance travelled), was measured as the great circle distance between the colony and centroid of the wintering area. For four individuals, the wintering area from one year was overlapping with multiple small polygons in another year. To make behaviour comparable across years, these fragmented polygons were grouped into single wintering areas.

Non-breeding distribution

To quantify intra-individual variation in non-breeding distributions, we calculated mean overlap in the 95% non-breeding season UDs (described above) between all possible paired combinations of non-breeding seasons per individual using Bhattacharyya’s affinity (BA; Bhattacharyya 1943), a recommended method for quantifying home-range overlap.
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(Fieberg and Kochanny 2005). BA is a function of the product of two UDs which quantifies their similarity, with 0 indicating no overlap and 1 being identical (as we are using 95% UDs, 0.95 would be the highest potential overlap). This metric is independent of area so is comparable across areas of different size (i.e. consistent use of a concentrated area ranks the same as consistent use of a larger, diffuse area). Because BA uses the complete probability distribution, individuals overlapping in areas with higher probability of occurrence (i.e. similar use of wintering and stopover sites across years), will have higher overlap than those overlapping in areas of low probability (i.e. if stopping over in different areas or for less time).

Inter-individual variation in non-breeding distribution was quantified by calculating non-breeding season overlap between pairs of individuals using similar migration strategies. Pairings were constrained so that neither the breeding colonies nor wintering areas used by paired individuals were further than 250 km apart. The 250 km constraint was chosen a-priori to any statistical analysis, and was selected because, considering the motion capacity of this species, the area within a 250 km range represent accessible alternatives for an individual while being large enough that most individuals could be paired to at least one other individual. The paired tracks were not required to be from the same year, and if multiple nonbreeding seasons were within the distance constraints for a pair of individuals, one non-breeding season per individual was randomly selected.

Following Guilford et al. (2011), to determine if individuals were significantly more consistent in their behaviour across years relative to the behaviour demonstrated by others, we used randomization tests. First, the difference between median variation between pairs of individuals and median variation within individuals was calculated. The data were then randomly re-arranged into new ‘between’ and ‘within’ groups and the difference between medians of these random groupings was found. Randomizations were repeated 10 000 times. The probability of the difference in medians from randomly generated groups being larger than that found between the actual within-individual and between-individual groups was then reported.

The relationship between migration distance and intra-individual variation in non-breeding season distribution was examined using a linear model of non-breeding season overlap against the median migration distance used by each individual. Individuals who had a wintering area which did not overlap with previous years were excluded from this, and all other comparisons of the influence of migration distance on intra-individual variation, so that the measured intra-individual variation could be associated with a single migration distance and wintering area. A likelihood ratio test between this model and a model with no explanatory variables was used to test whether migration distance significantly influenced individual variation.
However, short-distance migrants are more constrained in how much they can reasonably change their behaviour, and thus should demonstrate less variation regardless of their inclination for behavioural variation. To address this bias, the relationship between migration distance and overlap found between paired-individuals was used as a null model for expected variation at a given migration distance, assuming inter-individual variation should be similarly influenced by this spatial constraint. The variation predicted in this null model for a given migration distance was subtracted from the intra-individual non-breeding season overlap to determine whether intra-individual variation changed more or less than expected.

**Winter site fidelity**

As a measure of consistency in fine-scale space use, we calculated winter site fidelity. All GPS points between arrival and departure from the wintering area were used to maximise temporal resolution of movement data, rather than subsampling as done for non-breeding distributions. The biased random bridge approach was used to calculate a winter area UD, which considers the sampling interval of GPS points thus accounting for spatio-temporal autocorrelation in high frequency measurement schemes (Benhamou 2011). Winter area UDs were calculated on 500 m² grids using the BRB function in the R package “adehabitatHR”, with the plug-in method for estimating the diffusion coefficient. The maximum duration was set to 3 h, with a minimum distance of 20 m and a minimum smoothing parameter of 150 m. Site fidelity was then calculated using BA overlap of the winter area UD up to the 95th percentile, which is used as a measure of individual consistency (Wakefield et al. 2015, Abrahms et al. 2018).

A linear model of winter site fidelity against individual median migration distance was fit and compared to a model with no fixed effects to test whether migration distance significantly influences winter site fidelity (excluding individuals who changed wintering areas).

**Migration routes**

To quantify variation in migration routes, defined as the path recreated from the GPS track of an individual migrating between wintering and breeding areas, we computed an autumn and spring mean route for each individual. Based on a method by Freeman et al. (2010), the mean route is a sequence of 500 computed points that minimizes the distance to nearest-neighbour locations on the set of GPS tracks used by an individual across years. All points within stopover areas were removed and replaced by a single point at the centroid of the stopover area polygon so that these routes are composed of GPS points from migratory flights only. The variance of nearest-neighbour locations from
the GPS-tracked migration routes around each point on the mean route was calculated, and the mean of the variances along the mean route was used as a metric of migration route variation. Any migration route with a gap longer than 24 h when an individual was outside of a core area (i.e. during migratory flights) was removed, as were individuals who changed wintering area. Full methodology and illustrated example of mean route and migration route variation calculations are in the supplementary material (“Methodology: Calculation of mean routes”, Fig. S2.2).

Inter-individual variation in migration routes was calculated using the same between-individual pairing method used for non-breeding season overlap, and individual consistency was determined using randomization tests, as described above. Influence of migration distance on migration route variability was assessed using linear models for each season. Similar to non-breeding season overlap, short-distance migrants are expected to be more spatially constrained than long-distance migrants, so this relationship was also considered in comparison to that found for between-individual pairings.

**Timing of migration**

As measures of intra-individual variation in annual timing we report the range of dates individuals departed and arrived at their colony and wintering areas. One individual was removed from analysis of departure from colony and two individuals from arrival to wintering area as data gaps occurred during this transition.

To quantify individual consistency in timing we calculated repeatability, $R$, where

$$ R = \frac{s_\alpha^2}{s_\alpha^2 + s_\epsilon^2} $$

and $s_\alpha^2$ and $s_\epsilon^2$ are the variance among and within individuals, respectively. If individuals are highly consistent in their behaviour relative to variation occurring among individuals, $R$ is close to one. We calculated $s_\alpha^2$ and $s_\epsilon^2$ using linear mixed models (LMM) for each trait, with migration distance as a fixed effect and colony and individual as random effects (REML method using lme4 package in R; Bates et al. 2015), where variance of the individual-level random effect is $s_\alpha^2$ and variance of the random error is $s_\epsilon^2$ (Nakagawa and Schielzeth 2010). For arrival to wintering area, migration distance was excluded to achieve model convergence. As we were interested in the degree of behavioural variation an individual could exhibit, year was not included as a random effect so that behavioural variation in response to inter-annual changes in environmental conditions would contribute to intra-individual (residual) variation. We used the R package ‘rptR’ (Stoffel et al. 2017) to calculate repeatability with 95% confidence intervals based on parametric bootstrapping over 1000 iterations (presented as $R$ [Lower CI-Upper CI]).
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Figure 2.1. Mean individual migration routes in autumn and spring based on GPS tracking from two or more years. Variation around the mean route is shown by colour. Colonies are indicated with yellow diamonds.

For individual-level measures of variation in arrival and departure dates, using the LMMs above, we calculated an individual-level repeatability, $R_i$, by substituting the residual variance for the $i$th individual, $s_i^2$, for $s^2$ (excluding individuals who changed wintering areas; Potier et al. 2015, Wakefield et al. 2015). $R_i$ for each arrival or departure was then used as the response variable in the linear models with migration distance.

All analysis was completed in R version 3.5.1. Final sample sizes for each behaviour can be found in Table 2.1 and Table S2.1 in the supplementary material.
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Table 2.1. Summary of data included in this study by colony. Number of individuals (N. ind.) and number of seasons (N. seasons) used in the analysis are reported as: “overlap and timing”/“autumn routes”/“spring routes”.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Location</th>
<th>Years</th>
<th>N. ind.</th>
<th>N. seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walney, UK</td>
<td>54.0 N, 3.18 W</td>
<td>2014-2019</td>
<td>11/6/6</td>
<td>28/14/15</td>
</tr>
<tr>
<td>Orfordness, UK</td>
<td>52.1 N, 1.58 E</td>
<td>2010-2015</td>
<td>9/1/7</td>
<td>22/3/18</td>
</tr>
<tr>
<td>Schiermonnikoog, NL</td>
<td>53.5 N, 6.26 E</td>
<td>2017-2019</td>
<td>4/3/4</td>
<td>8/6/8</td>
</tr>
<tr>
<td>Texel, NL</td>
<td>53.0 N, 4.72 E</td>
<td>2010-2019</td>
<td>18/13/15</td>
<td>61/33/44</td>
</tr>
<tr>
<td>Vlissingen Oost, NL</td>
<td>51.4 N, 3.70 E</td>
<td>2015-2019</td>
<td>9/8/9</td>
<td>24/22/24</td>
</tr>
<tr>
<td>Zeebrugge, B</td>
<td>51.3 N, 3.18 E</td>
<td>2013-2019</td>
<td>24/17/22</td>
<td>74/54/67</td>
</tr>
<tr>
<td>Oostende, B</td>
<td>51.2 N, 2.93 E</td>
<td>2016-2019</td>
<td>2/2/2</td>
<td>5/5/5</td>
</tr>
<tr>
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<td>233/146/190</td>
</tr>
</tbody>
</table>

Results

Variation in migratory behaviour of lesser black-backed gulls

Individuals used between 1 – 3 core areas during the non-breeding season. For all but five individuals (n = 77, 94%), winter areas overlapped across all years. These five individuals switched wintering areas between France and Western Sahara (n = 1), Mauritania and Portugal (n=1), France and UK (n = 1), and Morocco and UK (n = 2). Migration distance was therefore highly repeatable (R = 0.81 [95% confidence interval: 0.57 - 0.93]). Sixty-two individuals (76%) used a stopover in at least one year, and 96% of total time spent in stopover areas occurred before arrival to the wintering area. Use of stopover areas was less consistent than wintering areas: 18 out of the 62 individuals using a stopover (29%) had a stopover area that did not overlap among years (compared to 6% individuals who had non-overlapping wintering areas).

Despite some variation in stopover area use, overlap in non-breeding distributions was generally high, with a median overlap of 0.91 (range: 0.51 – 0.95). Non-breeding distributions were considerably more similar within individuals across years than between individuals (median between-individual overlap = 0.61, range = 0.19 – 0.93, Fig. 2.2a and Fig. S2.3 in supplementary material), with none of the randomized sets producing a
difference in median more extreme than the actual data ($P < 0.001$). Site-fidelity within wintering areas was lower than non-breeding distribution overlap, with a median overlap of 0.62, and differed substantially among individuals (range: 0.00 – 0.91, Fig. 2.2b).

Individual variation in migration route was generally low in both autumn (median = 41 km, range = 3 – 169) and spring (median = 45 km, range = 11 – 211 ). Most intra-individual route variation occurred at the Bay of Biscay and over the arid centre of Spain (Fig. 2.1). Intra-individual variation was significantly lower than variation found between paired individuals (autumn: between-individual median = 107 km, range = 12 – 280; spring: between-individual median = 62 km, range = 11 – 236; Fig. 2.2c-d and Fig. S2.3 in supplementary material) with probabilities less than 0.001 of obtaining a difference in medians as extreme from a randomized set. Examples of high and low non-breeding distribution overlap and route variation for a range of migration distances can be found in the supplementary material (Fig. S2.1 and S2.4).

Individuals departed their breeding colonies within a 192-day period between 24 May – 2 December (Fig. 2.3a). The median range of departure dates within an individual was 20 days (range: 0 – 192) and was highly repeatable ($R = 0.51 \ [0.34 \ - \ 0.63]$). Arrival to wintering area occurred between 27 June – 24 January (a period of 211 days; Fig. 2.3b). Intra-individual arrival dates to wintering area ranged across years by 1 – 166 days (median = 16.5) and repeatability was high ($R = 0.77 \ [0.62 \ - \ 0.83]$). During spring, the range of departure dates from wintering areas and arrival dates to colony within individuals was narrower than in autumn. Departure dates from wintering areas occurred within a 90-day period between 24 January and 24 April (Fig. 2.3c). The median intra-individual range of departure dates was 11 days (range: 1 – 36). Repeatability of departure from wintering area was high ($R = 0.58 \ [0.39 \ - \ 0.74]$). Arrival to breeding colonies occurred between 24 January and 21 May (a period of 117 days; Fig. 2.3d). Intra-individual range in arrival dates to colony was 0 – 34 days (median = 10). Repeatability was also high ($R = 0.57 \ [0.38 \ - \ 0.74]$). Except for departure date from colony, migration dates were later in longer distance migrants (Fig. 2.3, Table S2.2 in supplementary material). Colony explained little variance in timing of migration. Linear mixed model results and partitioning of variance are reported in the supplementary material (Table S2.2).

While most individuals tended to be highly consistent, for each behaviour a few individuals demonstrated high variation (Fig. 2.2, Fig. S2.5 in supplementary material). The individuals demonstrating the most variation were not the same for each behaviour, with 26 different individuals (32%) being in the upper 5th percentile of variation for at least one behaviour (Table S2.3 in supplementary material).
Influence of migration distance on individual variation

Migration distances ranged from 53 – 4572 km (median = 1727 km, n = 77). Intra-individual non-breeding distribution overlap decreased with migration distance (overlap $= 0.936 - 2.0 \times 10^5 \cdot \text{migration distance}$, $F_{(1, 75)} = 28.142$, $p < 0.001$; Fig. 2.2a). However, intra-individual variation increased at a significantly lower rate than the increase between individuals (residual overlap $= 0.232 + 3.1 \times 10^5 \cdot \text{migration distance}$, $F_{(1, 75)} = 68.642$, $p < 0.001$; Fig. S2.6a in supplemental material), suggesting that longer distance migrants were less variable in their behaviour than expected when considering the total space traversed during their movements (and vice-versa for shorter distance migrants). Intra-individual route variation increased slightly but significantly with migration distance in spring (variation $= 22.652 + 0.014 \cdot \text{migration distance}$, $F_{(1, 67)} = 14.237$, $p < 0.001$; Fig. 2.2d), even after accounting for increasing between-individual variation (variation $= -46.208 + 0.010 \cdot \text{migration distance}$, $F_{(1, 67)} = 6.564$, $p = 0.013$, Fig S2.6c). Autumn route variation did not change with migration distance ($F_{(1, 52)} = 3.941$, $p = 0.052$; Fig. 2.2c), nor did it significantly differ from variation observed between individuals ($F_{(1, 52)} = 1.544$, $p = 0.220$; Fig S2.6b).

Winter site fidelity did not change significantly with migration distance ($F_{(1, 75)} = 1.269$, $p = 0.263$; Fig. 2.2b). Migration distance also did not correlate with individual repeatability in departure date from colony ($F_{(1, 74)} = 2.258$, $p = 0.137$; Fig. 2.2e), arrival to wintering area ($F_{(1, 73)} = 0.460$, $p = 0.500$; Fig. 2.2f), departure from wintering area ($F_{(1, 75)} = 1.422$, $p = 0.237$; Fig. 2.2g) or arrival to colony ($F_{(1, 75)} = 3.508$, $p = 0.065$; Fig. 2.2h), suggesting individual consistency of migration timing did not increase with migration distance.
Figure 2.2. Mean overlap in a) non-breeding distribution and b) winter areas, c) autumn and d) spring variation in migration routes, and individual repeatability in date of e) colony departure, f) arrival to winter area, g) departure from winter area, and h) colony arrival, across multiple non-breeding seasons from lesser black-backed gulls, versus their median migration distance. The y-axis for autumn and spring route variation (c and d) is reversed so that the order of variation is consistent among plots. Black lines showing trends predicted by the linear models were included if significant. Distributions from between-individual pairs used to calculate ‘residual’ intra-individual variation are shown in grey (only used for behaviours compared across multiple spatial scales). Individuals who changed wintering areas (n = 5) have been excluded.
Discussion

This study quantified inter- and intra-individual variation in non-breeding distributions, winter site fidelity, migration routes and timing of migration in lesser black-backed gulls at the individual-level, using high spatio-temporal resolution tracking data, and covering a broad-range of migration distances, to test the hypothesis that migratory behaviour should become more fixed as migration distance increases. However, we found that migration distance did not explain which individuals were most variable across years, contrasting with many previous inter-species comparisons of population phenology. Instead, we found that regardless of migration distance, individuals consistently differed from each other in their behaviour, suggesting that individuals predominantly follow learned and/or inherited behavioural strategies.

Figure 2.3. The range of a) departure dates from colony, b) arrival dates to wintering area, c) departure dates from wintering area, and d) arrival dates to colony used across non-breeding seasons by individual lesser black-backed gulls. Individuals who changed wintering areas (n = 5) are identified by white boxplots. Individuals are ordered by their median migration distance. Repeatability [95% confidence interval] is reported at the bottom of each plot.
Chapter 2 - Variation in migratory behaviour

Variation in migratory behaviour

For all behaviours examined, intra-individual variation was small compared to that of the population, resulting in distinct individual behavioural strategies, consistent with our hypothesis that gulls will be inclined to rely on past experience. Repeatability was high in comparison to findings across a range of taxa for diverse behavioural traits (Bell et al. 2009), but consistent with studies of avian migration (reviewed by Both et al. 2016 and Phillips et al. 2017). This suggests that many avian species preferentially use learned or inherited knowledge of previously reliable wintering and stopover areas, rather than risk searching for the best locations in a given year.

Winter area overlap demonstrated individuals also had high site fidelity at a fine scale (500 m resolution), suggesting repeated use of foraging areas and roosting sites among years. Individual consistency in space use may provide more stable energetic rewards than plastic behaviour (Abrahms et al. 2018), as familiarity with a site can improve foraging efficiency (Piper 2011, van den Bosch et al. 2019). Efficiency resulting from familiarity may be sufficient to balance the benefits of switching to a new location with better environmental conditions for a given year. Consistent individual differences in timing of migration may be a result of individual differences in foraging type and habitat quality at their respective wintering and stopover areas, resulting in different optimal migration times (Studds and Marra 2005), and it may also be a mechanism to reunite with mates in the breeding colony (Gunnarsson et al. 2004). Understanding how these individual strategies are determined (genetically inherited, socially transmitted, or learned) is important for assessing the adaptive scope of migratory animals to changes in their environment. Current studies on avian species suggest migratory behaviour may be under strong genetic influence in early life, but refined or replaced by learning as an individual gains experience (Sergio et al. 2014, Campioni et al. 2020).

Inter-individual variation for most behaviours examined was high. High inter-individual variation might suggest that selective pressure on these behaviours is low for this species (Verhoeven et al. 2019). Low selective pressure on migratory traits may be typical for generalist species, such as gulls, for whom the ability to use a range of behaviours at fine spatio-temporal scales (e.g. diet and habitat), and the ability to survive under a range of climatic conditions, may buffer the effects of inter-annual variation, enabling consistency in behaviours at mid-to-broad spatio-temporal scales (e.g. wintering and stopover regions, migratory period). This is conductive with the fact that spatial overlap measured at finer scales (winter site fidelity) was lower than regional-scale, non-breeding season overlap.

While most individuals follow a distinct strategy, the intra-individual variation observed suggests that gulls still adjust behaviour across years, and thus behaviour is not rigidly fixed. Instead, consistent behavioural strategies likely define a broad window in space
or time within which an individual can adjust its behaviour based on current conditions, thus allowing for the integration of information based on both past and current conditions (Åkesson & Helm, 2020). Additionally, for each behaviour examined, there were a few individuals with extremely high variation across years (i.e. a change in the behavioural strategy). The individuals which exhibited this high variation were not consistent across all behaviours, suggesting that the ability to change strategy could be common across all individuals. The causes of these drastic changes are unknown, but suggests that individuals can change strategies to adapt to shifting long-term conditions within their lifetime.

Intriguingly, for migration routes, inter- and intra-individual variation was low, suggesting the entire population is being constrained to the use of certain migratory corridors. Despite reduced inter-individual variation, intra-individual variation was still lower, suggesting individuals travelling between similar breeding and wintering areas consistently use different routes. This is in contrast to many migratory bird species who typically demonstrate high variation in migration routes, presumably as they adjust routes among years to current wind conditions (Stanley et al. 2012, Dias et al. 2013, López-López et al. 2014). This may suggest that there is high selection pressure for moving along coastlines in this species, implying an advantage to foraging or roosting in coastal habitats while migrating. Coastal areas may also represent energy efficient pathways, as the dunes and cliffs typical of these areas can generate orographic lift enabling gulls to switch from flapping flight to energetically cheap soaring flight (Sage et al. 2019).

**Influence of migration distance on individual variation**

No clear effect of migration distance on individual variation was found in lesser black-backed gulls from these populations. This is in contrast to numerous phenological studies, covering a range of avian taxa, which have found that species migrating long-distances are more fixed in their timing of spring migration compared to short-to-mid-distance migrants, both in response to long-term climate change (Hagan et al. 1991, Murphy-Klassen et al. 2005, Miller-Rushing et al. 2008, Rubolini et al. 2010) and year-to-year changes in environmental conditions (Rainio et al. 2006, La Sorte et al. 2016). However, these phenological studies are inter-specific comparisons focusing either on population means or ‘first individual’ observations, rather than examining individual-level variation using repeated measures. Similar to our study, Verhoeven et al. (2019) found no influence of winter region on intra-individual variation in migration timing. High intra-individual variation has also been reported for some long-distance migrants (e.g. Fraser et al. 2019), but not all (e.g. Conklin et al. 2013), providing poor support for a general trend for fixed migratory behaviour in long-distance migrants at the individual-level. This highlights the importance of integrating individual- and population-level data to better understand the
mechanisms and implications of how species react to changing climates (Visser et al. 2010).

While long distance migrants may not have reliable cues regarding remote environmental conditions, they may still adjust their migratory behaviour to changes in their intrinsic state or local conditions. Therefore, similar behavioural variability across individuals migrating different distances does not mean all migrants can respond equally well to environmental variation on short or long timescales. To draw such conclusions, deviations from an individual’s strategy should be correlated with changes in environmental conditions in breeding areas. Indeed, our study is limited by our inability to relate movement to a single preferred resource, as can be done for dietary specialists (Van der Graaf et al. 2006, Thorup et al. 2017, Abrahms et al. 2019). In the future, a better understanding of the underlying motivation and environmental cues gulls use to inform migratory behaviour would help further elucidate the mechanisms underlying migratory decision making in this species.

Given the readily accessible environmental information available to the shortest distance migrants, it is particularly surprising that we still observed individual consistency in space and time. Conditions on wintering areas are typically thought to be less reliable at higher latitudes (Danner et al. 2013), favouring behavioural flexibility and innovation in short-distance migrants (Sol et al. 2005). However, while availability of marine and terrestrial resources may be scarce at high latitudes during the winter, some anthropogenic resources (e.g. waste treatment centres) remain dependable year-round. Such consistency in the environment may limit the need to be plastic, instead favouring reliance on past experience leading to high site fidelity on even fine spatial scales such as we observed. Learned patterns and consistency may be a generally favourable strategy for species utilizing reliable and abundant anthropogenic resources.

**Conclusions**

Due to the challenge migrants face of determining when and where to move without comprehensive knowledge of environmental conditions at remote destinations, concern has been raised regarding whether migrants, particularly long-distance migrating species who are thought to be more fixed in their behaviour, can sufficiently adjust migratory behaviour to human-induced environmental change (Møller et al. 2008, Saino et al. 2011). Lesser black-backed gulls demonstrated consistent individual differences in migratory behaviours, suggesting a preference for relying on past conditions to guide movement, and we found no consistent influence of migration distance on intra-individual variation. Use of consistent strategies, even by individuals migrating short-distances who presumably have reliable information regarding current conditions, suggests that familiarity with a strategy may be
preferential to trying to track optimal conditions. While this may apply to species who use resources that are predictable year-round, such as anthropogenic resources (Riotte-Lambert and Matthiopoulos 2020), in unpredictable systems a consistent strategy may be detrimental (Abrahms et al. 2018). Importantly, despite an apparent preference for consistency, individuals, regardless of their migration distance, can vary behaviour within the confines for their individual strategies, and occasionally even change strategies. We encourage further examination of the influence of migration distance on behavioural plasticity at the individual-level to determine how universal our findings are, as well as extending this research to systems where behavioural variation can be linked with environmental variables to assess whether observed behavioural variation is equally adaptive across migration distances.

Acknowledgements

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Supplementary Materials for Chapter 2

**Figure S2.1.** Examples of relatively low (left) and high (right) nonbreeding distribution overlap for short (top), mid (middle) and long distance migrants (bottom). The 25, 50, 75 and 95% contours are delineated. The 50% contour used to identify core areas are shaded and outlined by the thicker line. The twice daily subsampled points used to make the utilization distributions are shown. Contours and points are coloured by season. The device number (id) and overlap are reported above each plot.
Methodology: Calculation of mean routes

Original (non-subsampled) GPS tracks were separated into autumn (from colony departure to arrival at the wintering area) and spring routes (from departure at the wintering area to colony arrival). GPS points between the entrance and exit from a core area (stopovers) were replaced with a single point at the polygon centroid (Fig S2.1a), smoothing the route. Any migration route with either a gap longer than 24 hours when an individual was outside of a core area (i.e. during migratory flights) or fewer than 10 GPS points remaining on the route were removed. Individuals that did not overlap in their wintering area (n = 5) were excluded from this analysis due to inability to compute a mean route. This resulted in a sample size of 58 individuals in autumn and 69 in spring.

Five-hundred points were created along each GPS route at equally spaced distances (Fig. S2.1b). To begin computing the mean route, point $i$ on the mean route was placed at the mean latitude and longitude of the $i^{th}$ points from the actual migration routes, resulting in 500 generated points (Fig. S2.1b). Each point along the mean route was then moved to the mean location of the nearest-neighbour points within ±1° of latitude on the GPS routes (Fig. S2.1c). The latitude range was created because, for c-shaped routes, such as around the Iberian Peninsula or Bay of Biscay, the nearest neighbour points for the mean route converge on the two points at the mouth of the sea, instead of capturing the shape of the route. Depending on the shape of the migratory routes, mean points may still converge to the same location. If points along the mean route became separated by more than 25 km, a new point was created midway between those two points (Fig S2.1d). Position averaging and adding of points continued for a total of 100 iterations, resulting in a mean route minimizing the mean squared distance between the GPS tracks (Fig. S2.1d).

Before calculating variance, 500 equally spaced points were placed along the mean route (total number of points and distances between them become uneven during the computing process). Variance was calculated for each point along the mean route using the distances between the points on the mean route and the nearest-neighbour points on the GPS route (Fig S2.1e).
Figure S2.2. An example of how mean routes were computed. Here two deviating routes were used for clarity, though this procedure can be applied to any number of routes. a) The GPS tracks (small points along a line) and core areas (shaded polygons) from ID 5524 during autumn. GPS points within the core area polygons were removed to create a smoothed route. Colour represents different years. Rectangle indicates area shown in b-d. b) A zoomed in section of the routes along which 100 equally spaced points were placed (500 points were used in actual analysis), and the beginning positions of the mean route (centre line). Points are coloured sequentially, such that the colour of the points along the GPS route that were averaged together correspond. Large points connected by lines indicate which points along the GPS tracks were averaged to create the mean route. Faded lines connecting large points on the mean track indicate the nearest-neighbour locations on the GPS track to these points. c) Location of mean route following 1 iteration, with solid line connecting the GPS points averaged to determine the position of select points along the mean route. The original mean route with nearest-neighbour points are indicated by faded points and lines. New points (blueish-green) were added if points along the mean route were separated by more than 25 km. d) The final mean route, after 100 points were equally placed along the route (500 points used in actual analysis). Points on the mean route are coloured based on their variance (low = purple, high = yellow). Lines indicate the distances between mean route and GPS routes used to calculate the variance for select points.
Table S2.1. The number of lesser black-backed gulls with a given number of nonbreeding seasons included in this study (post-processing). As the data processing steps differed depending on the behaviours, the number of individuals and seasons included differed between metrics based on the utilization distributions (and hence the wintering areas), thus migration distance, nonbreeding distribution overlap, and dates of departure and arrival (no gap longer than 21 days), and migration routes (no gap longer than 24 hours during migratory flights). On average 95% of days during a nonbreeding season had a GPS fix (range: 55-100%), and a total of 129 nonbreeding seasons had at least 1 GPS fix per day.

<table>
<thead>
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<th>Number of Seasons</th>
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</tr>
<tr>
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<tr>
<td><strong>Total</strong></td>
<td><strong>82</strong></td>
</tr>
</tbody>
</table>

Figure S2.3. A comparison of a) nonbreeding season distribution overlap, b) autumn route variation and c) spring route variation within versus between individuals. Differences between the categories (variation ‘between’ and ‘within’ individuals) were highly significant in all three cases, with p < 0.001 based on randomisation tests. The y-axis for autumn and spring route variation (b and c) is reversed so that the direction of variation is consistent with Fig. S2.3a and Fig 2.2 in the main manuscript.
Figure S2.4. Examples of relatively high (left) and low (right) route variation for short (top), mid (middle) and long distance migrants (bottom). Black paths show GPS migration routes and mean route is coloured based on variation (scale differs per plot). The device number (id) and mean variation are reported above each plot.
Table S2.2. Linear mixed model results for arrival and departure dates against migration distance with individual and colony as random effects. T-values are reported in brackets for fixed effects. Colony variance is the variance of the colony-level random effect, and individual variance is the variance of the individual-level random effect. Number of observations, n, and number of individuals, n_id used in the models are reported under each behaviour. Numbers differ because some individuals were removed due to gaps coinciding with departure or arrival time.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Intercept ± SE</th>
<th>Migration Distance (1000 km) ± SE</th>
<th>Colony variance</th>
<th>Individual variance</th>
<th>Residual variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony Departure</td>
<td>210.77 ± 5.51</td>
<td>1.73 ± 2.27 (t = 38.25)</td>
<td>43.12</td>
<td>410.65</td>
<td>357.63</td>
</tr>
<tr>
<td>n = 227, n_id = 79</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter Arrival</td>
<td>291.72 ± 6.47</td>
<td>-</td>
<td>44.88</td>
<td>2430.72</td>
<td>698.14</td>
</tr>
<tr>
<td>n = 225, n_id = 78</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter Departure</td>
<td>62.74 ± 3.41</td>
<td>4.55 ± 1.16 (t = 18.40)</td>
<td>35.84</td>
<td>134.06</td>
<td>61.55</td>
</tr>
<tr>
<td>n = 229, n_id = 80</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colony Arrival</td>
<td>63.16 ± 3.21</td>
<td>11.10 ± 1.04 (t = 19.67)</td>
<td>36.41</td>
<td>108.37</td>
<td>46.15</td>
</tr>
<tr>
<td>n = 229, n_id = 80</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure S2.5. Histograms of a) nonbreeding season overlap, b) wintering area site fidelity, c) autumn route variation, d) spring route variation, e) Individual-level repeatability ($R_i$) of departure date from colony, f) $R_i$ of arrival date to wintering area, g) $R_i$ of departure date from wintering area and h) $R_i$ of arrival date to colony. Lines indicate the 95th percentile used to identify the most variable individuals in Table S4. Note: x-axis in plots c and d are reversed so that the most variable individuals are on the left, consistent with the other subplots.
Table S2.3. Individuals (device number) in and above the 95th percentile for each measure of variation in the indicated behaviour. Individuals that were among the most variable for multiple behaviours are in bold. Asterisks indicate individuals that did not overlap in their wintering area in one year. All values for overlap and repeatability ($R_i$) range from 0 (high variation) to 1 (no variation).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Individual</th>
<th>Individual overlap/variability/repeatability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5593*</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>5027*</td>
<td>0.69</td>
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<tr>
<td>Nonbreeding distribution overlap</td>
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<td>0.73</td>
</tr>
<tr>
<td></td>
<td>854</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>1400</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>606*</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>1402*</td>
<td>0.00</td>
</tr>
<tr>
<td>Winter area site fidelity overlap</td>
<td>5593*</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>5555</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>478</td>
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<tr>
<td>Autumn Route Variability (km)</td>
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</tr>
<tr>
<td></td>
<td>4024</td>
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<td></td>
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<td>Spring Route Variability (km)</td>
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<td>5009</td>
<td>121 km</td>
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<tr>
<td></td>
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<td>112 km</td>
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<td></td>
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<tr>
<td></td>
<td>854</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>833</td>
<td>0.33</td>
</tr>
<tr>
<td>R$_i$ of colony departure date</td>
<td>4047</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>484</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>853</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>1402*</td>
<td>0.265</td>
</tr>
<tr>
<td>R$_i$ of winter arrival date</td>
<td>606*</td>
<td>0.349</td>
</tr>
<tr>
<td></td>
<td>5027*</td>
<td>0.422</td>
</tr>
<tr>
<td></td>
<td>534*</td>
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<tr>
<td></td>
<td>606*</td>
<td>0.337</td>
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<td>1402*</td>
<td>0.381</td>
</tr>
<tr>
<td>R$_i$ of winter departure date</td>
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<td>0.37</td>
</tr>
<tr>
<td></td>
<td>5334</td>
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<tr>
<td></td>
<td>503</td>
<td>0.35</td>
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<tr>
<td></td>
<td>608</td>
<td>0.51</td>
</tr>
<tr>
<td>R$_i$ of colony arrival date</td>
<td>1400</td>
<td>0.53</td>
</tr>
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<td></td>
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<td>0.55</td>
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<td></td>
<td>5550</td>
<td>0.546</td>
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Figure S2.6. a) Residual non-breeding distribution overlap, and residual migration route variation in b) autumn and c) spring across multiple non-breeding seasons from lesser black-backed gulls, versus their mean migration distance. Please note: the y-axis for autumn and spring route variation (b and c) is reversed so that the order of variation is consistent (less variation at the top of the plot). Black line showing trend predicted by the linear models were included if significant. Negative residuals in figures b and c mean that within-individual variation is lower than between individual variation. Individuals who changed wintering areas (n = 5) have been excluded.
CHAPTER 3

Acceleration as a proxy for energy expenditure in a facultative-soaring bird: comparing dynamic body acceleration and time-energy budgets to heart rate

J. Morgan Brown, Willem Bouten, Kees C. J. Camphuysen, Bart A. Nolet, Judy Shamoun-Baranes

Submitted Manuscript
Abstract

1. Energy expenditure is a unifying currency in animal ecology, used for assessing the consequences of different behavioural strategies, life-history events, or environments. Animals can also influence their energy expenditure through instantaneous behavioural responses to changes in their external environment. Thus, measuring energy expenditure of free-ranging animals at high temporal resolutions and across seasons is useful. The heart rate method has historically been used for this, but requires invasive surgery. Dynamic body acceleration (DBA) is an alternative proxy that is simpler to deploy, yet few studies have examined how it performs for species using different locomotory modes, particularly for passive locomotion like soaring flight.

2. We measured DBA alongside heart rate in free-ranging lesser black-backed gulls, a seabird that moves using flapping flight, soaring, and walking, and rests on both land and water. Our objectives were to compare the relative changes in DBA and heart rate among and within behaviours and to examine how accelerometers can be used to estimate daily energy expenditure by comparing DBA to time-energy budgets.

3. DBA and heart rate were sampled at 2.5 and 5 min intervals throughout the breeding season, though measurements were not synchronised. Behaviour was identified from accelerometer measurements, and DBA and heart rate were averaged over bouts of consecutive behaviour. Heart rate was converted to metabolic rates using an allometric calibration, after confirming its fit using metabolic measurements taken in captivity and values from existing literature.

4. Both proxies showed similar changes among behaviours, though DBA overestimated costs of floating, likely due to waves. However, relationships between DBA and heart rate were weak within a behaviour mode, possibly due to a lack of synchrony between our measurements.

5. On daily scales, DBA and time-energy budgets perform comparably for estimating daily energy expenditure. Accelerometry methods deviated from a 1:1 relationship with heart rate because acceleration could not measure variation in resting metabolic costs.

6. We conclude DBA functions well as a proxy for energy expenditure in species using different locomotory modes, including soaring flight. We discuss scenarios where one method (DBA versus time energy-budgets) may be preferred for estimating daily energy expenditures.
Chapter 3 - Acceleration as a proxy for energy expenditure

Introduction

Living organisms constantly expend energy. Energy is used to fuel resting processes such as basal metabolism, thermoregulation, production (e.g. growth, body maintenance), and digestion, as well as physical activity (e.g. locomotion). The balance between energy gain and use determines an individual’s ability to survive, grow, and reproduce, and thus energy is considered to be a unifying currency in biology (McNamara and Houston 1996, Ricklefs 1996, McNab 2002). In animal ecology, determining patterns of daily or seasonal energy expenditure can reveal the consequences of inhabiting different environments or employing different behavioural strategies (Anderson and Jetz 2005, Careau and Garland 2012), as well as exploring how energy requirements vary throughout the year or between life-history stages (Rotics et al. 2016, Dunn et al. 2020). Organisms can also influence their daily energy expenditures (DEE) through fine-scale responses to their environment. For example, animals may be able to reduce energy expenditure by avoiding landscape features that increase locomotion costs (Shepard et al. 2013), or by moving at times when environmental conditions facilitate passive movement (Gibson 2003, Shamoun-Baranes et al. 2016). As such, measuring metabolic rates of free-ranging animals at both high temporal resolutions and continuously throughout the annual cycle provides a mechanistic explanation of the internal and external drivers influencing the ecology, behaviour and evolution of species (Tomlinson et al. 2014).

Several proxies have been developed to estimate metabolic rates in free-ranging animals, including mass loss, isotopic turnover (e.g. doubly-labelled water technique), heart rate ($f_h$), dynamic body acceleration (DBA), and time-energy budgets (reviewed by Elliott 2016). Of these techniques, only $f_h$ and DBA have the capacity to both detect near-instantaneous changes in energy expenditure (i.e. resolutions of several seconds; Bishop et al. 2015), while being remotely monitored so that energy expenditure can be continuously measured at seasonal or annual time-scales (Green et al. 2009a, Flack et al. 2016).

Measuring $f_h$ in the wild for long periods typically requires surgical implantation, making it invasive and logistically challenging in field conditions. The $f_h$ method relies on the Fick’s equation, which states that rate of oxygen consumption ($\dot{V}O_2$) is equal to the product of heart rate and the $O_2$ consumed by the animal per heartbeat. Heart rate is therefore only a partial measure of oxygen uptake from the blood, thus the relationship between $f_h$ and $\dot{V}O_2$ in an individual can change with, for example, body mass, heart volume, activity mode, and stress (Green 2011). As such, derivation of energy estimates from $f_h$ typically requires species and activity specific calibrations (Green 2011). When measured alone, $f_h$ provides limited information regarding activity mode, though coarse identification of resting and active periods might be possible (Pelletier et al. 2007, Green et al. 2009b).
Dynamic body acceleration is measured via tri-axial accelerometers, which can be incorporated into existing bio-logging devices, and thus require no additional effort or invasive protocols to deploy. DBA is the sum of the dynamic acceleration along three axes of the body (Yoda et al. 2001, Wilson et al. 2006). Acceleration is achieved through mechanical work performed by muscles, which should be proportional to the amount of energy being used to move (Gleiss et al. 2011, Halsey et al. 2011a). As such, DBA does not provide information on fluctuations in resting metabolic rate, unless these changes are accompanied by some form of acceleration (e.g. shivering; Green et al. 2009a, Hicks et al. 2017, Wilson et al. 2019). Further, the efficiency with which mechanical work can be fuelled by chemical energy can differ depending on the mode of locomotion, thus behaviour-specific calibrations are likely needed (Halsey et al. 2011b, Gómez Laich et al. 2011). Accelerometers can also detect environmental acceleration (e.g. from wind or waves), which may bias energy estimates during passive forms of locomotion (e.g. soaring flight) or in certain environments (e.g. waves while floating).

In addition to being applied as a measure for fine-scale changes in energy expenditure, DBA has been demonstrated to be a good predictor of DEE (Elliott et al. 2013, Stothart et al. 2016, JeanniardduDot et al. 2017, Sutton et al. 2021). These validation studies, comparing average DBA to field metabolic rates determined using doubly-labelled water, typically conclude that behaviour-specific DBA calibrations significantly improve the accuracy of estimating DEE in species that use a range of locomotory modes. Instead of calculating DBA, acceleration patterns can also be used to identify different behaviours (e.g. locomotory modes), allowing for detailed partitioning of time between activities. A constant energetic cost can then be assigned to each behaviour, either measured in captivity or based on biomechanical models or allometric relationships, which can be integrated in time to estimate DEE (i.e. a time-energy budget, TEB). The TEB approach thus ignores changes in energetic costs within a behaviour caused by, for example, changes in speed or body mass (Pennycuick 2008), though circumvents the need for calibration relationships to interpret DBA.

The use of accelerometers is rapidly gaining popularity as an alternative method for measuring energy expenditure in free-ranging animals (Brown et al. 2013, Joo et al. 2020). However, while DBA has been successfully validated across a range of taxa for walking (Wilson et al. 2006, Halsey et al. 2009), the relationship between DBA and energy expenditure during other modes of locomotion has been less extensively explored, particularly for flapping and soaring flight (Hicks et al. 2017). Heart rate, having equally high temporal resolution and potential to record over extended time scales as accelerometers, presents a good standard against which we can assess the effectiveness of using acceleration as a proxy for energy expenditure on both fine- and daily- scales (Hicks et al. 2017).
In this study, we concurrently measure acceleration and $f_h$ on free-ranging lesser black-backed gulls (*Larus fuscus*), a seabird species that uses a range of locomotory behaviours (flapping flight, soaring flight, walking), and rests on both land and water. Heart rate is converted to metabolic rates using an allometric calibration equation (Bishop and Spivey 2013), the fit of which we confirmed using metabolic measurements of lesser black-backed gulls in captivity and expected values based on published literature. Our first objective is to examine how DBA corresponds to energy expenditure when measuring both across and within different behaviour modes in a wild setting, by comparing it to the $f_h$ method. This includes two parts: a) We compare the relative changes within both proxies among different behaviour modes (flapping, soaring, walking, floating, and resting on land). Here, both soaring flight (being a passive vs powered locomotory mode) and floating (being susceptible to environmental variation) are of particular interest as DBA may be less able to predict metabolic rate of these behaviours. We report average energetic costs of these behaviour modes, which can be used in TEB analyses. b) We examine the relationships between DBA and metabolic rate estimated from $f_h$, both separately within a behaviour, as well as across bouts of all behaviours. Our second objective is to determine how acceleration data can best be used to estimate DEE. To do so, we compared DEE from DBA and TEB methods to that from the $f_h$ method, using the average costs per behaviour and relationships between DBA and metabolic rate found in objective 1. We explore how variation in resting metabolic rate, based on daily minimum $f_h$, influences the relationship between $f_h$-based and acceleration-based estimates of DEE.

**Methods**

**Capture, tagging and implantation**

Four male and two female lesser black-backed gulls were captured during incubation using a walk-in trap between 28 – 31 May, 2019 in their breeding colony (Texel, the Netherlands, 53°00′N, 04°43′E). The birds were colour-ringed and measured, and solar-powered GPS trackers with tri-axial accelerometers (13.5 g, 5CDLe trackers, UvA Bird tracking system; Bouten et al. 2013) were attached to the back of the birds using a Teflon ribbon ‘wing harness’ (Thaxter et al. 2014). This GPS tagging method does not appear to impact breeding productivity (Kavelaars et al. 2018) or colony return rates (Thaxter et al. 2016), though nest desertion occasionally occurs after capture and handling of both tagged and untagged birds. Heart rate ($f_h$) was derived from electrocardiograms measured with implantable loggers (15 g, size M Stellar implants, TSE systems, www.tse-systems.com). Heart rate loggers were surgically inserted in the field under full anaesthesia immediately
following ringing and GPS attachment (see supplementary materials S3.1 for implantation methods).

GPS fixes, including location, altitude, instantaneous speed and direction, were recorded every 15 min within the colony, and every 5 min outside of the colony. Acceleration was recorded in 1 s segments at 20 Hz every 2.5 min as well as directly following each GPS fix. An electrocardiogram (ECG) was recorded for a 4 s interval at 500 Hz, with 82% of the data being collected at a 5 min interval, and the remainder at a 10 min interval. Because we used separate systems, acceleration and ECG measurements could not be synchronized.

Data was collected throughout the incubation and chick rearing periods. Base-stations in the colonies were used to remotely program recording schedules and download data. Long data gaps sometimes occurred in $f_h$ data as a result of breaking contact during download.

The combined weight of the GPS trackers and heart-rate loggers was 3.2 - 4.6 % of body mass. Five birds resumed incubation following release. The sixth bird abandoned its nest and no $f_h$ data was recovered. All six birds returned to the colony in 2020, demonstrating birds can successfully migrate and survive with these devices long term. As captured individuals will not re-enter traps during the same breeding season, we are trying to recapture individuals during subsequent breeding seasons to remove both devices. Currently three birds have been successfully recaptured and released following sensor removal.

**Processing of bio-logging data**

Overall dynamic body acceleration (ODBA) and vectoral dynamic body acceleration (VeDBA) were calculated as in Wilson et al. (2019). ODBA and VeDBA were highly correlated ($r = 0.999$). Since VeDBA has a theoretical mathematic basis, we used VeDBA for the final results (hereafter DBA). Heart rate was derived from ECG segments using either peak detection or fast-Fourier transforms on a filtered signal, depending on signal characteristics (see supplementary material S3.2 for full methodology).

Behavioural classifications were assigned to each accelerometer segment using a random forest classifier previously developed for lesser black-backed gulls (Shamoun-Baranes et al. 2016) which identifies nine behaviours based on metrics derived from the pattern of acceleration and GPS speed. Where no GPS fix was paired with an acceleration measurement, speed was interpolated in time from the GPS fix directly before and after. We combined classifications into six behaviour modes: flapping, mixed-flight, soaring, walking, floating and resting (see Table S3.1 for mapping of behaviour classifications).

As $f_h$ and DBA measurements could not be synchronized in time (see ‘Capture, tagging and implantation’), we identified bouts from periods where consecutive accelerometer measurements were classified as the same behaviour, and averaged DBA and $f_h$ over
the bout. Bouts were required to have a minimum of two $f_h$ measurements and three acceleration measurements, with point-to-point speeds appropriate to the behaviour (see supplementary material S3.3 for full methodology). Mixed flap-soar flight was excluded from the comparison of behaviour costs (Objective 1a). For analyses examining the relationship between $f_h$ and DBA at behavioural and daily scales (Objectives 1b and 2), mixed-flight segments with DBAs below the mean DBA during mixed-flight (0.492 g) were reclassified as soaring, and those above the mean DBA were reclassified as flapping. Bouts were then reprocessed to include these reclassified segments.

**Estimating energy expenditure**

A pilot study was carried out in captivity with four individuals in 2018, to ensure the suitability of heart rate implantation in the field situation, as well as to assess the possibility of calibrating $f_h$ and DBA to rate of oxygen consumption measured ($\dot{V}O_2$) with respirometry using treadmill and temperature challenges. Full methodology and results of the pilot study are in the supplementary material (S4).

From treadmill data ($n = 2$), we derived a linear relationship between DBA and $\dot{V}O_2$ of:

$$\dot{V}O_2 = (70.61 \pm 8.24) \cdot \text{DBA} + (10.86 \pm 1.92)$$

(± standard error, $r^2 = 0.94$, Fig. S3.1a) which we used to convert DBA to metabolic rate ($MR_{DBA}$) in the comparison of behaviour costs (Objective 1a).

We assessed the fit of the lab-derived $f_h$ calibrations by plotting $f_h$ measured in the field versus estimates of $\dot{V}O_2$ either estimated from DBA in the field (walking, this study), measured in captivity (resting, this study), estimated from related species (field metabolic rate, FMR), biomechanical models (flapping flight) or allometric equations (maximum metabolic rates, supplementary materials S3.5). The estimated $\dot{V}O_2$ from lab-derived $f_h$ calibrations fit the expected values poorly (Fig. S3.2). Combined with elevated heart rates in captivity relative to in the field (Fig. S3.3), this suggests the $f_h - \dot{V}O_2$ relationship was decoupled by stress.

Therefore, we used a general allometric relationship between $\dot{V}O_2$ and $f_h$ reported from 24 species of birds and mammals exercising in their primary mode of locomotion (equation 9 in Bishop and Spivey 2013):

$$\dot{V}O_2 = 0.0402 \cdot M_h^{0.328} \cdot M_h^{0.913} \cdot f_h^{2.065}$$

(3.2)
where $M_b$ is the body mass and $M_h$ is the heart mass in kg. For $M_b$ we used the body mass measured at capture. We assumed $M_h = 0.010 \cdot M_b$ based on the mean $M_h$ to $M_b$ ratio reported for five species in the *Larus* genus (Magnan 1922, Crile and Quiring 1940, Hartman 1961). This allometric relationship fit the expected values well for most behaviours, though may underestimate $\dot{V}O_2$ for the lowest measured $f_h$ (supplementary materials S3.5 and Fig. S3.2). Overall we conclude that equation 3.2 is a reasonable approximation for shape of the $f_h - \dot{V}O_2$ relationship and was therefore used to estimate energy expenditure from $f_h$. $\dot{V}O_2$ estimated from DBA and $f_h$ using equations 3.1 and 3.2 were converted to a metabolic rate ($MR_{DBA}$ and $MR_{hr}$, respectively, in W) assuming 19.8 J ml$^{-1}$ O$_2$ (Bartholomew 1982), based on a respiratory quotient of 0.71 (supplementary materials S4).

**Data Analysis**

Linear models (LMs) were the primary statistical test used to compare among proxies. Typically mixed models are employed to control for individual effects, however, due to the low number of individuals, estimates of individual random effects were sometimes singular. Instead, individual was included as a fixed effect, and the data were centred over the individual factor so the model intercept falls at the group centre (Schielzeth 2010). For LMs without convergence issues, Akaike’s information criterion (AIC; Burnham and Anderson 2010) usually indicated that it was more parsimonious to include individual as a fixed factor than a random effect, so we use fixed factors throughout for consistency. Instead of reporting parameters estimated for all levels of the individual factor, we report standard deviation of individual intercepts. To account for potential effects of post-surgical recovery on $f_h$, the four days following surgery were excluded from analyses. All analysis was performed in R version 4.0.2.

**1a. Comparison of DBA to heart rate: Relative changes among behaviours**

To compare the relative changes in DBA and $f_h$, $MR_{hr}$ and $MR_{DBA}$ among bouts of flapping, soaring, walking, floating and resting, the proxies and estimated MRs were used as the response variable in a LM with behaviour and individual as fixed factors. Significant differences between behaviours within a given proxy were assessed for each method using Tukey’s post-hoc test.

**1b. Comparison of DBA to heart rate: Linear relationships**

$MR_{hr}$ of behavioural bouts was modelled as a function of DBA, behaviour mode, and their interaction, using LMs with individual as a fixed factor, to assess whether the relationship between DBA and energy expenditure changes across behaviours. AIC was used to assess the most parsimonious groupings of behaviours (i.e. whether some or all
behaviours demonstrate the same DBA - MR$_h$ relationship). To examine the relationship within a behavioural mode, we used separate LMs of MR$_h$ as a function of DBA per behaviour, including individual as a factor.

2. Using acceleration to estimate DEE

To examine how acceleration can best be used to estimate DEE, we averaged MR$_h$ over the course of a day (Portugal et al. 2016), weighted by the interval between $f_h$ measurements, to obtain an average daily metabolic rate (DMR$_h$). We then estimate DMR from four acceleration-based methods. Method 1 converts DBA to MR using a single calibration relationship across all behaviours (DBA$_{single}$) and method 2 uses behaviour-specific calibrations to convert DBA to MR (DBA$_{behave}$). The LMs calculated in section 1b were used for these conversions. Method 3 estimates DMR using a TEB differentiating five behaviour modes (TEB$_{behave}$), and method 4 uses a simplified TEB only differentiating flight, floating and resting, such as can typically be reconstructed from GPS data (TEB$_{GPS}$). The mean MR$_h$ for each behaviour calculated in 1a and reported in Table 3.1 were used in TEB$_{behave}$. For TEB$_{GPS}$, a single cost of flight was estimated from the mean of MR$_h$ while flapping and soaring, weighted by the flap-soar ratio over the study (65.9% flapping). Walking was combined with resting and assigned the mean MR$_h$ while resting. Unclassified accelerometer measurements were excluded. Acceleration-based estimates of MR were averaged over the day and weighted by the time until the next acceleration measurement. In case of a data gap, only periods with both proxies were used in daily averages. Days with less than 12 hrs of coverage were discarded.

As both measurement methods contain error, we used major axis regression to examine whether the relationship between each accelerometry method and DMR$_h$ falls along the line of equality. Similarity between slopes and elevation were estimated using likelihood ratio tests comparing independently calculated slopes or elevation to a combined slope or elevation (Warton et al. 2006). Confidence intervals around predicted values were estimated by bootstrapping (n = 1000 resampled datasets). We also explored how daily minimum $f_h$ (as an indicator of variation in resting metabolic rate), calculated as the mean of the lowest three consecutive $f_h$ measurements per day, influenced DMR$_h$, the acceleration-based estimates of DMR, and their relationship.

**Results**

We collected a total of 1285 hrs of overlapping heart rate-accelerometer recordings. A summary of the individuals, number of bouts per individual, and their resting and
flapping heart rates are in the supplementary material (Table S3.2). Air temperatures during this period ranged between 11.1 - 32.7°C, within the thermal neutral zone for this species (supplementary material S4), and sea surface temperatures ranged between 12.3 - 18.6°C (ERA5; Hersbach et al. 2018).

Resting was the most common activity exhibited (63.3% of accelerometer measurements). Floating accounted for 8.7% of measurements, resulting in 71.9% of measurements being taken while inactive. Flapping flight was the most common form of locomotion (12.8% of measurements), followed by soaring (5.8%), walking (5.6%), and mixed flight (1.4%), with 2.4% of segments being unclassified.

1a. Comparison of DBA to heart rate: Relative changes among behaviours

A total of 1742 behaviour bouts were retained in the analysis. During flapping flight \( f_h \) was significantly higher compared to other behaviours (Tukey’s test: \( p < 0.001 \) for all comparisons, Fig. 3.1a). Heart rates for the remaining behaviours were more similar and overlapping. Walking had the next highest \( f_h \), followed by soaring, while floating and resting had similar \( f_h \) ranges. Heart rate while floating was statistically indistinguishable from soaring (\( p = 0.17 \)) and resting (\( p = 0.48 \)), but the other behaviours were significantly different (\( p < 0.02 \)). After converting to \( \text{MR}_{hr} \), walking remained significantly different from resting (\( p < 0.001 \)), though not from soaring or floating (\( p = 0.61 \) and \( p = 0.14 \)), and soaring and floating were not statistically different from resting (\( p = 0.23 \) and \( p = 0.12 \); Fig. 3.1c).

Changes in DBA (and \( \text{MR}_{DBA} \)) followed a similar pattern to \( f_h \) though with less overlap between behaviours: flapping was noticeably higher than all other behaviours, followed by walking, then soaring, and resting being lowest (all significantly different with \( p < 0.001 \), Fig. 3.1b). However, unlike \( f_h \), DBA while floating was significantly higher than resting (t-test: \( p < 0.001 \)), instead being similar to DBA during soaring (\( p = 0.89 \)).

The mean \( f_h \), DBA, and metabolic rates of each behaviour mode, along with their ratio to resting metabolic rate measured in captivity (\( \text{RMR}_{lab} = 4.59 \text{ W} \), supplementary material S3.4), are reported in Table 3.1. Mass-specific metabolic rates are reported in Table S3.3. Applying the DBA calibration derived while walking (eq. 3.1) to other behaviours severely underestimated the costs of flapping flight (Fig. 3.1c), and mean values while soaring and resting were also underestimated (differences of 1.5 and 2 W, respectively). This lab-derived calibration is not used further in this study.
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Table 3.1. Number and median and maximum durations (dur.) of behavioural bouts, along with mean (± standard deviation) heart rates ($f_h$) and DBA, and metabolic rates estimate from $f_h$ (MR$_{hr}$) and DBA (MR$_{DBA}$), per behaviour. Ratio to RMR was based on MR$_{hr}$ and the resting metabolic rate measured in the lab (RMR$_{lab}$ = 4.59 W).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>N. of Bouts</th>
<th>Med. Dur. (min)</th>
<th>Max. Dur. (min)</th>
<th>Mean. $f_h$ (beats min$^{-1}$)</th>
<th>Mean. DBA (g)</th>
<th>MR$_{hr}$ (W)</th>
<th>MR$_{DBA}$ (W)</th>
<th>Ratio to RMR$_{lab}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flap</td>
<td>290</td>
<td>15</td>
<td>119</td>
<td>360 ± 60</td>
<td>0.661 ± 0.052</td>
<td>32.0 ± 11.1</td>
<td>19.0 ± 1.2</td>
<td>7</td>
</tr>
<tr>
<td>Walking</td>
<td>75</td>
<td>12</td>
<td>49</td>
<td>200 ± 37</td>
<td>0.199 ± 0.036</td>
<td>8.5 ± 3.2</td>
<td>8.2 ± 0.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Soar</td>
<td>68</td>
<td>11</td>
<td>88</td>
<td>181 ± 37</td>
<td>0.123 ± 0.038</td>
<td>7.9 ± 3.8</td>
<td>6.4 ± 0.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Float</td>
<td>201</td>
<td>15</td>
<td>100</td>
<td>162 ± 44</td>
<td>0.121 ± 0.030</td>
<td>6.6 ± 3.8</td>
<td>6.4 ± 0.7</td>
<td>1.4</td>
</tr>
<tr>
<td>Rest</td>
<td>1108</td>
<td>27</td>
<td>396</td>
<td>160 ± 42</td>
<td>0.028 ± 0.021</td>
<td>6.2 ± 3.4</td>
<td>4.2 ± 0.5</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Figure 3.1. Violin and boxplots of a) heart rate, b) DBA, and c) metabolic rate estimated from each proxy (heart rate in purple and DBA in teal) for different behavioural modes (n = 1742 bouts). Violin plots outline kernel probability densities and boxplots show median and interquartile range (IQR) with whiskers denoting 1.5x IQR. Significant differences based on Tukey’s tests per proxy are indicated above boxplots (in c, differences between proxies were not tested, indicated by letter case).
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Table 3.2. AIC comparison and $r^2$ values of linear models of MR$_{hr}$ by DBA and behaviour, with all five behavioural classification used. All models include individual as a fixed factor.

<table>
<thead>
<tr>
<th>Model</th>
<th>Degrees of Freedom</th>
<th>Δ AIC</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>MR$_{hr}$ ~ DBA + Behaviour + DBA*Behaviour + ID</td>
<td>15</td>
<td>0.00</td>
<td>0.766</td>
</tr>
<tr>
<td>MR$_{hr}$ ~ DBA + Behaviour + ID</td>
<td>11</td>
<td>14.27</td>
<td>0.763</td>
</tr>
<tr>
<td>MR$_{hr}$ ~ Behaviour + ID</td>
<td>10</td>
<td>40.70</td>
<td>0.759</td>
</tr>
<tr>
<td>MR$_{hr}$ ~ DBA + ID</td>
<td>7</td>
<td>145.57</td>
<td>0.743</td>
</tr>
</tbody>
</table>

Table 3.3. Results of linear models between MR$_{hr}$ and DBA with individual included as a fixed factor, for each behavioural mode as well as when combining across all behaviours. Intercept was centred over the individual factor. Standard deviation of the estimated individual factor parameters is reported. t- and p-values are given for the slope.

<table>
<thead>
<tr>
<th>Behaviour (DF)</th>
<th>Intercept (95% CI)</th>
<th>Individual SD</th>
<th>Slope (95% CI)</th>
<th>t-value</th>
<th>p-value</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flapping (295)</td>
<td>24.51 (11.45 – 37.56)</td>
<td>3.34</td>
<td>10.82 (-8.70 – 30.34)</td>
<td>1.091</td>
<td>0.276</td>
<td>0.078</td>
</tr>
<tr>
<td>Walking (70)</td>
<td>5.74 (1.55 – 9.94)</td>
<td>0.54</td>
<td>14.19 (-6.55 – 34.92)</td>
<td>1.364</td>
<td>0.177</td>
<td>0.047</td>
</tr>
<tr>
<td>Soaring (79)</td>
<td>6.76 (1.55 – 9.94)</td>
<td>0.54</td>
<td>10.63 (-2.32 – 23.57)</td>
<td>1.633</td>
<td>0.106</td>
<td>0.047</td>
</tr>
<tr>
<td>Floating (195)</td>
<td>6.66 (4.53 – 8.78)</td>
<td>2.75</td>
<td>-0.16 (-17.21 – 16.89)</td>
<td>-0.019</td>
<td>0.985</td>
<td>0.163</td>
</tr>
<tr>
<td>Resting (1102)</td>
<td>4.80 (4.50 – 5.09)</td>
<td>1.34</td>
<td>49.80 (41.21 – 58.39)</td>
<td>11.371</td>
<td>&lt; 0.001</td>
<td>0.195</td>
</tr>
<tr>
<td>Combined (1766)</td>
<td>4.38 (4.07 – 4.70)</td>
<td>1.54</td>
<td>39.89 (38.78 – 41.00)</td>
<td>70.586</td>
<td>&lt; 0.001</td>
<td>0.743</td>
</tr>
</tbody>
</table>

1b. Comparison of DBA to heart rate: Linear relationships

The top LM for predicting MR$_{hr}$ based on AIC includes an interaction between behaviour and DBA, indicating that the relationship between DBA and MR$_{hr}$ changes depending on the behavioural mode (Table 3.2, Fig. 3.2). Grouping behavioural classes did not increase parsimony, with the top ranked model including all five behavioural modes (Table S3.4). DBA without any behaviour-specific adjustments was positively correlated with MR$_{hr}$ ($r^2$ = 0.743, expected given similarity in relative changes among behaviours, Fig. 3.1), though this was the lowest performing model. The model including just behaviour classification explained slightly more variation in MR$_{hr}$ than that with only DBA, suggesting DBA did
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Figure 3.2. MR$_{hr}$ versus DBA of behavioural bouts (n = 1772). Centred intercept and slope of linear models per behaviour are represented by coloured lines, and across all bouts by the dashed black line (p < 0.001, $r^2 = 0.743$). Model parameters and statistics are reported in Table 3.3.

not improve upon using a single cost per behaviour (Table 3.2). Moreover, when the MR$_{hr}$ - DBA relationship was considered separately for each behaviour, MR$_{hr}$ and DBA were poorly correlated for most behaviours (Table 3.3). Only resting had a significant positive relationship between MR$_{hr}$ and DBA, while other behavioural modes had no significant relationship (Fig. 3.2, Table 3.3). Plots of MR$_{hr}$ versus DBA per behaviour along with confidence intervals and individual intercepts are in supplementary material (Fig. S3.4).

2. Using acceleration to estimate DEE

Sixty-nine bird-days had coverage from both proxies for more than 12 hrs. DMR estimated by any acceleration method increased significantly with DMR$_{hr}$ (MA slope: p < 0.001). Slopes between methods did not significantly differ (LRT: df = 3, p = 0.08) but elevations did (LRT: df = 3, p < 0.001). DBA$\text{single}$ consistently overestimated DMR relative to DMR$_{hr}$ (Fig. 3.3a, Table 3.4). The other three models, DBA$\text{behave}$, TEB$\text{behave}$, and TEB$\text{GPS}$ resulted in similar DMR estimates, with models overlapping in their 95% confidence
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Intervals throughout the range of data (Fig. 3.3a). Slopes of these models fell between 0.55 - 0.69, underestimating DMR on days with high DMR$_{hr}$, and overestimating on days with low DMR$_{hr}$. TEB$\_GPS$ explained less variation in DMR$_{hr}$ than the other acceleration methods.

To understand why the acceleration methods had slopes shallower than a 1:1 relationship with DMR$_{hr}$, we explored the influence of daily minimum $f_h$ on our DMR estimates. Minimum $f_h$ was positively correlated to DMR$_{hr}$ ($r = 0.29$), but not to the acceleration estimates ($-0.18 < r < -0.05$ for all methods). As such, days with high minimum $f_h$ tend to be days with high DMR$_{hr}$, and days with high minimum $f_h$ tend to fall below the line of equality (i.e. underestimated by acceleration), and vice versa (see Fig. 3.3b-d for an example using DBA$\_behave$ for other acceleration methods see Fig. S3.5 in supplementary material). Thus, the limited ability of acceleration methods to detect variation in resting metabolic rates partially explains why the slope of the relationship between DMR$_{hr}$ and DMR estimated from acceleration is shallower than the line of equality.

Table 3.4. Summary of major axis regression models of daily metabolic rate estimated from acceleration-based measures of energy expenditure (DBA and time-energy budgets) versus estimated from heart rate. DBA$\_single$ is DBA calibrated with a single relationship across all behaviours, DBA$\_behave$ is calibrated with behaviour-specific relationships, TEB$\_behave$ is a five-behaviour time-energy budget and TEB$\_GPS$ is a simplified time-energy budget that could be reconstructed using only GPS data.

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept (95% CI)</th>
<th>Slope (95% CI)</th>
<th>Model r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBA$_single$</td>
<td>3.59 (1.58 – 5.59)</td>
<td>0.86 (0.68 – 1.08)</td>
<td>0.54</td>
</tr>
<tr>
<td>DBA$_behave$</td>
<td>2.26 (0.70 – 3.82)</td>
<td>0.70 (0.56 – 0.87)</td>
<td>0.56</td>
</tr>
<tr>
<td>TEB$_behave$</td>
<td>2.89 (1.40 – 4.37)</td>
<td>0.64 (0.50 – 0.80)</td>
<td>0.54</td>
</tr>
<tr>
<td>TEB$_GPS$</td>
<td>3.65 (2.13 – 5.17)</td>
<td>0.55 (0.41 – 0.71)</td>
<td>0.4</td>
</tr>
</tbody>
</table>
Figure 3.3. a) Major-axis regressions of acceleration-based estimates of daily metabolic rates (DMR) versus daily mean metabolic rate from heart rate (DMR_{hr}). Methods include DBA converted to MR with a single relationship across all behaviours (DBA_{single}), DBA converted with behavior-specific calibrations (DBA_{behave}), a five-behaviour time-energy budget (TEB_{behave}) and a simplified time-energy budget that could be derived from only GPS (TEB_{GPS}). Acceleration methods are distinguished by colour. 95% confidence intervals are identified by the shaded regions with dashed lines. The line of equality is shown with a black line. b) A scatterplot showing the relationship between daily metabolic rates estimated DBA_{behave} versus DMR_{hr}. Points are coloured by daily minimum heart rate (min. f_{hr}). Major-axis regression line with 95% confidence intervals is shown in pink. The line of equality is shown in black. c) Boxplots showing distribution of min. f_{hr} on days in plot b that fall above and below the line of equality. d) Boxplots showing distribution of min. f_{hr} on days where DMR_{hr} is below or above the mean DMR_{hr} (9.9 W). Scatterplots as shown in 3b for the other three methods can be found in Fig. S3.5 in supplementary material.
Discussion

While the use of DBA as an estimate of metabolic rate in free-ranging animals is becoming increasingly popular (Brown et al. 2013, Joo et al. 2020), few studies have investigated how well it functions across multiple behaviour modes in the wild, particularly at high temporal resolutions (Hicks et al. 2017) and in a species that uses a passive mode of locomotion such as soaring flight (Duriez et al. 2014). In this study, we measured DBA alongside \( f_h \) in five free-ranging lesser black-backed gulls. We found DBA generally suggested similar relative differences between behaviours as the \( f_h \) method, except during floating, which was overestimated by DBA. DBA was thus positively correlated to MR\(_{hr}\) when all behaviours are considered together, though correlations within a behaviour mode were insignificant. At a daily scale, DBA performed similarly to TEBs for predicting DEE, though did not follow a 1:1 relationship with \( f_h \) based estimates. This was at least partially due to undetected fluctuations in resting metabolic rates.

Comparison of DBA to heart rate

While accelerometry provides great potential for measuring energy invested into physical activity in the wild, many studies overlook the crucial step of determining the relationship between DBA and energy expenditure (Halsey and Bryce 2021). This is particularly important for systems where a range of behaviour modes and habitats are utilised, as variation in muscle efficiency and environmental noise may result in deviations from a single linear fit (Gómez Laich et al. 2011). In our study, the relative changes in both proxies among behaviour modes were generally similar, with the exception of floating which was overestimated by DBA.

We were particularly interested in whether DBA would properly represent energy expenditure while soaring. During soaring flight, animals capture rising air with wings held out isometrically, manoeuvring using small adjustments to wing and tail position (Gillies et al. 2011). As isometric muscle contractions do not result in acceleration, DBA cannot detect the work done by the animal (Gleiss et al. 2011). Instead much of the measured acceleration is likely resulting from air turbulence. However, DBA and \( f_h \) both showed similar relative differences between soaring and other behaviours, falling between walking and resting. This suggests that environmental acceleration is similar to energy required to statically control wing position, though this may be subject to deviations under different wind conditions or soaring styles (e.g. orographic, thermal and dynamic soaring). Two other studies that record DBA and \( f_h \) simultaneously in obligate soaring birds also found a good relationship between DBA and \( f_h \) during flight (Duriez et al. 2014, Weimerskirch et al. 2016).
In contrast, we found that DBA during floating was higher than at rest on land, whereas $f_h$ was not significantly different between floating and resting. Higher DBA is presumably due to added acceleration from waves. When environmental acceleration may influence DBA estimates, calibrating DBA in the environment which it is being used could partially correct this bias, for instance we found floating has a higher intercept than resting on land. However, this cannot account for spatial or temporal variation in environmental conditions, such as differences in wave action across various bodies of water and weather conditions. From a physiological stand point, it is interesting that we found no significant difference between $f_h$ on land and on water. Metabolic rates of diving and floating animals are often elevated because water has higher thermal conductance and a greater specific heat capacity than air, requiring more energy to maintain body temperature (Bevan et al. 1995, Humphreys et al. 2007). Our results suggest that there is no increased thermoregulatory costs of resting on water at temperatures above 12°C in lesser black-backed gulls.

Corresponding with similar relative changes in both proxies among behaviours, when all behaviour bouts were pooled, we found that DBA was positively correlated with $MR_{hr}$. However, the top model for predicting $MR_{hr}$ from DBA of behavioural bouts included an interaction term between all five behavioural modes, indicating that the relationship between $MR_{hr}$ and DBA changes by behaviour. In line with our results, previous studies on diving seabird species have demonstrated that DBA tends to be a robust proxy when comparing across different behaviour modes, either by comparing it to the high resolution $f_h$ method (Hicks et al. 2017) or to the lower resolution doubly-labelled water method (Elliott et al. 2013, Stothart et al. 2016, Sutton et al. 2021), with the general consensus that behaviour-specific calibrations will improve estimation of energy expenditure. These studies focus on species that can use some or all of diving, terrestrial locomotion, and flapping flight, while our study now additionally adds an animal that can travel using soaring flight.

When comparing behaviour bouts within a single behaviour mode we did not find significant positive relationships between DBA and $MR_{hr}$. Due to the imperfect temporal pairing between $f_h$ and DBA, we cannot conclude whether this is because DBA ($or f_h$) do not properly depict changes in energy expenditure within a behaviour mode, or because gulls adjust their effort on finer-temporal resolutions than we could capture with our recording schedules. The latter is highly probable given the fluid flap-soar flight style of gulls. Even considering this we may still expect some average differences in effort between behaviour bouts. For example, gulls commuting over sea flap continuously along direct routes, where effort across the entire flight bout may vary depending on whether the bird is experiencing head-, tail- or crosswinds (McLaren et al. 2016), or with changes in body mass before and after foraging. The average effort while flapping during a commuting flight may likewise
differ from the effort during competitive interactions while foraging behind a fishing vessel or at a refuse site. Hicks et al. (2017), who also continuously recorded and compared DBA to energy expenditure estimated from $f_h$ in wild European shags *Phalacrocorax aristotelis* found positive relationships within a behaviour for flapping flight and resting, though not diving behaviour. They also had high error around their behaviour regression lines, though demonstrated that much of the error could be accounted for by the uncertainty around the $f_h$ to energy expenditure conversion, rather than necessarily originating from the DBA method.

Differences in body mass both among and within an individual can also influence overall energy expenditure, as well as the relationship between energy expenditure and both $f_h$ and DBA. The allometric $f_h$ equation and individual intercepts should account for some of the influence of among-individual differences in body mass on energy expenditure and the calibration relationships, though we cannot account for fluctuations of body mass within an individual over time, which can be substantial (i.e. following consumption of food during a foraging trip). Work, the mechanical equivalent of energy expenditure, is proportional to the product of body mass and acceleration (Gleiss et al. 2011). Thus, the slope of the relationship between DBA and energy expenditure should increase with body mass (i.e. a heavier mass will show a smaller increase in acceleration for a given increase in energy expenditure compared to a lighter mass; Halsey et al. 2009). As we have a small number of individuals with only a single body mass measurement each, we cannot properly account for the influence of body mass in our study.

Overall, our comparison between DBA and MR$_{hr}$ across behaviour bouts suggests that DBA does perform reasonably well as a proxy for energy expenditure across a range of behaviour modes, including soaring flight. However, DBA did overestimate energy expenditure when floating on the water, likely as a result of environmental acceleration from waves. While within a behaviour mode we did not find significant, positive correlations between DBA and MR$_{hr}$, sources of methodological error may be obscuring our ability to detect these relationships. We encourage more validation studies with either continuous or synchronised recording of these methodologies at high temporal resolutions to determine the degree to which either $f_h$ or DBA can detect fine-scale variation in energy expenditure for various modes of locomotion.

**Using acceleration to estimate DEE**

On a daily scale, TEBs performed similarly for estimating DMR$_{hr}$ as DBA calibrated with behavioural interactions, while the DBA model without activity-specific calibrations consistently overestimated DEE. This is in contrast to validation studies comparing DBA to energy estimated from doubly labelled water in diving seabird species, where DBA
predicted total energy expenditure better than TEBs, at least when behaviour-specific slope parameters were estimated (Elliott et al. 2013, Stothart et al. 2016, Sutton et al. 2021). The slope of the relationship between acceleration-based estimates of DEE and the $f_b$ estimates was shallower than 1, which we demonstrate is at least partially caused by day-to-day fluctuations in resting rates which are better detected using the heart-rate method.

A simplified activity budget (TEB$_{GPS}$, where flight mode was pooled, had a comparable relationship with DMR$_{hr}$ as the complete TEB, albeit with more error. This was surprising given the large difference in energetic cost between soaring and flapping flight. This suggests that gulls were using a relatively similar flap-to-soar ratio throughout the study. However when comparing across season or locations, flap-soar ratio may become less predictable. For example, Flack et al. (2016) demonstrated that DBA during migration for white storks (Ciconia ciconia) migrating south of the Sahara was lower than those north of the Sahara, corresponding to increased thermal uplift facilitating soaring at lower latitudes. Metabolic rates estimated from DBA without a behaviour-specific calibration fell furthest from the line of equality, though its slope was similar and even slightly closer to a slope of 1 than the other methods. This suggests that uncalibrated DBA may still be useful to make qualitative comparisons across days. We caution that our finding may not be extrapolated to all systems. For example, JeanniardduDot et al. (2017) found DBA did not correlate with DEE in foraging fur seals unless behaviour-specific relationships were applied.

The predictive power of all models at the daily level ($r^2 = 0.48 - 0.56$) were lower than those reported in doubly labelled water studies (Elliott et al. 2013, Stothart et al. 2016, Sutton et al. 2021). Assuming activity compensates for resting metabolism, then the error caused by variation in resting metabolic rates when using acceleration-based methods will be more significant in a bird with low versus high activity levels. The gulls in this study spent on average 72% of the day in inactive behaviours (resting or floating). Thus, DBA may not perform as well in our system compared to animals with higher activity levels (or costs). Further, for both of our proxies we were relying on samples over the day rather than continuous recording. This adds additional sampling error to both of our proxies compared to other validation studies where DBA was recorded continuously and doubly-labelled water provides a cumulative estimate of energy expenditure covering the entire measurement period.

Given that detailed TEBs perform similarly to DBA at estimating DEE, there are situations where TEBs may be preferable: i) For studies examining how energy is partitioned among behaviours, TEBs can provide a clear link to the underlying cause behind variation in energy expenditure between individuals, habitats, or strategies (Sage et al. 2019). ii) For studies where the accelerometer is not located near the centre of mass (e.g.
neck collars, mounted to tail feathers), where DBA accuracy may be decreased (Wilson et al. 2019). Additionally, the TEB method can be used to compare energy expenditure across systems where different attachment methods have been used (Garde et al. 2021). iii) For species using activities which may be unduly influenced by environmental acceleration (e.g. floating).

DBA, however, is advantageous because it does not require categorising behaviour into discrete categories, leading to unknown or intermediate behaviours being discarded from TEBs. Also, if DBA is used without classifying behavioural modes, which typically requires raw acceleration profiles, it can be calculated on the tracker, reducing the amount of data collected per bout and thus permitting more frequent or longer recording periods (Nuijten et al. 2020). Note however, that this would preclude the use of behaviour-specific calibration equations. For studies spanning seasons or years, where body mass of animals may fluctuate systematically causing changes in activity costs, DBA should detect some of the resulting change in effort. Finally, the accuracy of the TEB approach depends on reliable estimates of the costs of various locomotory modes for the species of interest (Elliott 2016), which may not be available for all species.

None of the accelerometry-based methods accounted for variation in resting metabolic rates, as can be captured using the $f_h$ method. This is a drawback of all acceleration-based methods, particularly if the purpose is to quantify an absolute value of energy expenditure. However, while activity may be highly unpredictable, variation in resting costs such as thermoregulation, digestion, and production may be more easily modelled and added to activity costs measured via acceleration (Gleiss et al. 2011). Further, for questions relating to behavioural strategies and decisions making, where fluctuations in resting process may be independent of the behaviour being examined, acceleration-based methods are likely still suitable. Preferably, the combined use of $f_h$ and acceleration presents an opportunity to examine changes in both activity and resting costs throughout the year and across diverse environmental conditions (Grémillet et al. 2005, Bishop et al. 2015).

Acknowledgments

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Supplementary Materials for Chapter 3

S3.1: Implantation of heart rate loggers

The TSE Stellar implants typically have long flexible electrodes which need to be sutured into place. We modified the electrodes by shortening them and reinforcing them with silicone so that they did not require additional suturing, allowing for faster, lower impact surgeries.

Implantation surgeries were performed under sterile conditions by a licenced veterinarian. Birds were anaesthetised with isoflurane gas and local analgesics (Xylocaine and Lidocain) were administered around the incision site. The heart rate implants were inserted into the abdominal cavity via an incision along the linea alba, slightly caudal of the sternum with the antennas pointing cranially. The implants were held in place using non-absorbable sutures into the abdominal wall. Following surgery, the birds were given a short recovery period of around 10 minutes immobilized on the table following termination of isoflurane gas, and a further 10 -15 minutes in a small cage until behaviour returned to normal (head up, standing, alert and displaying aggression/escape behaviour), after which they were released. Explant surgeries followed the same protocol, cutting out the remaining suture material.

S3.2: Extracting heart rate from electrocardiograms

The TSE Stellar heart rate implants recorded an electrocardiogram (ECG) at 500 Hz for an interval of 4 s in the wild, and 6 s in captivity. For each ECG interval, the baseline was removed and the signal normalized. To derive heart rate, we took the first derivative of the signal and converted it to absolute values. A first order Butterworth bandwidth filter was then applied to the signal, using thresholds of 12 and 0.5 Hz (equivalent to 720 and 30 beats min\(^{-1}\) respectively, which were considered to be the highest and lowest possible heart rates for this species based on both literature and manual exploration of our ECG recordings).

We used two different methods to derive heart rate from the ECG signal: 1) by identifying high peaks created by the QRS complex, and 2) by extracting signal frequency using a fast-Fourier transform (FFT). To identify QRS peaks, the filtered signal was rescaled so that it ranged from 0 to 1. Peaks were identified as potential QRS candidates using two thresholds: 0.52 and 0.68, and the time between peaks was calculated. If heart rate was accelerating over the course of the 4s recording, no heart rate was calculated. If the maximum absolute mean deviation of the time between peaks is greater than 0.2s, the most deviated time is dropped. This helped control for missed QRS peaks or if other components of the ECG signal were past the threshold. The deviated peak distances were
dropped until all peak distance deviated by less than 0.2s or until fewer than 5 distances remained. The mean time between peaks was then calculated and used to calculate heart rate.

To extract the heart rate using FFT, the discrete Fourier transform was computed using a fast-Fourier transform algorithm. The single-sided amplitude spectrum was calculated by taking the absolute of the Fourier transform divided by its length and selecting the first half of the spectrum. Heart rate was determined based on the frequency of the highest peak in the amplitude spectrum that fell within the range of 35 and 1000 beats min⁻¹.

The peak distance method was preferred over the FFT method because it allows for more precision, and was used if the difference between heart rate calculated from the two different thresholds was low (indicating a reasonably clear signal) and if the result was within 20 beats min⁻¹ of the FFT result, otherwise the result from the FFT method was used.

S3.3: Processing behaviour bouts

To ensure no undetected flights occurred between accelerometer measurements during walking, floating, and resting bouts, if the bird moved between two GPS fixes with a net ground speed exceeding 2 m s⁻¹ (walking, floating) or 1 m s⁻¹ (resting), that bout was discarded (n = 115 removed). No speed limits were applied to flight modes or bouts with only one GPS fix. To reduce the influence of heart rate measurements that may have been taken while another behaviour was being performed between acceleration measurements, as well as elevated heart rates due to stress responses unrelated to energy expenditure, we removed all bouts with heart rate exceeding 1.5-times IQR for each behaviour (n = 16 bouts removed).

S3.4: Laboratory Vo₂ measurements and calibrations

Methods

Respirometry trials

Four lesser black-backed gulls (Larus fuscus) were captured in Den Helder, The Netherlands prior to the breeding season (1 May, 2018), using a leg noose. The birds were housed in outdoor aviaries nearby at the NIOZ, Texel, The Netherlands, to acclimate to captivity, and heart rate transmitters were implanted on 8 May, 2018 (two with TSE Stellar S transmitters, 8 g, and two with Star Oddi DST micro-HRT loggers, 3.3 g, https://www.staroddi.com/products/data-loggers/heart-rate-sensor-animals). Birds were ringed and
GPS-accelerometers (UvA-BiTS) were attached following the same methodology used in the field. The birds were driven to the NIOO in Wageningen, The Netherlands, on 16 May (~ 2 hours), where respirometry trials were conducted. They were housed indoors in individual cages (180 x 120 x 100 cm) with a large water bath for bathing and were fed an ad lib diet of fatty fish.

Individuals were used for one treadmill trial and one climate chamber trial each, performed between 8 – 13 June, 2018. Measurement days were arranged so that each individual had at least 1 rest day between trials. Individuals were given three trainings on the treadmill over a three-week period, with several rest days in between to reduce handling stress. During trials, rate of oxygen consumption \( \dot{V}_O_2 \), rate of carbon dioxide production \( \dot{V}_C O_2 \), water vapour pressure (WVP) and barometric pressure (BP) were measured using an open-circuit respirometer (Sable Systems FMS; https://www.sablesys.com/products/classic-line/new-fms-field-metabolic-system-classic/). Prior to every trial, the \( H_2 O \) and \( CO_2 \) sensors were zeroed using \( N_2 \) gas. The \( CO_2 \) sensor was spanned using a calibration gas (0.5% \( CO_2 \) + 99.5% \( N_2 \)). The \( O_2 \) sensor was spanned to 20.95% using outdoor air dried with Magnesium Perchlorate. Water was spanned as \( WVP = BP \times (20.95 - \%O_2_{wet})/20.95 \) (Lighton 2018).

For treadmill trials, birds were placed in a 56 x 39 x 42 cm polypropylene box with an open bottom, placed on a treadmill. Draught excluders were attached to the base of the chamber. A treadmill trial consisted of 4 stages: walking at 0.22 m s\(^{-1}\), 0.39 m s\(^{-1}\), 0.56 m s\(^{-1}\), and 0.56 m s\(^{-1}\) with an 8% incline. The order in which the tests were presented were randomized. For a test, the birds walked at the given speed and incline for 10 minutes, allowing the air in the chamber to equilibrate. Between walking trials, birds rested on the treadmill for 10 - 15 minutes to recover. Air was pulled through the respirometer at a rate of 15 L min\(^{-1}\) (measured using a mass-flow meter, FK – 100 Field, Sable systems). A subsample of air was drawn from the main flow, then pushed through the water vapour pressure sensor, \( CO_2 \) analyser and \( O_2 \) analyser in series. Ambient air was sampled before and after each stage of the trial as a baseline. A cardboard box was placed over the respirometer with a window at the top to calm and direct the birds forward. Acceleration was recorded throughout trials at 20 Hz in 16 s chunks every 32 s. Star Oddi loggers measured ECG at 500 Hz over 1.2 s chunks every 5 minutes. TSE Stellar transmitters recorded ECG at 500 Hz over 6 s chunks every 1 minute. Accelerometer data was measured at 20 Hz over 1.5 s chunks every 1 minute. Gas concentrations were averaged once air concentrations had reached equilibrium, approximately the final 2 minutes of each walking and resting stage.

For climate chamber trails, food was withheld for 12 h so that birds were in a post-absorptive state. Measurements were taken mid-morning through early afternoon, in the dark. Birds were placed in a smaller, 51 x 30 x 38 cm polypropylene box, placed
inside a climate chamber. Climate chamber trials started at room temperature, which was progressively lowered in steps of approximately 7°C to a minimum temperature of -15°C. Air temperature was recorded inside the respirometry box. Climate chamber air was drawn in through a small hole in the lid, and air from the respirometry box was drawn out from the base of the box, from the side the bird was facing. Air was pulled through the respirometer at a rate between 5-10 L min⁻¹. The ambient air used for baseline air concentrations was taken from within the climate chamber, but outside the respirometry box. For each step, once temperature in the respirometer reached an equilibrium, gas concentrations were measured for 15 – 45 min, and values over a steady portion of this period were used for analysis. Heart rate recording schedules were the same as used for treadmill trials.

Following respirometry trials, the birds were returned to Texel and released into a large outdoor aviary to collect measurement under more natural housing conditions for a week. The heart rate loggers were then surgically explanted by the veterinarian and GPS loggers removed (27 June), and the bird were released into the wild following an observation period in the aviary (3 July).

**Respirometer data processing**

Time lags between WVP, CO₂ and O₂ sensors were corrected visually. The partial pressures of O₂ and CO₂ were ‘dried’ by multiplying by BP/(BP-WVP). Baseline drift was corrected and O₂ spanned to 0.2095. Flow rate was ‘dried’ using (BP-WVP)/BP. \( \hat{V}_o \) was then calculated according to:

\[
\hat{V}_o = FR_{D}(O_2 - 0.2095 + CO_2)/(1-0.2095)
\]

and \( \hat{V}_{CO_2} \) was calculated as:

\[
\hat{V}_{CO_2} = FR_{D}(CO_2 - F_iCO_2) + F_iCO_2 \times \frac{CO_2}{1 + F_iCO_2}
\]

where \( FR_{D} \) is the dried flowrate in L min⁻¹, CO₂ and O₂ are the dried fractional concentrations measured from the chamber, and \( F_iCO_2 \) is the dried, fractional concentration of CO₂ measured from the ambient air (Lighton 2018). Plots of O₂ and CO₂ were examined to determine when gas levels reached an equilibrium, and values after this point until the end of the trial were averaged to produce a single \( \hat{V}_o \) and \( \hat{V}_{CO_2} \) value per temperature or treadmill test setting. Initial data analysis was performed in ExpeData (Sable Systems International), then mean \( \hat{V}_o \) and \( \hat{V}_{CO_2} \) data for each trial were input into a spreadsheet for subsequent analysis.
Data analysis

Heart rates from TSE stellar loggers were derived following methods in section S3.2. Heart rates from Star Oddi loggers are calculated onboard the logger along with a quality index, with only measurements within the two highest quality categories (0 and 1) being used in analysis.

The relationship between DBA and $\dot{V}O_2$ and heart rate and $\dot{V}O_2$ while walking on a treadmill appeared to be linear (Fig. S3.1). The $\dot{V}O_2$ during each treadmill speed was modelled as a function of the mean DBA value during that speed using a linear model (LM) with individual being included as a centred factor.

Climate trials were used to attempt resting calibrations for both DBA and heart rate, as well as to estimate the influence of ambient temperature on $\dot{V}O_2$. Calibration relationships also appeared linear, and were modelled as per the treadmill trials. To determine the lower critical temperature (LCT), a loess regression (span = 0.95) was calculated between ambient temperature in the climate chamber ($T_a$) and $\dot{V}O_2$. The inflection point in the smoothed loess regression was taken as the LCT. A LM was calculated between $\dot{V}O_2$ and $T_a$ for all measurement in the climate chamber below the LCT, with individual as a centred factor.

All data analysis was performed in R. Standard deviation of individual intercepts are reported instead of individual parameter estimates (see methods in main manuscript).

S3.4

Results

A summary of the four individuals captured is in Table S3.5. All birds appeared stressed in the indoor cages, and most lost some weight. One individual was particularly effected (KCJW), and demonstrated decreased activity and food consumption while in captivity, resulting in body mass decreasing to 82% of his capture weight. Due to welfare concerns, no treadmill measurements were taking for this individual. The behaviour of KCJW did not change following release into the outdoor aviary, though the other three birds appeared less stressed and body mass of all individuals increased. KCJW was released along with the other three birds in the hope that it would recover better outside of captivity. Unfortunately, two weeks following release this individual was found emaciated and ultimately died. The respirometry measurements made at room temperature were significantly lower for KCJW than the resting rates for the other three individuals (statistical outlier based on 1.5x IQR, Fig. S3.6), so data from this individual was discarded. Another individual (KCJZ)
repeatedly caught its bill under its tracker harness, so the transmitter was removed and no acceleration data was recorded for this individual. For future studies with wild-caught gulls we recommend they be housed together in a large outdoor aviary, or alternatively suggest the use of captive raised individuals.

The three individuals included in analyses were all males, with a mean mass during trials of 793 ± 41 g (± standard deviation, Table S3.5). The mean respiratory quotient (RQ) across all measurements in both climate chamber and treadmill trials was 0.710 ± 0.007. This is a typical RQ value for seabirds due to their high fat diets (Ellis and Gabrielsen 2002).

Comparison of lab and field heart rates

Heart rates in captivity were elevated compared to those measured in the field (Fig. S3.3). Daily mean heart rates (on days with no gap in heart rate coverage greater than 60 minutes) in captivity averaged 235 beats min\(^{-1}\), compared to 190 beats min\(^{-1}\) in the field. This was despite having no flight or foraging-related activity while in captivity. Daily minimum heart rates were also elevated while in captivity, with the mean daily minimum heart rate in the lab being 163 beats min\(^{-1}\), 1.7 times higher than the average daily minimum heart rate in the field of 94 beats min\(^{-1}\).

Resting Metabolic Rate (RMR)

Rate of oxygen consumption (\(\dot{V}_O_2\)) measured in the climate chamber trials at room temperature and measured during rest intervals between treadmill trials were taken as measurements for resting metabolic rates (Fig. S3.6). The mean of these measurements resulted in a resting \(\dot{V}_O_2\) of 13.91 ± 0.68 mL min\(^{-1}\), with 95% confidence intervals ranging from 10.98 to 16.84 mL min\(^{-1}\). Using an RQ of 0.71, this is equivalent to 4.59 W. The mass-specific resting \(\dot{V}_O_2\) was 17.60 ± 1.08 mL min\(^{-1}\) kg\(^{-1}\).

This resting rate of 13.91 mL min\(^{-1}\) is similar to or lower than the basal metabolic rate (BMR) that would be estimated for similar sized birds based on allometric equations available for seabirds (Ellis and Gabrielsen 2002), though the conditions of our trials do not meet requirements for BMR. For climate chamber trials, birds were in a post-absorptive state and birds were relatively still during the trials, however, the measurements were not made overnight, and elevated heart rates indicated a stress response. Resting rates during treadmill trials were taken between periods of intense exercise. Birds were alert, and often pecking at the edges of the box. Resting rates measured in the climate chamber were lower than on the treadmill for two of the three birds (Fig. S3.6). Averaged individual heart rates at room temperature in the climate chamber ranged between 180 – 244 and during rest intervals on the treadmill ranged between 226 – 282, higher than the median resting rate in
the field (160 beats min\(^{-1}\)). Based on this, we anticipate that the resting \(\dot{V}_O_2\) combined across climate and treadmill trials should be a reasonable estimate of average resting metabolic rates in the field, and higher than true BMR for these individuals.

**DBA calibration**

The relationship between \(\dot{V}_O_2\) (mL O\(_2\) min\(^{-1}\)) and DBA (g) while walking was \(\dot{V}_O_2 = 70.61 \pm 8.24 \cdot \text{DBA} + 10.86 \pm 1.92\) with the standard deviation of individual intercepts = 1.0 (n = 2 individuals, \(r^2 = 0.94\); Fig. S3.1a). The 95% confidence interval around the slope ranged between 49.41 – 91.81, and around the centred intercept ranged between 5.93 – 15.78.

The relationship between \(\dot{V}_O_2\) and DBA (g) while resting in the climate chamber was \(\dot{V}_O_2 = 249.14 \pm 106.39 \cdot \text{DBA} + 10.81 \pm 3.23\) with the standard deviation of individual intercepts = 0.29 (n = 2 individuals, \(r^2 = 0.41\); Fig. S3.1b). The 95% confidence interval around the slope was wide and included 0, ranging between -20.59 – 529.4, while the centred intercept ranged between 2.32 – 18.99.

**Heart rate calibration**

The relationship between \(\dot{V}_O_2\) and heart rate (\(f_h\), beats min\(^{-1}\)) while walking was \(\dot{V}_O_2 = 0.07 \pm 0.01 \cdot f_h + 2.83 \pm 2.91\) with the standard deviation of individual intercepts = 2.68 (n = 3 individuals, \(r^2 = 0.90\); Fig. S3.1c). The 95% confidence interval around the slope ranged between 0.05 – 0.08, and around the centred intercept between -3.87 – 9.53. During the climate chamber trials, the relationship between \(\dot{V}_O_2\) and heart rate was \(\dot{V}_O_2 = 0.08 \pm 0.02 \cdot f_h - 2.55 \pm 3.61\) with the standard deviation of individual intercepts = 1.95 (n = 3 individuals, \(r^2 = 0.80\); Fig. S3.1d). The 95% confidence interval around the slope ranged between 0.05 – 0.011, and around the centred intercept ranged between -10.50 – 5.41. Comparison of these equations with expected values suggests that elevated heart rates caused by stress decoupled the heart rate to \(\dot{V}_O_2\) relationship, and these equations were ultimately discarded (Section S3.4, Fig. S3.2).

**Effect of temperature on metabolic rate**

The lower critical temperature (LCT) for this species was estimated to be 9.5°C (Fig. S3.7). The relationship between \(\dot{V}_O_2\) (mL min\(^{-1}\)) and \(T_a\) below the LCT was \(\dot{V}_O_2 = 17.88 \pm 0.47 - 0.43 \pm 0.08 \cdot T_a\) with SD of individual intercepts = 2.9 (n = 3 individuals, \(r^2 = 0.92\), Fig. S3.7). The 95% confidence interval for the slope was between -0.63 – -0.23, and the centred intercept between 16.69 – 19.08.
S3.5: Comparison of heart rate calibrations to expected values

To examine how well the allometric heart rate calibration calculated by Bishop and Spivey (2013) (equation 3.2 in main manuscript) fits for lesser black-backed gulls, we compared heart rates measured in the field to expected $\dot{V}O_2$ values (Fig. S3.2), following Weimerskirch et al. (2016). The mean body mass of the five birds in the field were used in allometric relationships ($M_b = 869$ g). A heart mass ($M_h$) of $0.010\cdot M_b$ was used for the allometric calibration, with dashed lines showing the relationship for the highest and lowest $M_h$ to $M_b$ ratio reported for $Larus$ sp. For resting behaviour, we plotted the mean heart rate while resting in the field (160 beats min$^{-1}$, “Rest”) versus $RMR_{lab}$ (13.91 mL min$^{-1}$). The mean heart rate while walking was plotted against $MR_{DBA}$ values measured in the field while walking (200 beats min$^{-1}$ and 24.9 mL min$^{-1}$, respectively, “Walk”). Mean heart rate while flapping (356 beats min$^{-1}$, “Flap”) was plotted against the chemical power estimated from the biomechanical model in (Klein Heerenbrink et al. 2015) and implemented in their R package “afpt”. We assumed body mass equal to $M_b$, with a wing span of 1.45 m and a wing area of 0.21 m$^2$, based on values reported in the flight database (Pennycuick 2008) and adjusted proportionally on body mass, and using the minimum power speed based on these dimensions (10.5 m s$^{-1}$; Pennycuick 2008). Chemical power was converted to $\dot{V}O_2$ assuming an RQ of 0.71 to obtain an estimated cost of 107.1 mL O$_2$ min$^{-1}$. The mean of the highest heart rate measured for each of the five individuals in the wild (548 beats min$^{-1}$, “Max”) was plotted against estimated maximal energy expenditure based on an allometric equation by Bishop (1997) using $M_b$ for mass (213 mL min$^{-1}$). Finally, mean daily heart rate $f_{h.24}$ (190 beats min$^{-1}$), was compared to field metabolic rate measured in ring-billed gulls ($L. delawarensis$) which were measured under similar environmental conditions and had comparable time budgets (Martinson et al. 2015, “FMR”). The average of the male and female mass-specific FMRs reported therein was 0.78 kJ g$^{-1}$ d$^{-1}$, which was multiplied by $M_b$, and converted to mL O$_2$ min$^{-1}$ assuming an RQ of 0.71, resulting in a FMR of 23.8 mL min$^{-1}$. Discarded heart rate calibrations calculated on captive animals (section S3.4) are shown for comparison.

The allometric heart rate calibration showed good fit for resting, field, walking and maximal rates of energy expenditure (Fig. S3.2). Flight costs were underestimated compared to predictions from biomechanical models, though biomechanical models often do not correspond well with empirical data (Elliott 2016). Overall this suggests that over the majority of heart rate values recorded in our study, this allometric curve is a good estimate of the relationship between heart rate and $\dot{V}O_2$.

However, the allometric heart rate calibration applied to the mean of the lowest heart rate measured per day in the field per day (81 beats min$^{-1}$) predicted a metabolic rate of 1.4 W, one third of $RMR_{lab}$, while the lowest measured heart rate (43 beats min$^{-1}$) predicted a
\( \hat{V}_{O_2} \) of 0.4 W, one tenth of RMR\textsubscript{lab}. While we do not have a reasonable estimate of BMR for this species, given that an allometric relationship derived for seabirds in Ellis and Gabrielsen (2002) predicts a BMR of 4.8 W, this seems unrealistically low, suggesting the allometric heart rate calibration may not perform well on the lower range of heart rates. As such, reported metabolic rates for resting and floating behaviours should be interpreted with caution. Further, note that estimated values are sensitive to heart mass (Bishop and Spivey 2013), particularly at higher heart rates, as shown by the dashed lines in Fig. S3.2.

The lab-derived heart rate calibrations showed poor fit, suggesting the stressful conditions during captivity decoupled the heart rate - \( \hat{V}_{O_2} \) relationship, and these relationships are not used in the study.
Table S3.1. Mapping of behaviours identified from accelerometer segments using the random forest classifier (Shamoun-Baranes et al. 2016) to behaviour modes used in this analysis. For objective 1a, mixed flight was excluded from analysis. For objectives 1b and 2, mixed flight segments were reclassified as flapping flight if that segment’s DBA was above the mean DBA during mixed flight (0.492 g), and soaring if the DBA was below the mean mixed flight DBA.

<table>
<thead>
<tr>
<th>Original classifications</th>
<th>Definition</th>
<th>Behaviour modes used in this paper</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Obj. 1a</td>
</tr>
<tr>
<td>Extreme Flapping</td>
<td>Flight with deep wingbeats, typical of take-offs and landings</td>
<td>Flap</td>
</tr>
<tr>
<td>Flapping</td>
<td>Flight with regular wingbeats</td>
<td>Flap</td>
</tr>
<tr>
<td>Mixed flight</td>
<td>Flight with infrequent flaps, and aerial manoeuvres</td>
<td>DBA &gt; mean mixed DBA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DBA &lt; mean mixed DBA</td>
</tr>
<tr>
<td>Soaring</td>
<td>Flight with no wingbeats</td>
<td>Soar</td>
</tr>
<tr>
<td>Terrestrial locomotion</td>
<td>Walking</td>
<td>Walk</td>
</tr>
<tr>
<td>Pecking</td>
<td>Walking while pecking the ground</td>
<td>Walk</td>
</tr>
<tr>
<td>Floating</td>
<td>Sitting on water</td>
<td>Float</td>
</tr>
<tr>
<td>Sitting or standing</td>
<td>Sitting or standing on a solid surface terrestrial or marine platforms)</td>
<td>Rest</td>
</tr>
<tr>
<td>Boat</td>
<td>Sitting or standing on a boat</td>
<td>-</td>
</tr>
<tr>
<td>Other</td>
<td>Unclassified behaviour</td>
<td>-</td>
</tr>
</tbody>
</table>
Table S3.2. Summary of individuals used in the field study along with their mean heart rates and DBA while at rest and during flapping flight (standard deviation reported with brackets).

<table>
<thead>
<tr>
<th>ID</th>
<th>Mass (g)</th>
<th>Sex</th>
<th>Number of behavioural bouts</th>
<th>Number of days</th>
<th>Resting Heart Rate (beats min⁻¹)</th>
<th>Flapping Heart Rate (beats min⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5697</td>
<td>895</td>
<td>M</td>
<td>461</td>
<td>22</td>
<td>176 (36)</td>
<td>377 (61)</td>
</tr>
<tr>
<td>5698</td>
<td>895</td>
<td>M</td>
<td>113</td>
<td>4</td>
<td>134 (34)</td>
<td>351 (58)</td>
</tr>
<tr>
<td>5699</td>
<td>945</td>
<td>M</td>
<td>424</td>
<td>17</td>
<td>157 (44)</td>
<td>355 (56)</td>
</tr>
<tr>
<td>5700</td>
<td>745</td>
<td>F</td>
<td>407</td>
<td>20</td>
<td>162 (41)</td>
<td>371 (56)</td>
</tr>
<tr>
<td>5701</td>
<td>865</td>
<td>M</td>
<td>337</td>
<td>14</td>
<td>146 (44)</td>
<td>347 (65)</td>
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<tr>
<td>5702</td>
<td>645</td>
<td>F</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table S3.3. Mean ± standard deviation mass-specific estimates of metabolic rate from heart rate (MRₜ) and DBA (MR_{DBA}) for different behaviour modes of free-ranging lesser black-backed gulls. The mass-specific resting metabolic rate of 5.79 W kg⁻¹ measured in captivity was used for ratio to RMR, and the ratio was calculated with MRₜ.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Mass-specific MRₜ (W kg⁻¹)</th>
<th>Mass-specific MR_{DBA} (W kg⁻¹)</th>
<th>Ratio to RMR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flap</td>
<td>36.4 ± 12.3</td>
<td>21.9 ± 2.0</td>
<td>6.3</td>
</tr>
<tr>
<td>Walk</td>
<td>10.7 ± 4.1</td>
<td>10.3 ± 1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>Soar</td>
<td>9.1 ± 4.3</td>
<td>7.5 ± 1.3</td>
<td>1.6</td>
</tr>
<tr>
<td>Float</td>
<td>7.5 ± 4.2</td>
<td>7.3 ± 1.1</td>
<td>1.3</td>
</tr>
<tr>
<td>Rest</td>
<td>7.2 ± 3.8</td>
<td>4.9 ± 0.7</td>
<td>1.2</td>
</tr>
</tbody>
</table>
Table S3.4. Comparison of linear models where different behavioural classes are used to estimate metabolic rate with a DBA and behaviour interaction. ‘Flight’ combines flapping and soaring bouts, ‘Active’ combines flapping, soaring, and walking bouts, ‘RestF’ combines resting on land and floating, while ‘Other’ combines all remaining behaviours.

<table>
<thead>
<tr>
<th>Behaviour Classes used</th>
<th>Degrees of Freedom</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flap + Soar + Walk + Float + Rest + ID</td>
<td>15</td>
<td>0</td>
</tr>
<tr>
<td>Flap + Float + Other + ID</td>
<td>11</td>
<td>10.1</td>
</tr>
<tr>
<td>Flap + Other + ID</td>
<td>9</td>
<td>12.7</td>
</tr>
<tr>
<td>Flap + Soar + Walk + RestF + ID</td>
<td>13</td>
<td>20.2</td>
</tr>
<tr>
<td>Flight + Walk + Float + Rest + ID</td>
<td>13</td>
<td>61.6</td>
</tr>
<tr>
<td>Active + Float + Rest + ID</td>
<td>11</td>
<td>66.9</td>
</tr>
<tr>
<td>Flight + Other + ID</td>
<td>9</td>
<td>76.7</td>
</tr>
<tr>
<td>Rest + Other + ID</td>
<td>9</td>
<td>77.2</td>
</tr>
<tr>
<td>Flight + Walk + RestF + ID</td>
<td>11</td>
<td>80.7</td>
</tr>
<tr>
<td>Active + RestF + ID</td>
<td>9</td>
<td>85.7</td>
</tr>
<tr>
<td>Float + Other + ID</td>
<td>9</td>
<td>103.2</td>
</tr>
<tr>
<td>Soar + Other + ID</td>
<td>9</td>
<td>116.9</td>
</tr>
<tr>
<td>Walk + Other + ID</td>
<td>9</td>
<td>119.4</td>
</tr>
</tbody>
</table>

Table S3.5. Summary of individuals used in the captive study.

<table>
<thead>
<tr>
<th>ID</th>
<th>Sex</th>
<th>Heart rate implant</th>
<th>Mass at capture (g)</th>
<th>Mass during climate trial (g)</th>
<th>Climate trial</th>
<th>Treadmill trial</th>
</tr>
</thead>
<tbody>
<tr>
<td>KCJV</td>
<td>M</td>
<td>TSE Stellar</td>
<td>830</td>
<td>787</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>KCJW</td>
<td>M</td>
<td>TSE Stellar</td>
<td>820</td>
<td>677</td>
<td>Y, discarded</td>
<td>N</td>
</tr>
<tr>
<td>KCJX</td>
<td>M</td>
<td>Star Oddi</td>
<td>835</td>
<td>742</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>KCJZ</td>
<td>M</td>
<td>Star Oddi</td>
<td>875</td>
<td>822</td>
<td>Y</td>
<td>Y, no DBA</td>
</tr>
</tbody>
</table>
Figure S3.1. Rate of oxygen consumption versus a) dynamic body acceleration walking on a treadmill and b) sitting in a climate chamber, and c) heart rate while walking on a treadmill and d) sitting in a climate chamber. Raw DBA and heart rate data are shown with open circles, and the mean measurement used in the linear model is shown by a filled circle. Individuals are identified by colour. The linear models reported in section S3.4 (excluding individual intercepts) are shown by the black line, with dashed lines indicating 95% confidence intervals around the slope and centred intercept.
Figure S3.2. Heart rate – rate of oxygen consumption ($\dot{V}_{O_2}$) relationships, based on an allometric relationship (black line, equation 3.2 in main text, published in Bishop and Spivey 2013), and calibrations performed on captive gulls in 2018 while resting and walking (coloured lines). Points show maximal (Max), mean flapping (Flap), walking (Walk), resting (Rest), and daily (FMR) heart rate values measured in the field, plotted against expected values based on $\dot{V}_{O_2}$ measurements in captivity (Walk, Rest), or values derived from an allometric relationship (Max), a biomechanical model (Flap), or measured in related species (FMR). The mean body mass of the five birds in the field were used in allometric relationships ($M_b = 869$ g). A heart mass of $0.010\cdot M_b$ was used for the allometric calibration, with dashed lines showing the relationship for the highest and lowest $M_b$ to $M_h$ ratio reported for Larus sp. Shaded area around the calibration curves from captivity are 95% confidence intervals.
Figure S3.3. Comparison of a) daily mean heart rate and b) daily minimum heart rate values in captivity (yellow) versus in the field (purple).
Figure S3.4. Metabolic rate (from heart rate, MR$_h$) versus DBA with a) flapping (n = 301), b) walking (n = 74), c) soaring (n = 85), d) floating (n = 201), e) resting (n = 1108) and f) combined across all behaviours (n = 1769). Results of linear model predicting MR$_h$ from DBA with individual as a factor are shown. The black line shows the centred intercept and slope with 95% confidence intervals represented by dashed lines. Coloured lines represent the individual intercepts. Note the different ranges on the axes.
Figure S3.5. Daily mean metabolic rate from heart rate ($\text{DMR}_{hr}$) versus metabolic rate estimated from a) dynamic body acceleration (DBA), DBA calibrated with a single relationship across all behaviours (DBA$_\text{single}$), b) a five-behaviour time-energy budget (TEB$_\text{behave}$), and c) a simplified time-energy budget that could be reconstructed using only GPS (TEB$_\text{GPS}$). Point colour shows minimum heart rate. Pink lines show results of major axis regression with shaded area demarking 95% confidence intervals. Black line shows line of equality.
Figure S3.6 Rate of oxygen consumption of three lesser black-backed gulls at room temperature versus body mass. Round points are measurements made during climate trials, and triangular points were made during treadmill trials. Individuals are identified by colour. KCJW (blue) was discarded from analysis.
Figure S3.7. Rate of oxygen consumption of three lesser black-backed gulls in a climate chamber over a range of ambient temperatures. The vertical red line marks the lower critical temperature (LCT, 9.5 °C), and the loess smoother used to determine the LCT is shown by the dashed red line. The linear mixed model results for the effect of temperature on rate of oxygen consumption below the LCT \( (\text{Vo}_2 = 17.88 - 0.43 \cdot T_a) \), and the resting metabolic rate above the LCT (13.91 ml min\(^{-1}\)), are shown by solid black lines, with 95\% confidence intervals indicated by black dashed lines. Individuals are identified by colour.
Chapter 3 - Acceleration as a proxy for energy expenditure
Migrating further does not affect annual energy expenditure but increases variation in daily energy expenditure in lesser black-backed gulls

J. Morgan Brown, Willem Bouten, Kees C. J. Camphuysen, Bart A. Nolet, Judy Shamoun-Baranes

To be submitted
Abstract

Life-history events, such as reproduction, moult, migration and periods of quiescence, have their own behavioural and energetic requirements. Animals should adjust their daily time-budgets throughout the year to account for different stages in the annual cycle, while managing their energy budgets at sustainable levels. Migrating costs both time and energy, and hence, how, when and where animals migrate may influence how energy expenditure and behaviour is distributed throughout the year. Lesser black-backed gulls *Larus fuscus* are a generalist seabird that use a diversity of migration strategies. Using year-round GPS and accelerometer data combined with a bioenergetics model to estimate thermoregulatory costs, we compare average annual energy expenditure and its variability through time among individuals migrating to different wintering areas (West Africa, North Africa, Iberia, and France or the UK). We also explore how gulls with different migration strategies adjust activity budgets to accommodate the needs of their annual cycle stages and regulate energy expenditure. Annual energy expenditure was unaffected by migration strategy, though daily, weekly and monthly energy expenditure deviated more from the average as migration distance increased. High variability in energy expenditure may be more challenging to balance, as energy expenditure is concentrated into intense periods (during migration and breeding). However, individuals of all strategies seem to manage their activity budgets to maintain energy expenditure within sustainable levels. For example, long distance migrants increased the number of migration days instead of flight time per day, resulting in similar daily energy expenditures during migration as short distance migrants. Further, individuals from all strategies had similar activity patterns throughout the year, which corresponded with annual cycle stages. This demonstrates how animals can adjust behaviour to meet the behavioural requirements of different annual cycle stages while regulating their energy expenditure when experiencing different environmental conditions.
Introduction

An animal’s energy budget determines its ability to survive, grow, and reproduce. In many parts of the world, weather conditions, and thus resource abundance, fluctuate seasonally, resulting in periods of energetic abundance and scarcity throughout the year. Life-history stages (such as periods of growth or reproduction) are energetically demanding, as well as having their own distinct morphological, physiological or behavioural requirements (Wingfield 2005, Barta et al. 2008). In animals whose lives span multiple years, these stages can be organised throughout the year (‘annual cycle stages’) to correspond with seasonal fluctuations in their environment (Jacobs and Wingfield 2000, McNamara and Houston 2008, Varpe 2017).

The reproductive stage is typically the most energetically or nutritionally demanding stage of the annual cycle, because individuals must acquire sufficient resources not only for themselves, but also to fuel both the maintenance, growth and development of their young (Bryant 1997). Breeding is thus timed to coincide with peaks in food resources in high latitude breeding areas (Lack 1954). Moult is an energetically demanding growth stage in avian species (Lustick 1970, Murphy and King 1992, Lindström et al. 1993). High moult costs not only result from growing new feathers, but also from indirect costs such as impaired body insulation which increases thermoregulatory costs (Buttemer et al. 2003), or reduced flight performance due to loss of flight feathers (Hedenström and Sunada 1999). To compensate for this, birds may reduce flight activity (Cherel et al. 2016) or move to more productive habitats to complete moult (Rohwer et al. 2005). Finally, animals may benefit from having time for a quiescent (‘winter’) stage. This may be important for survival when resource levels are limited, creating energetic bottlenecks (Fort et al. 2013), while winter conditions are also important for preparing for the subsequent breeding season (Norris et al. 2004).

Seasonal migrations are a life-history strategy that has evolved in many animal taxa where, by moving between two distant areas, they can exploit resource peaks and reduced competition at high latitudes, while avoiding deteriorating conditions in the other part of the year (Alerstam et al. 2003, Somveille et al. 2015). This effectively reduces the variation in resource abundance and weather conditions experienced by the animal during the year (Somveille et al. 2019). However, migrating also introduces two more annual cycle stages (autumn and spring migration), which also cost both energy and time (Alerstam et al. 2003). Thus, the benefits of migrating (improved resources and weather conditions), which should increase with migration distance, likely trade-off with the energy and time required to access those regions, creating a range of potential migration strategies.
For example, as migration distance increases, animals must invest more energy into migrating. Reduced thermoregulatory costs for individuals wintering at lower latitudes could balance the energetic costs of migrating, resulting in similar annual energy expenditures across a range of migration strategies. Results from other avian migrants have demonstrated this trade-off (Garthe et al. 2012, Alves et al. 2013, Fort et al. 2013, Carneiro et al. 2017, Pelletier et al. 2020), but see Fayet et al. (2016) who found longer migration routes increased energy expenditure. However, even if annual energy expenditure is similar among migration strategies, it may be distributed differently throughout the year. As migration distance increases, energy expenditure may shift from being relatively constant throughout the year to more variable, with energy expenditure being concentrated during migration stages, balanced by below average energy expenditure during the winter. Animals must be capable of finding, digesting, assimilating and metabolizing sufficient energy to balance their energy budget. If energy expenditure is concentrated into certain periods, resulting in days with above average daily energy expenditure (DEE), animals may reach limits to time available for foraging (Tinbergen and Verhulst 2000), or exceed the limits of their metabolism (Drent and Daan 1980, Weiner 1992, Hammond and Diamond 1997), thus increasing risk of mortality (Deerenberg et al. 1995, Daan et al. 1996).

Additionally, the further an animal migrates, the more time it takes away from other annual-cycle stages (Newton 2011). This may limit when animals can carry out other annual cycle stages, or require overlap between some of these stages (Wingfield 2005). For example, long distance migrants often return later to breeding areas, leaving less time to transition into breeding condition (Ramenofsky and Wingfield 2006). If insufficient time is available to separate moult, long-distance migrants may have to begin moulting during the breeding season, or end during migration (Kiat et al. 2019). On the other hand, migrating to more productive regions may enable moulting in wintering areas, whereas short distant migrants or residents should complete moult before resources become limited in winter (Barta et al. 2008, Newton 2011, Kiat et al. 2019). Also, if resource type or abundance differs across wintering regions, this may result in different foraging efforts or methods among regions.

The aim of this study is to examine how an individual’s energy requirements throughout the year, as well as their ability to adjust their behaviour to different annual-cycle stages, are influenced by their migration strategy. To do so, we use GPS and accelerometer data in combination with a bioenergetics model to estimate daily energy expenditures (DEE) and activity budgets year-round of lesser black-backed gulls (Larus fuscus) breeding in the Netherlands, where individuals range from short distance migrants wintering in the UK (< 250 km) up to long distance migrants that travel to West Africa (> 4500 km; Klaassen et al. 2012). Lesser black-backed gulls are a mid-sized sized seabird that can forage on a range
of different resource types, including marine, agricultural, and urban food sources (Tyson et al. 2015, Baert et al. 2018, Spelt et al. 2019, Martín-Vélez et al. 2020). Gulls move using predominantly flapping flight, but also by soaring and walking (Chapter 3). Climate conditions, as well as types of available resources, should differ substantially within their winter range. We divide gulls into four migration strategies based on their geographical wintering regions: France and UK (short-distance, urban and terrestrial winter resources, cold climate), Iberia (mid-distance, urban, agricultural or marine resources, cold interior or moderate coastal climate), North Africa (mid-distance, urban or marine resources, hot climate), and West Africa (long-distance, marine resources, hot climate). Despite this vast range in migration distances, a previous study on this gull population found that cumulative distance travelled throughout the year was not explained by migration distance (Shamoun-Baranes et al. 2017), though this study did not account for differences in flight mode (flapping vs soaring flight), nor thermoregulatory costs. West African migrants also return later to the breeding colony (Shamoun-Baranes et al. 2017), which may be an indication of time limitation within that strategy.

Our first objective is to compare energy expenditure among different migration strategies. First, we compare annual energy expenditure (AEE), which we hypothesize will be equal across strategies due to a trade-off between energy allocated towards activity versus resting (i.e. thermoregulatory) costs. Next, we examine how constant or variable DEE is throughout the year. We expect energy expenditure will deviate more from AEE as distance to wintering areas increases, as a result of high energy expenditure being concentrated into migratory periods and below average DEEs during winter periods. Our second objective is to explore whether migration strategies differ in patterns of energy expenditure and time allocated towards different behaviours, in relation to time of year, and the habitat and weather conditions gulls experience.

**Methods**

**Capture and Tagging**

Breeding adults from three colonies in the Netherlands (IJmuiden 52°27’54N 4°34’34E: 35 individuals between 2019 – 2021; Texel 53°00’33N 4°43’10E: 104 individuals between 2008 – 2021; and Schiermonnikoog 53°30’00N 6°15’34E: 29 individuals between 2017 – 2018) were captured in a walk-in trap set over a nest during the incubation stage as a part of long-term monitoring studies. Solar-powered GPS and acceleration trackers (UvA-BiTS; Bouten et al. 2013) were attached using a Teflon wing harness (Thaxter et al. 2014). Combined mass of tracker and harness were less than 3% of body mass.
fixes followed by 1 s of tri-axial acceleration at 20 Hz were taken year-round at an interval between 2.5 – 60 minutes, depending on location, time of year, battery level and available memory. Measurements are stored on the logger and transmitted to a base station in the colony during the breeding season.

**Data processing**

‘Bird-years’ (starting and ending on June 1) that had GPS and acceleration data for at least 75% of the year were selected from the complete dataset for processing. A behaviour was assigned to each acceleration measurement using a random forest classifier previously developed for lesser black-backed gulls (Shamoun-Baranes et al. 2016). Following methods in Chapter 3, behaviours identified by the classifier were combined into four behaviour modes: flapping, soaring, walking and stationary (sitting, standing or floating on water).

Data were subsampled to an interval between 20 – 60 minutes, based on the lowest sampling frequency on that given day. To assess whether sample frequency biased our results, we used a high-resolution acceleration dataset from the 2019 breeding season to estimate daily energy expenditure (DEE, see below) for data measured at a 2.5 minute interval (highest resolution available), a 20 minute interval (most common annual sampling interval) and a 60 minute interval (lowest resolution in this study). Precision of DEE decreased with sample interval (r = 0.94 between DEEs estimated from 2.5 versus 20 min interval, and r = 0.85 between 2.5 and 60 min interval), though distribution of high and low frequency data did not significantly differ, suggesting resampled data were not biased (paired t-tests: df = 208, t = -0.11, p = 0.97 and df = 208, t = 0.11, p = 0.91 for 2.5 versus 20 and 60 minute intervals, respectively).

Net displacement over each day was calculated as the great circle distance between GPS fixes closest to midnight to distinguish between ‘relocation’ versus ‘stationary’ days. There was no clear bimodal distribution in net distance travelled per day, but there was a drop in the frequency of days with net displacements exceeding 70 km, which was used as a threshold to separate relocation and stationary days.

Data gaps commonly occur at high latitudes during autumn and winter when tracker batteries are unable to charge due to short daylight hours and poor weather. Discarding all bird-years with a gap, or periods of years containing a gap, would bias our thermoregulatory estimates towards fair-weather years and regions. Data exploration suggested that gulls tend to allocate time similarly between activities within a stationary period (consecutive stationary days), coinciding with extremely high repeatability in space used observed within wintering areas across all migration strategies (Chapter 2). Therefore, we filled gaps with simulated time-activity budgets by randomly sampling GPS-acceleration fixes.
from that bird-year within the same stationary period and at ± one hour of the missing measurement time. Energy expenditure during filled gaps was estimated using the behavioural classification of the sampled fix, and thermoregulatory costs were calculated using the weather experienced at the sampled location using the date and time of the missing fix (see below). As assessing the contribution of potentially elevated energy expenditures during migration is central to our research question, any bird-year that relocated during a gap was discarded.

Habitat classifications were extracted from Copernicus Global Land Service (updated annually between 2016-2019, 100m resolution; Buchhorn et al. 2020) for each GPS fix at the closest available year. We reduced the number of classifications to six: marine, built-up (i.e. urban), agricultural (croplands, includes most landfill sites), terrestrial open (herbaceous vegetation, bare/sparse vegetation, shrubland), inland wet (permanent inland water and herbaceous wetland), and forest (all forest classification types). Misclassified habitat within the breeding colonies were corrected to terrestrial open habitat.

**Estimating Energy Expenditure**

Metabolic rates for each measurement were estimated using two approaches: the first was from acceleration data, as an estimate of activity costs, and the second is based on thermoregulatory costs, using a bioenergetics model. To estimate metabolic rate from activity, we calculated the vectoral sum of the dynamic body acceleration measured on three-axes (DBA; Wilson et al. 2019). First, we removed the baseline acceleration from each axis by subtracting the mean acceleration across the recording chunk. DBA was then calculated as $DBA = \sqrt{x^2 + y^2 + z^2}$, where $x$, $y$, and $z$ are remaining dynamic acceleration in the surge, sway and heave directions. For flapping, soaring, walking, and non-floating stationary behaviour, we converted DBA to metabolic rate using calibration equations derived in Chapter 3 (Table S4.1 in supplementary materials for Chapter 4). With the exception of resting, the slopes of these equations were not statistically significant. However, we used them instead of average activity costs as DBA should partially account for the influence of seasonal fluctuations in body mass on activity costs. Waves interfere with DBA measurements while floating, so we used the average metabolic rate of all other stationary points that day as an estimate of metabolic rate while floating.

The metabolic rate required to maintain body temperature was estimated using a model based on heat exchange theory developed by (Cartar and Morrison 1997) for *Calidridis* sandpipers, and subsequently adapted for waterfowl (*Anseriformes*, Baveco et al. 2011). The model estimates thermal metabolic rate based on ambient air temperature at 2 m ($T_{\text{a}}$, °C), wind speed at 10 m ($u$, m s$^{-1}$) and surface solar radiation ($R_{\text{g}}$, W m$^{-2}$), which were extracted for each GPS fix at the nearest hour and 0.25 degree latitude-longitudinal grid
from the ERA5 dataset (Hersbach et al. 2018). The model was followed as reported in Baveco et al. 2011, modifying the species specific constants for gulls (see ‘Constants used in heat-exchange model’ in supplementary material). We did not account for potential increased thermoregulatory costs while floating, which can result from water having higher thermal conductance and greater specific heat capacity than air (Stahel and Nicol 1982, Bevan and Butler 1992, Bevan et al. 1995, Humphreys et al. 2007). We found gulls did not incur extra thermoregulatory costs while floating in water around 12°C (Chapter 3), though this may lead to underestimation of thermoregulatory costs while floating in colder water. We also did not account for potential increased thermoregulatory costs while floating in water around 12°C (Chapter 3), though this may lead to underestimation of thermoregulatory costs while floating in colder water.

We assumed thermoregulatory costs are compensated by activity, so the highest of these two estimates was selected per fix, and averaged over the day to estimate DEE. Daily time-budgets were estimated based on the proportion of fixes per day classified as a given behaviour. Mean annual energy expenditure (AEE) was calculated by averaging DEE throughout the year. Flight metabolic rate was the mean metabolic rate of all flight fixes during a day (in W). Stationary metabolic rate was the mean metabolic rate of all stationary fixes during a day (including estimated thermoregulatory costs when they exceeded activity costs, in W).

Simulated time and energy budgets during stationary gaps were included in analyses of annual summaries, DEE, and stationary metabolic rate, to account for weather (and thermoregulatory costs) during gaps, as well as ensuring the proportion of time spent in each stage is properly reflected (for annual summaries). Simulated time-budgets were excluded from analyses of time spent per activity (as time values are constant with respect to weather).

**Data analysis**

We partitioned the annual cycle into four stages: breeding, autumn migration, wintering, and spring migration following methods in Chapter 2, based on GPS locations. Breeding was considered the stage when individuals had an association with the breeding colony. The last detection within 10 km of the colony was used for the transition from breeding to autumn migration, and the first detection within 10 km of the colony the following year was the transition from spring migration to breeding. Wintering areas for each bird year were identified from the 95% kernel density estimates of GPS locations taken between colony departure and arrival following methods in Chapter 2. This approach identifies
core-areas of several hundred km in diameter where gulls spend a substantial amount of time. When multiple core areas were identified, the most southerly is assumed to be the wintering area. The winter period was defined between the first and last stationary day within the wintering area. Migration stages were defined as the periods in the annual cycle between breeding and wintering. Relocation days within the migratory periods are referred to as migration days and stationary days as stopover days.

Migration distance was defined as the great circle distance between the breeding colony and the centroid of the wintering area (i.e. direct versus actual distance flown along route). Bird-years were separated into four migration strategies based on the location of their wintering area: Birds wintering in Africa south of 25° latitude (“West African”), birds wintering in Africa north of 25° latitude (“North African”), birds wintering in Spain or Portugal (“Iberian”) and those wintering in France and UK.

Linear mixed models (LMM) with migration strategy as a fixed factor were used to examine whether migration strategy influences AEE and annual mean time and energy allocated to flapping, soaring, walking or stationary behaviour per day. Individual was included as a random effect and we used a gaussian probability distribution. Models were estimated using r package lme4 (Bates et al. 2015). Likelihood ratio tests (LRT) were performed against a null model with no fixed effects to test whether migration strategy explained a significant amount of variation in the models.

To examine whether distribution of DEE becomes more concentrated within certain periods versus constant as migration distances increase, the deviance between DEE and AEE was summed for each bird-year. To take the temporal sequence of DEE into account, the deviance was also calculated using a 7-day and 30-day moving mean of DEE, to examine whether energy expenditure during periods of a week or month deviated more from AEE as migration distance increased (i.e. opposed to above average DEEs being balanced by below-average DEEs during a given time period). Sum of deviance per bird-year was modelled in response to migration strategy (fixed factor) using LMMs with individual included as a random effect and a gaussian probability distribution, and significance of migration strategy was assessed by comparing to a null model using a LRT.

Patterns of DEE, daily time spent flapping, soaring, walking or stationary, stationary and flight metabolic rate, and experienced temperature and solar radiation, were modelled as a function of calendar date using generalized additive mixed models (GAMM), including individual as a random effect and assuming a gaussian probability distribution, using r-package mgcv (Wood 2021). To control for temporal autocorrelation, an auto-regressive moving average (ARMA) correlation structure with one auto-regressive parameter and one moving average parameter was included in all additive models, selected using Akaike’s Information Criterion (AIC) comparing all ARMA correlation structures up to a maximum
of two parameters and validated by plotting the autocorrelation function of normalized residuals (Zuur 2017). Models were estimated containing either a smoothing function per migration strategy, a single smoothing function combining all migration strategies, or a null model with no smoothing function with time, as well as with and without migration strategy as a fixed factor, and compared using AIC.

To relate periods of extreme high or low energy expenditure to stages in the annual cycle, the annual cycle stages of the weeks with the three highest and lowest average DEE were reported per bird-year. The extreme weeks were determined using a 7-day moving average, and the three highest or lowest weeks could not overlap in time (so no day can contribute towards two high or low weeks), with extreme weeks being determined consecutively from most to least extreme. All analyses and figures were generated using R version 4.0.2.

**Results**

A total of 59 bird-years (starting and ending June 1) spanning five years (2016 – 2021) had sufficient data to be used in this study. Most of these individuals migrated to either Iberia or North Africa (Table 4.1, Fig. 4.1). Migration distances ranged between 360 to 4583 km (Table 4.1).

**Energetic consequences of different migration strategies**

As hypothesised, AEE did not significantly differ among migration strategies (LRT: df = 3, $\chi^2 = 0.22$, $p = 0.84$; Table 4.1, Fig. 4.2a), and was predicted to be 782 kJ day$^{-1}$ (1.97-times the resting metabolic rate, RMR, measured in captivity within their thermoneutral zone, Chapter 3), albeit with large variation among bird-years within a migration strategy (Fig. 4.2a). For all strategies, the majority of the day was spent stationary (Fig. 4.2b). Time stationary increased slightly, but not significantly, with distance to wintering area (LRT: df = 3, $\chi^2 = 5.50$, $p = 0.14$; Fig. 4.2b). Differences in thermoregulatory costs between winter regions were insufficient to cause significant differences in resting metabolic rates between strategies (LRT: df = 3, $\chi^2 = 4.62$, $p = 0.20$), so average energy allocated towards stationary behaviour was likewise not significantly different (LRT: df = 3, $\chi^2 = 0.46$, $p = 0.93$; Fig. 4.2d).

Average time walking per day differed by migration strategy (LRT: df = 3, $\chi^2 = 20.93$, $p < 0.001$; Fig. 4.2b). Individuals using the French/UK strategy spent the most time walking, with LMMs predicting them to walk $2.94 \pm 0.27$ h day$^{-1}$ ($\pm$ standard error), almost an hour more than other strategies (Iberia: $2.01 \pm 0.19$; North Africa: $1.87 \pm 0.23$; West
Table 4.1 Number of individuals and bird-years included in the study by migration strategy, along with mean migration distance and annual energy expenditure (AEE; presented as mean ± standard deviation)

<table>
<thead>
<tr>
<th>Winter Area</th>
<th>N. Individuals</th>
<th>N. bird-years</th>
<th>Migration Distance (km)</th>
<th>AEE (kJ day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>West Africa</td>
<td>5</td>
<td>10</td>
<td>4174 ± 291</td>
<td>771 ± 43</td>
</tr>
<tr>
<td>North Africa</td>
<td>15</td>
<td>22</td>
<td>2303 ± 239</td>
<td>781 ± 37</td>
</tr>
<tr>
<td>Iberia</td>
<td>15</td>
<td>18</td>
<td>1709 ± 206</td>
<td>790 ± 40</td>
</tr>
<tr>
<td>France/UK</td>
<td>7</td>
<td>9</td>
<td>685 ± 228</td>
<td>782 ± 33</td>
</tr>
</tbody>
</table>

Figure 4.1 GPS tracks and centroids of wintering areas (open circles) of bird-years, coloured by migration strategy (West Africa = red, North Africa = orange, Iberia = teal, France/UK = blue). Breeding colonies are marked with yellow diamonds.
Africa: 1.74 ± 0.18). Average time spent in either flapping or soaring flight did not differ by migration strategy (Flap LRT: df = 3, $\chi^2 = 2.53$, p = 0.47, predicted time flapping = 2.22 h day$^{-1}$; Soar LRT: df = 3, $\chi^2 = 4.72$, p = 0.19, predicted time soaring = 1.39 h day$^{-1}$). Despite only a small portion of time being allocated towards flapping flight, it accounted for a large portion of the daily energy budget (Fig. 4.2d).

**Figure 4.2** Annual summary of energy expenditure and time-energy budgets by migration strategy. Violin and boxplots show variation in (a) annual energy expenditure (AEE) across bird-years, and (c) the sum of deviance between AEE and 7-day average DEE. Stacked bar plots show allocation of time (b) and energy (d) towards different behaviours where purple is proportion flapping, blue soaring, green walking and yellow stationary.
While AEE was unaffected by migration strategy, the sum of deviance between AEE and daily, weekly and monthly energy expenditure, all increased significantly with migration distance (daily LRT: df = 3, $\chi^2 = 12.20$, $p = 0.007$; 7-day LRT: df = 3, $\chi^2 = 12.69$, $p = 0.005$; 30-day LRT: df = 3, $\chi^2 = 12.64$, $p = 0.005$). This means that, as hypothesised, longer distance strategies have more days, weeks and months during the year with higher and lower than average DEE compared to shorter distance strategies (Fig. 4.2c).

Activity-budgets and DEE throughout the year

DEE (Fig. 4.3), and time per day spent flapping, soaring, walking and stationary (Fig. 4.4), fluctuated throughout the year. Migration strategies generally showed similar temporal patterns in DEE and time allocated towards different locomotory modes, with Akaike information criterion (AIC) indicating that a single smoothing function combining all strategies was more parsimonious than strategy-specific smoothing functions for all GAMM models, except for stationary metabolic rate (mean metabolic rate of all stationary points during the day, including thermoregulatory costs) and weather models (Table S4.2 in supplementary material). The top model for walking included strategiespecific intercepts, with the French/UK migration strategy walking 0.90 - 1.16 h day$^{-1}$ more throughout the year compared to the other strategies (Table S4.2, Fig. 4.4a). Timing of the main stages in the annual cycle also varied widely between individuals, even when migrating to the same wintering areas (Fig. 4.3b), diffusing some of the mean patterns within a strategy, particularly the impact of migratory flights. Within-stage differences among strategies of potential biological significance may have been insufficient to support strategy-specific models when considering the entire annual cycle together. As we are interested in identifying periods of potential divergence between strategies during the year, we present the strategy-specific models (Fig. 4.3 & 4.4bh).

Among individuals using the same migration strategy, both DEE (Fig. 4.3a) and time-budgets (Fig. S4.14 in supplementary material) show high variation at a given time. Daily stationary metabolic rates explained little variation in DEE (correlation, $r = 0.24$). Instead, DEE was highly correlated with time spent flapping ($r = 0.97$). Soaring flight, which is an energetically cheaper alternative to flapping flight, accounted for 39% of time in flight. Flight metabolic rate (the mean metabolic rate of all flight points during a day) was highly variable but did show a trend throughout the year, with predicted cost of flight exceeding 22 W in autumn, 2 W more than flight metabolic rate during the rest of the year (Fig. 4.4c). Variation in daily activity budgets could also be partially explained by time spent in the three primary foraging habitats used by this species (marine, agricultural and urban/built-up areas). Time in flapping flight was weakly correlated with time in marine habitats ($r = 0.30$), while time walking was moderately correlated with time in agricultural habitats.
(r = 0.52) and weakly negatively correlated with time in marine habitats (r = -0.32). Time stationary or soaring were unrelated to any of the three habitat types (all r < 0.3).

Patterns of DEE generally reflect transitions between annual cycle stages. Peaks in DEE typically coincided with the migration stages or breeding depending on migration strategy, while the magnitude of the peak increased with migration distance (Fig. 4.3, see also sum of deviance in the previous section).

**Figure 4.3** a) Daily energy expenditure (DEE) of lesser black-backed gulls throughout the year by migration strategy (WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK). Bold black line shows Gamm prediction per strategy with approximate 95% confidence intervals. Coloured lines show 7-day mean DEE per bird-year, coloured by latitude. Points mark the three highest and lowest 7-day mean DEEs per bird-year, with point size indicating rank (most extreme being larger), and colour indicating the annual cycle stage of the central day of that week. The horizontal line indicates the annual mean DEE across all strategies. b) Timing of annual cycle periods of each bird-year, ordered from longest (top) to shortest migration distance per strategy. Stopover days during autumn and spring are differentiated from migration days by the darker tone. c) Boxplots showing value of three highest and lowest weeks per migration strategy (indicated by coloured points in panel a). d) Stacked bar plot showing distribution of annual cycle stages of the 7 days contributing to the three highest and lowest weeks per strategy.
Figure 4.4 Time or energy spent flapping, soaring, walking and stationary in lesser Black-backed Gulls throughout the year along with experienced weather, predicted using GAMM models. a) General pattern across all migration strategies (top model based on AIC), with behaviour models distinguished by colour. The top model for walking included strategy-specific intercepts, with the French/UK migration strategy walking 0.90 - 1.16 h day\(^{-1}\) more throughout the year compared to the other strategies, though for consistency we show the model without strategy-specific intercepts b) Time walking, c) flight metabolic rate. d) time flying, e) stationary metabolic rate, f) time stationary, g) ambient temperature, and h) solar radiation, by migration strategy (distinguished by colour). Point-wise approximate 95% confidence intervals shown around GAMM predictions. Bottom panel shows violin plots of probability density for the start dates of annual cycle stages for each migration strategy, with points indicating the mean per strategy (stage distinguished by point shape, and migration strategy by colour where WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK).
Demonstrating this, the magnitude of average DEE during the three highest and lowest weeks of the year generally became more extreme as distance to wintering area increased (Fig. 4.3c). West African migrants spent on average $1300 \pm 155$ kJ day$^{-1}$ (3.28-times RMR) during their highest weekly energy expenditure, which typically occurred during spring migration (Fig. 4.3d). In comparison, the week with the highest energy expenditure in French/UK individuals typically occurred during the breeding season, and averaged $1064 \pm 101$ kJ day$^{-1}$ (2.69-times RMR), a similar level reached by the other strategies during that period. Generally, as distance to wintering area decreased, weekly energy expenditure during the migratory periods became more similar to energy expenditure during the late breeding season (Fig. 4.3a). Accordingly, the proportion of high energy expenditure weeks occurring during the breeding stage versus during one of the migration periods increased with winter latitude (Fig. 4.3d). The weeks of the years where DEE was at its lowest generally occurred during autumn stopovers or on wintering areas for all strategies (Fig. 4.3d). Mean DEE during the lowest weeks of the year also decreased with migration distance, though differences were less extreme (Fig. 4.3c), with West African migrants having the lowest weekly mean DEE of $584 \pm 29$ kJ day$^{-1}$, and French/UK migrants having the most moderate mean DEE of $627 \pm 45$ kJ day$^{-1}$ during their lowest week (1.48 and 1.58-times RMR, respectively).
Patterns in time allocated towards different activities likewise reflected different annual-cycle stages. Daily time-budgets changed throughout the breeding season. Following arrival to the colony, time in flight initially decreased to moderate levels while time walking briefly increased during the early breeding season (Fig. 4.4a). As the breeding season progressed, time walking decreased while time in flight increased, with GAMMs predicting a peak of 3.18 h day$^{-1}$ flapping and 2.09 h day$^{-1}$ soaring. West African migrants spent slightly less time in flight during the breeding season compared to the other strategies (Fig. 4.4d). Around half the time during breeding season was spent in terrestrial open habitat (i.e. the colony), with individuals from all strategies using a range of foraging habitats (marine, built-up and agricultural, Fig. 4.5a).

Following the breeding season, time spent in flight plateaued at 1.55 h day$^{-1}$ flapping and 0.80 h day$^{-1}$ soaring, while use of walking became more common for a period of approximately two months during autumn and early winter, peaking at 2.90 h day$^{-1}$. During autumn stopovers, most individuals were residing in the UK, Belgium, or Northern France (see latitude in Fig. 4.3a), where use of agricultural and built-up areas increased compared to the breeding season, and occurrence in marine areas decreased compared to breeding (Fig. 4.5). This behavioural pattern is absent in the strategy-specific model for the West African strategy (Fig. 4.4). Instead, the West African strategy slowly decreased both time walking and in flight throughout the autumn period until activity reached an annual low in early November, when most individuals had already crossed the Sahara. Among-strategy differences in behaviour during this period correspond with patterns found in individual bird-years (See ‘Individual-level exploration of autumn time-budgets’ in the supplementary materials).

As mentioned previously, peaks in DEE and activity-budgets during migration were not well captured by GAMM models. However, peaks in energy expenditure corresponding with autumn and spring migratory flights are apparent in the 7-day moving mean of individual bird-years in all strategies except French/UK migrants (Fig. 4.3a). A summary of migration days (Table 4.2) shows that the length of the migratory period (i.e. time between departure and arrival) was shorter in spring than in autumn, but otherwise seasons did not differ greatly in number or intensity of migration days within a migration strategy. The number of migration days in a migratory period increased with migration distance, while mean DEE and time in flight during migration days was similar across strategies (Table 4.2). However, French/UK migrants reached lower maximum DEE and flight times during migration days compared to individuals using other strategies. Flight metabolic rates on migration days were highly variable (i.e. high standard deviations), thus trends are unlikely to be significant (Table 4.2).
Table 4.2. Mean and maximum daily energy expenditure and flight time during migration days by winter area during autumn and spring (± 1 standard deviation). Migration days were days with a net displacement greater than 70 km during the migratory period.

<table>
<thead>
<tr>
<th>Winter Area</th>
<th>Season</th>
<th>Length mig. period (days)</th>
<th>N. Mig. days</th>
<th>Mean mig. DEE (kJ)</th>
<th>Max mig. DEE (kJ)</th>
<th>Mean flight time (h day^-1)</th>
<th>Max flight time (h day^-1)</th>
<th>Mean flight MR (W)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAf</td>
<td>Autumn</td>
<td>123 ± 48</td>
<td>18 ± 4</td>
<td>1043 ± 255</td>
<td>203 ± 38</td>
<td>7.7 ± 3.8</td>
<td>16.6 ± 3.6</td>
<td>24.8 ± 4.7</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>21 ± 5</td>
<td>14 ± 4</td>
<td>1172 ± 297</td>
<td>271 ± 37</td>
<td>10.6 ± 3.7</td>
<td>17.3 ± 2.6</td>
<td>22.7 ± 4.7</td>
</tr>
<tr>
<td>NAf</td>
<td>Autumn</td>
<td>96 ± 46</td>
<td>9 ± 2</td>
<td>1183 ± 311</td>
<td>337 ± 40</td>
<td>9.9 ± 3.7</td>
<td>17.1 ± 2.8</td>
<td>24.0 ± 4.6</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>19 ± 9</td>
<td>10 ± 3</td>
<td>1098 ± 296</td>
<td>193 ± 34</td>
<td>9.3 ± 3.2</td>
<td>15.5 ± 2.1</td>
<td>21.5 ± 4.9</td>
</tr>
<tr>
<td>IB</td>
<td>Autumn</td>
<td>106 ± 43</td>
<td>7 ± 2</td>
<td>1141 ± 301</td>
<td>248 ± 41</td>
<td>9.3 ± 3.2</td>
<td>16.1 ± 2.6</td>
<td>23.6 ± 4.8</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>23 ± 14</td>
<td>9 ± 3</td>
<td>1074 ± 222</td>
<td>218 ± 32</td>
<td>8.7 ± 3.2</td>
<td>14.2 ± 2.8</td>
<td>22.2 ± 4.5</td>
</tr>
<tr>
<td>FRUK</td>
<td>Autumn</td>
<td>33 ± 48</td>
<td>5 ± 5</td>
<td>990 ± 217</td>
<td>242 ± 32</td>
<td>7.8 ± 3.2</td>
<td>11.9 ± 3.0</td>
<td>21.5 ± 5.1</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>16 ± 16</td>
<td>5 ± 3</td>
<td>975 ± 169</td>
<td>162 ± 24</td>
<td>6.6 ± 2.4</td>
<td>10.1 ± 2.1</td>
<td>22.9 ± 4.3</td>
</tr>
</tbody>
</table>
The winter period was generally the most restful time of the year, with time spent stationary peaking at 19.81 h day\(^{-1}\) in mid-January. Time walking decreased compared to autumn stopovers, while flight time increased slightly. Activity budgets remained stable during winter for most strategies, while French and UK migrants steadily increased time in flight as winter progressed. Expectedly, weather conditions differed between wintering areas (Fig. 4.4g-h). West African migrants never experienced temperatures below 10°C (their approximate lower critical temperature), while some Iberian and French/UK migrants experienced mean temperatures below 10°C throughout the winter period. Winter solar radiation and ambient temperature increased with migration distance. As a result, birds overwintering in France, UK and parts of Iberia had higher stationary metabolic rates during winter (Fig. 4.4e) than birds overwintering further south. The use of different foraging habitats also diverged between strategies (Fig. 4.5c). Use of marine habitats was highest in the West African strategy, and decreased in higher latitude winter areas. The French/UK strategy spent half their time in agricultural areas, the use of which decreased as migration distance increased. Use of built-up habitats was highest in the North African strategy, and lowest in West Africa. Despite these differences, all strategies reduced their activity-levels during winter, albeit with French and UK migrants continuing to walk more compared to other strategies.

**Discussion**

In this study we compared the annual energy expenditure of lesser black-backed gulls migrating to different wintering areas, while examining how variable energy expenditure is through time. We found that AEE was not significantly different among migration strategies, while variation among individuals was high within a strategy. Further, the sum of deviance between daily, weekly, and monthly energy expenditure increased with migration distance, demonstrating that individuals migrating further have their energy requirements concentrated into bursts which are balanced by periods of below-average energy expenditure, as opposed to being constant throughout the year. We also explored how DEE and time allocated towards different activities varied throughout the year. We showed that DEE and activity budgets changed with different stages in the annual cycle, with DEE and time in flight being highest during migration and late breeding, walking increasing during autumn stopovers, and winter being a highly stationary period. Individuals from all migration strategies showed similar behavioural adjustments to most of these stages.
Energetic consequences of different migration strategies

Despite the diversity in migration strategies demonstrated by lesser black-backed gulls, choice of wintering region did not influence annual energy expenditure. This was expected due to a trade-off between additional flight costs resulting from migrating further and higher thermoregulatory costs in short distance migrants (Somveille et al. 2019). However, in this species, energy allocated towards both active and resting processes was not affected by migration strategy. Differences in thermoregulatory costs between wintering regions were insufficient to influence AEE, suggesting that weather conditions experienced throughout the winter range of lesser black-back gulls remain relatively moderate given their body size and insulation. Rather, increased flight time during migration as migration distance increased was balanced by slightly lower activity during other annual cycle stages.

Instead of clear divisions among wintering areas in annual time and energy allocation, there was high inter-individual variation in annual energy expenditure among individuals migrating to the same wintering areas. This suggests that other behavioural strategies that influence time spent in flapping flight (the main determinant of DEE), influence annual energy requirements more than migration. Among-individual differences in foraging strategy, for example, can lead to high inter-individual variation in activity budgets within a region (Spelt et al. 2019), also demonstrated on a coarse-scale in this study through correlations between time in different behaviours and foraging habitats. Habitat use and foraging behaviour of lesser black-backed gulls can be complex and variable even within a winter region (Martín-Vélez et al. 2020), and a more in-depth analysis is required to properly quantify the contribution of foraging strategy towards DEE (and thus inter-individual differences in AEE).

While annual energy requirements were balanced across strategies, as distance to wintering area increased, individuals had more days, weeks and months with energy expenditures that deviated from their annual mean (i.e. energy expenditure was increasingly concentrated into certain periods versus constant throughout the year). Periods of elevated energy expenditure may make obtaining sufficient calories to meet these energy requirements more challenging, while if energy expenditure increases above the limit at which the body can assimilate and metabolise energy, fitness could be negatively impacted (Weiner 1992, Hammond and Diamond 1997, Tinbergen and Verhulst 2000). The annual cycle stages where gulls experience above average energy requirements were during late breeding and migration, with increasing migration costs for long distance migrants likely contributing to the increased deviance between DEE and AEE throughout the year. However, even in gulls migrating to West Africa, DEE seldom exceeded 4-times RMR (measured in captivity at rest in room temperature) during migration days, while weekly peaks were maintained below 3-times RMR, suggesting that even during periods
of concentrated energy expenditure gulls remain within a sustainable limit. The fact that all migration strategies demonstrated similar mean and maximal DEEs on migration days suggests that gulls do limit their daily effort to stay within a sustainable threshold, with long distance migrants instead choosing to allocate more time (via total number of migration days) to complete their longer migrations.

During the long autumn migration period, migrating birds could have further dispersed their migration days more evenly to spread out these high energy expenditure days, however typically migration days were clustered on either side of long autumn stopovers. Many gulls can be seen undergoing their post-nuptial moult during this period (Sept-Oct, Camphuysen CJ, unpublished data). This tactic may enable more separation between migration and moult, emphasising the importance of separating energetically demanding stages in the annual cycle (Wingfield 2005).

Increased time in flight during the late breeding stage resulted in it being one of the more energetically demanding periods during the annual cycle. While a peak period of energy expenditure, lesser black-backed gulls also do not appear to be maximizing (energetic) effort during this stage, remaining well below 4-times RMR. Supporting this, gulls have been observed outside of their breeding colony for long periods during the breeding season, emphasising that they are not devoting all their time towards breeding efforts (Shamoun-Baranes et al. 2011, Kavelaars et al. 2021). Elevated DEE as a result of increased breeding effort has been linked to reduced annual survival (Deerenberg et al. 1995, Daan et al. 1996). As a long-lived species with low annual reproductive output, maintaining lower levels of energy expenditure may be a mechanism to optimise long-term survival, and thus future potential breeding opportunities versus investing in survival of current offspring (Drent and Daan 1980).

When interpreting DEE reported here, it is important to consider that while variation in activity was likely reasonably well accounted for throughout the year in this study, many resting costs are not (e.g. feather moult, and fluctuation in basal metabolic rate due to plastic changes in morphology, physiology, and body mass during different annual cycle stages). Also, our bioenergetic model likely underestimates increased thermoregulatory costs from floating on cold water (due to the higher heat capacity and thermal conductance of water; Humphreys et al. 2007), as well as resulting from heat stress at elevated atmospheric temperatures (Lustick et al. 1978). Variation in resting costs throughout the year have been found to significantly influence DEE through time in other species, sometimes more-so than activity (Green et al. 2005, 2013, White et al. 2011, Guillemette and Butler 2012). In particular, early autumn stopovers appear to be a time of low energy expenditure, however the metabolic costs of feather moult likely do pose an energetic challenge during this stage. In future, measuring of physiological parameters (e.g. heart rate) along-side activity could
provide a more detailed picture of variation in energy requirements between annual cycle stages and migration strategies.

**Activity-budgets and DEE throughout the year**

Fluctuations in DEE and daily activity budgets through time were similar enough that there was not sufficient support for strategy-specific patterns when comparing across the entire year. Changes in DEE and activity-budgets also coincided with transitions between different annual cycle stages, demonstrating the need for behavioural flexibility to satisfy changing behavioural and energetic requirements of each stage (Dunn et al. 2020). Similarity in behavioural patterns among migration strategies suggests that conditions throughout the entire range currently used by lesser black-backed gulls can appropriately satisfy the behavioural and energetic requirements of the annual cycle stages during which those regions are occupied.

Time-budgets shifted throughout the breeding season. During the incubation period (typically beginning in May), gulls tend to stay closer to the colony and spend more time attending the nest (Camphuysen 2011). Chicks begin to hatch in June, when we saw a progressive reduction in time walking with time flapping increasing to the highest level obtained outside of migration, making this one of the more energetically demanding periods during the year. Increased time in flight likely results from increased foraging effort required to provision growing chicks (Camphuysen et al. 2015). Increasing energy expenditure as the stages of breeding progress from incubation through chick care is commonly found in energetic studies of seabirds (Dunn et al. 2018). We also found that West African migrants had slightly lower flight time compared to other strategies. Combined with the fact that this strategy returns later to the colony (Shamoun-Baranes et al. 2017), we speculate this may be because individuals wintering in West Africa are capital breeders, benefitting from their presumably more marine diet during winter, whereas the other strategies may be income breeders, investing more time into foraging throughout the breeding period. This could be explored further using stable isotope signatures (Whiteman et al. 2021).

During early autumn, time in flight dropped to an annual low, accompanied by a marked increase in time spent walking. This behavioural change is consistent with reduced activity observed during the non-breeding season of other seabird species and generally attributed to flight feather moult (Gutowsky et al. 2014, Cherel et al. 2016). Increased resting energy expenditures resulting from moult likely favours a reduction in energy invested in activity, especially flight, to help manage total DEE. During this period, most individuals remained at higher latitudes for several months after departing their breeding colonies, residing in the UK, Belgium or Northern France. Gulls spent a high proportion of time foraging in the ample agricultural and anthropogenic habitats available in those regions, which may
facilitate reducing time spent in flight, resulting in overall lower DEE during this period (before accounting for metabolic costs of feather moult, see below).

Longer-distance migrants, particularly the West African strategy, were less likely to demonstrate behavioural accommodations suggestive of moult than individuals migrating to nearer wintering areas. Long-distance migrants spent more days migrating, reducing time available for other annual cycle stages. This can result in increased temporal overlap between stages (Wingfield 2005). A greater portion of individuals migrating to West Africa showed a moult-like behavioural pattern during the breeding season, which may indicate they overlap moult with breeding. Alternatively, individuals migrating to West Africa may delay or suspend moult until reaching wintering areas, where they likewise are able to substantially reduce both flight and walking activity. This has previously been suggested for colonies in the UK, where gulls were found to have a bimodal pattern in onset of moult, hypothesised to be associated with whether individuals were resident (or short-distance migrants), versus migratory (Harris 1971, Verbeek 1977).

The migration strategies only diverged spatially following autumn stopovers. Despite residing in different wintering areas, individuals from all migration strategies managed to reduce activity and energy expenditure during winter months, with a remarkably high proportion of the day spent stationary. While activity and energy expenditure did not differ greatly between wintering areas, foraging habitats and environmental conditions did. Weather conditions experienced within the northern parts of winter range increased stationary metabolic rate, but not to a degree that it had a strong influence on DEE. Occurrence in winter foraging habitats shifted from primarily agricultural in French/UK migrants to marine or built-up areas in African migrants. Unfortunately, we are unable to account for differences in resource abundance or energy intake rates between wintering areas in this system, which may influence winter survival. However, food from agricultural areas tend to be of lower caloric value than food from marine or urban areas (van Donk et al. 2019). Variation in nutritional quality of resources during the wintering periods could also potentially lead to carry over effects on reproductive success (Sorensen et al. 2009). A comparative analysis of survival and reproductive outputs may illuminate long-term fitness consequences of using different wintering areas (Lok et al. 2011, Reneerkens et al. 2020, Pelletier et al. 2020, Carneiro et al. 2021).

Conclusions

Energy requirements were not influenced by migration strategy when averaging across the entire year, though as migration distance increases individuals have more days, weeks
and months during the year with higher and lower than average DEE. However, even during periods of elevated energy expenditure, individuals managed their time budgets to stay within what is likely a sustainable level. As such, we do not expect any strong consequences of migrating long versus short distances in lesser black-backed gulls arising from energetic challenges. High inter-individual variation in energy expenditure suggests that individual differences in foraging behaviour may be more influential to daily and annual energy requirements than migration strategy. Time budgets throughout the year were similar across all strategies, showing that for all migration strategies behaviour is appropriately adjusted to accommodate the main stages in their annual cycle. Generally, this demonstrates the ability of animals to adjust behaviour on fine- (e.g. daily activity budgets), meso- (e.g. habitat use) and coarse- (e.g. wintering locations) spatio-temporal scales throughout the year to regulate their energy expenditures in relation to fluctuating external conditions and key life-history events.

Acknowledgements

We are grateful to many people for their help with data collection, including Fred Cottaar, Maarten van Kleinwee and Jose Verbeek for their substantial ringing and monitoring efforts in the IJmuiden colony, Kees Oosterbeek (Sovon) and Elspeth Sage (UvA) for their work on Schiermonnikoog, as well as Rosemarie Kentie (UvA) for her work on Texel and help deploying GPS loggers on IJmuiden. JSB and the tracking projects were supported by Open Technology Programme, project Interactions between birds and offshore wind farms: drivers, consequences and tools for mitigation (project number 17083), which is financed by NWO Domain Applied and Engineering Sciences, in collaboration with the following private and public partners: Rijkswaterstaat and Gemini Windpark. JMB was supported by NSERC (PGSD3-503551-2017). UvA-BiTS studies are facilitated by infrastructures for e-Ecology, developed with support of NLeSC and LifeWatch and carried out on the Dutch national e-infrastructure with the support of SURF Cooperative. We thank the Staatsbosbeheer and PBN for to access the colonies on Texel and IJmuiden, respectively. The work was done under licence number A VD8020020174225, following the Dutch Animal Welfare Act Articles 9, 10 and 11 of animal experiment documents. (Hersbach et al. 2018 p. 5) was downloaded from the Copernicus Climate Change Service (C3S) Climate Data Store. (Buchhorn et al. 2020) was generated by the Global component of the Land Service of Copernicus, the Earth Observation programme of the European Commission.
Supplementary Materials for Chapter 4

Methods

Constants used in heat-exchange model

We updated the following constants used in Baveco et al (2011) to adapt our model to lesser black-backed gulls (following their notation). For body temperate $T_b$, we used a value of 40.4°C, which was measured using implantable loggers in free-range lesser black-backed gulls (Brown JM, unpublished data). Body radius $r$ was calculated from body mass at capture using an empirical relationship (Birkbeback, 1966, reported in Baveco et al 2011). Height of center of mass $h_b$ was 0.2 m. Our plumage resistance $r_p$ is based on the thermal conductance reported for herring gulls *L. argentatus* (0.0385 mL O$_2$ g$^{-1}$ h$^{-1}$ °C$^{-1}$, reported in Ellis and Gabrielsen 2002, based on measurements in Lustick et al 1978). We convert thermal conductance into Watts assuming 19.8 kJ L$^{-1}$ O$_2$ based on a respiratory quotient of 0.71 (Bartholomew 1982, Ellis and Gabrielsen 2002), and express it in terms of surface area by multiplying by the mass of the bird and dividing by surface area ($C$, in W m$^{-2}$ °C$^{-1}$). Plumage resistance (s m$^{-1}$), $r_p$, was then calculated as $r_p = \rho \cdot cp \cdot C^{-1}$, where $\rho$ (g m$^{-3}$) is the density of dry air at air temperature, $T_a$: $\rho = 1292 - (5 \cdot T_a) + (0.01567 \cdot T_a^2)$ (reported in Baveco et al. 2011, based on Robinson et al. 1976), and $cp$ is the specific heat of air (1.010 J g$^{-1}$ °C$^{-1}$). Because gulls stand or perch in open habitats, we assume a vegetation height, $h_v$, of 0 m and a surface roughness $z_o$ of 0.0005 m, the roughness value reported for sandy dunes and intertidal areas in (De Jong et al. 1999).

Results

Individual-level exploration of autumn time-budgets

The general trend during the autumn period shows a period of elevated walking with reduced time in flight. However, strategy-specific model results for the West African strategy suggest they do not follow this pattern, instead maintaining higher levels of walking during breeding, with both walking and time in flight decreasing throughout the autumn season. Individual bird-years were subsequently explored for this behavioural pattern, using the criterion of a minimum 30-day period where average time walking exceeded 2.5 hours while average time in flight was below 2.5 hours (Fig. S4.1 – 4.3). In accordance with the strategy-specific model, only two out of ten bird-years in the West African strategy demonstrated this behavioural pattern during autumn or winter, compared
to 59% in North African migrants, 67% of Iberian migrants all nine bird-years in French/UK migrants (Table S4.3). Instead, three of ten West African bird-years demonstrated this pattern during the breeding season (compared to < 10% in other strategies), while half of the West African bird-years never demonstrated this pattern (compared to 32% of North African migrants, 28% of Iberian migrants, and none of the French/UK migrants).

### Supplementary Tables and Figures

**Table S4.1.** Equations used to convert dynamic body acceleration (DBA, in G) to metabolic rate (MR, in W), based on behavioural classification.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Calibration Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flapping</td>
<td>$MR = 24.51 + 10.82 \cdot \text{DBA}$</td>
</tr>
<tr>
<td>Soaring</td>
<td>$MR = 6.76 + 10.63 \cdot \text{DBA}$</td>
</tr>
<tr>
<td>Walking</td>
<td>$MR = 5.74 + 14.19 \cdot \text{DBA}$</td>
</tr>
<tr>
<td>Stationary, excluding floating</td>
<td>$MR = 4.80 + 49.80 \cdot \text{DBA}$</td>
</tr>
</tbody>
</table>

**Table S4.3.** Number of bird-years showing a behavioural pattern suggestive of flight feather moult by annual cycle stage and wintering area.

<table>
<thead>
<tr>
<th>Winter Area</th>
<th>Breeding</th>
<th>Autumn or winter</th>
<th>No moult pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAf</td>
<td>3 (30%)</td>
<td>2 (20%)</td>
<td>5 (50%)</td>
</tr>
<tr>
<td>NAF</td>
<td>2 (9%)</td>
<td>13 (59%)</td>
<td>7 (32%)</td>
</tr>
<tr>
<td>IB</td>
<td>1 (6%)</td>
<td>12 (67%)</td>
<td>5 (28%)</td>
</tr>
<tr>
<td>FRUK</td>
<td>0 (0%)</td>
<td>9 (100%)</td>
<td>0 (0%)</td>
</tr>
</tbody>
</table>
Table S4.2. AIC comparison of GAMM models of daily energy expenditure, flight metabolic rate, time flapping, soaring, in flight (all flight combined), walking, and stationary, flight and stationary metabolic rate, and experienced weather condition, of lesser black-backed gulls throughout their annual cycle. Strat = migration strategy. Models shown in Fig. 4.3 and 4.4 are in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>n. par.</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Daily Energy Expenditure</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>f(day)</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>f(day) + strat</td>
<td>9</td>
<td>5.4</td>
</tr>
<tr>
<td>f(day*strat)</td>
<td>9</td>
<td>24.1</td>
</tr>
<tr>
<td>f(day*strat) + strat</td>
<td>12</td>
<td>29.5</td>
</tr>
<tr>
<td>null</td>
<td>5</td>
<td>186.0</td>
</tr>
<tr>
<td>strat</td>
<td>8</td>
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**Chapter 4 - Annual energy expenditure**

*Figure S4.1* Daily time in flapping flight by migration strategy (WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK). Bold black line shows GAMM prediction per strategy with approximate 95% confidence intervals. Coloured lines show 7-day mean daily energy expenditure per bird-year, coloured by latitude.

*Figure S4.2* Daily time spent soaring by migration strategy (WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK). Bold black line shows GAMM prediction per strategy with approximate 95% confidence intervals. Coloured lines show 7-day mean daily energy expenditure per bird-year, coloured by latitude.
Figure S4.3 Daily time spent walking by migration strategy (WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK). Bold black line shows GAMM prediction per strategy with approximate 95% confidence intervals. Coloured lines show 7-day mean daily energy expenditure per bird-year, coloured by latitude.

Figure S4.4 Daily time spent stationary by migration strategy (WAf = West Africa, NAf = North Africa, IB = Iberia, FRUK = France and UK). Bold black line shows GAMM prediction per strategy with approximate 95% confidence intervals. Coloured lines show 7-day mean daily energy expenditure per bird-year, coloured by latitude.
CHAPTER 5

Equal survival and reproductive parameters between short- and long-distance migrating lesser black-backed gulls

J. Morgan Brown*, Rosemarie Kentie*, Kees C. J. Camphuysen, Judy Shamoun-Baranes
* both authors contributed equally

To be submitted
Chapter 5 - Survival and reproductive parameters

Abstract

Seasonal migrations have evolved in a wide range of animal taxa, and migrating animals show remarkable diversity in their migration strategies, even between individuals from the same population. Migration is assumed to be costly in terms of time, energy and mortality risk, and long distance migrants often arrive later to breeding areas, often reducing reproductive success. These costs are expected to be balanced by increased survival due to higher quality wintering areas at lower latitudes. Alternatively, migration strategy may be dependent on an individual’s condition, where unequal fitness between strategies may occur. These assumptions are widely accepted within evolutionary theories of migration, though empirical evidence regarding the costs and benefits of migration is mixed. In this study we compare reproductive parameters (laying date, egg volume, hatching success) and apparent survival of lesser black-backed gulls (*Larus fuscus*) breeding in the Netherlands and whose winter range extends from the UK to West Africa, resulting in one-way migration distances that differ by more than 4500 km. We found no evidence of an effect of migration distance on reproductive parameters, despite previous work showing long distance migrants return later to breeding colonies. This may be because gulls are colonial breeders with socially induced lay dates, or perhaps because winter habitat quality offsets the consequences of returning later to the colony in long distance migrants. We also found no support for an effect of migration distance on apparent survival, corresponding with previous research showing that annual energy expenditure and behaviour throughout the year is similar across strategies in lesser black backed gulls. Combined, our results suggest equal fitness payoffs across strategies. Empirical support for fitness consequence of migration are conflicting, some finding survival or reproductive costs of migrating further, but others likewise find little effect of migration strategy on either survival or reproductive success. Considering that migratory species range widely in fundamental aspects of their biology, we conclude that the survival and reproductive consequences of migration will not apply universally to all migratory species, leading to a diversity in migration strategies among and within species.
**Introduction**

Seasonal migration is a life history strategy that enables animals to exploit peaks in resource abundance in seasonal environments for breeding while avoiding deteriorating environmental conditions during other parts of the year (Lack 1968, Alerstam et al. 2003). Migration has evolved in a wide range of animal taxa (Dingle 2014), but is epitomized by avian migrants whose capacity for flight allows them to efficiently travel thousands of kilometres (Alexander 1998, Newton 2008). There is remarkable variation in migration patterns among species, but also among individuals from the same breeding population. In extreme cases, wintering regions can span entire flyways, leading to inter-individual variation in both distance travelled during migration, as well as conditions experienced on wintering areas, creating different ‘migration strategies’. Migratory populations that demonstrate diverse migration strategies provide a natural comparison with which we can assess the fitness trade-offs (i.e. survival and reproductive performance) resulting from migrating to different wintering areas.

The migratory periods of the year are generally assumed to be costly, in terms of time, energy and mortality risk (Alerstam et al. 2003, Buehler and Piersma 2008), and these costs should increase with migration distance. Many, but not all, empirical studies examining seasonal variation in survival of migrating birds find that seasonal survival is decreased during one or both migratory stages; for example, diverse studies (Sillett and Holmes 2002, Klaassen et al. 2014, Lok et al. 2015, Rushing et al. 2017, Watts et al. 2019) found reduced survival during migration in raptor, songbird and wader species, while others found constant survival throughout the year in waterfowl, a crane and a wader species (Gauthier et al. 2001, Rakhimberdiev et al. 2015, Ely and Meixell 2016, Pearse et al. 2019). Typically adult mortality is highest during spring migration (Klaassen et al. 2014, Lok et al. 2015, Rushing et al. 2017), but see Sergio et al. (2019) who found higher mortality in autumn. Higher mortality during spring migration may be caused by spring migration being condensed into a shorter period (Nilsson et al. 2013), prevailing winds opposing the direction of travel (Klaassen et al. 2014, Lok et al. 2015), or late winter food-scarcity limiting the building of fat reserves needed to fuel migratory flights (Studds and Marra 2007). Interspecies variation in mortality risk during migration may indicate that elevated mortality is a property of the route’s environmental conditions (e.g. presence or absence of geographical barriers, prevailing wind conditions), rather than a generalizable consequence for all migration strategies (Klaassen et al. 2014, Senner et al. 2019).

In addition to direct fitness costs from mortality, increased time and energy expenditure as migration distances increase may influence reproductive success. Migrating further is expected to result in later arrivals to breeding areas compared to short-distance migrants.
(Ketterson and Nolan 1983), which has been found in comparisons among species (Schmaljohann 2019) as well as within populations using different migration strategies (Mazerolle and Hobson 2007, Rolshausen et al. 2009, Woodworth et al. 2016, 2017, Grist et al. 2017, Lok et al. 2017, Shamoun-Baranes et al. 2017), but see Kentie et al. (2017) and Reneerkens et al. (2020) who did not find long-distance migrants arrive later in spring. There is substantial evidence from a range of avian taxa, including songbirds, waterfowl, kestrels and some shorebird species, that later arrival to a breeding area, and subsequent later clutch initiation dates, decreases reproductive success (Dijkstra et al. 1990, Lepage et al. 2000, Brinkhof et al. 2002, Verhulst and Nilsson 2008, Kwon et al. 2018). Shorter time-spans between arrival and laying date can result in decreased egg volumes (Crossin et al. 2010), which in turn decreases hatchling survival (reviewed by Krist 2011). Empirical support for a link between migration distance and reproductive parameters is mixed, with some studies supporting the assumption that wintering closer to breeding areas increases reproductive success (Bearhop et al. 2005, Grist et al. 2017, Lok et al. 2017, Gow et al. 2019) while others found no or non-linear effects of migration distance on breeding parameters (Bregnballe et al. 2006, Pelletier et al. 2007, Kentie et al. 2017, Carneiro et al. 2021, Dufour et al. 2021).

To counter-balance potentially increased mortality during migration and reduced reproductive performance, migration should provide a fitness advantage for it to have evolved (Lack 1954). Winter habitat quality is expected to increase with migration distance as a result of greater abundance of prey (Mathot et al. 2012, Carneiro et al. 2021), milder weather and thus decreased maintenance metabolism (Castro et al. 1992), and increased stability in environmental conditions (Sanz-Aguilar et al. 2012, Acker et al. 2021a). Migration could be adaptive if winter habitat quality increases winter survival probability sufficiently to overcome the risks of migrating. Fitness could also be unbalanced across strategies. Migration could still have evolved if fitness is conditional on characteristics of the individual, e.g. subordinate individuals are not sufficiently competitive to remain near breeding areas and thus ‘make the best of a bad job’ by migrating to less competitive areas (Adriaensen and Dhondt 1990, Kaitala et al. 1993, Gillis et al. 2008). Otherwise, formerly adaptive migration strategies may have become maladaptive due to contemporary changes to the environment (e.g. resulting in increased survival at higher latitudes), with individuals continuing to use traditional migration strategies that now provide lower fitness (Lok et al. 2013, Reneerkens et al. 2020). Correspondingly, some empirical studies of species with partial or differential migration have found higher wintering or annual survival probabilities for those migrating further (Fernández et al. 2004, Alves et al. 2013, Zúñiga et al. 2017, Buechley et al. 2021), but others have found no effect or decreased survival with migration distance (Lok et al. 2013, Ely and Meixell 2016, Reneerkens et al. 2020).
Few studies weighed the costs and benefits of migration distance in terms of both survival and reproductive success within a population (but see Pelletier et al. 2020, Acker et al. 2021b).

In this study, we investigated whether migration distance influences the survival and reproduction of lesser black-backed gulls (*Larus fuscus*), a mid-sized coastal seabird that uses diverse migration strategies. A rapid increase in number of breeding pairs began in the 1960s (Spaans 1998), coinciding with an increase in the number of individuals overwintering at high latitudes (Baker 1980), with population growth stabilizing during the past 20 years (Koffijberg 2018). The winter range of Dutch breeding populations now extends from the UK to West Africa (a one-way difference of more than 4500 km). Typically individuals are highly site faithful during winter, and timing of migration and migratory routes are highly repeatable across years (Chapter 2). Lesser black-backed gulls are foraging generalists, with individuals using a varying proportion of marine, agricultural, and anthropogenic food resources (Camphuysen et al. 2015, Baert et al. 2018, Spelt et al. 2019). Changes in population size and winter range are both presumed to be a response to increased availability of anthropogenic food sources resulting from changing agricultural practices, fishing regulations, and waste management (Baker 1980, Spaans 1998). Wintering regions vary in primary foraging habitat types (Chapter 4), though migration strategy is not associated with individual foraging specialization during the breeding season, nor sex or size of the individual (Baert et al. 2018). Migration strategy does not influence annual energy expenditures, however, long-distance migrants do have a period of concentrated energy expenditure during spring migration, which could influence their body condition on arrival (Chapter 4), and they also consistently return later to the breeding colony compared to short-distance migrants (Chapter 2, Shamoun-Baranes et al. 2017).

To quantify fitness consequences associated with different migration strategies we use a combination of colour-ring resightings and GPS tracking to examine whether migration strategy affects reproductive parameters, including laying date, egg volumes and hatching success, and apparent survival of lesser black-backed gulls breeding in the Netherlands. Because gulls wintering further away arrive later to their breeding colonies than those wintering close-by, we hypothesized that longer distance migrants will either have later laying dates, and/or lay smaller eggs. Additionally, long-distance migrants may have lower hatching success if they are required to spend more time foraging to recover from migration, thus making their nests more susceptible to predation. If long-distance migrants winter in habitats of higher quality, we anticipate they will have higher apparent survival. Alternatively, contemporary anthropogenic changes to winter conditions in the northern extent of the winter range may have created new wintering foraging opportunities and
improved climatic conditions offering equal or better survival in short distance migrants, with some individuals continuing to use traditional, if suboptimal, strategies.

**Methods**

**Marking individuals**

Gulls were individually marked during their breeding season in two mixed herring gull (*L. argentatus*) and lesser black-backed gull colonies: between 2006-2020 in a coastal dune area on the Wadden Sea island Texel (‘Texel’, 53°01’N, 04°43’E), and between 2008-2020 on an artificial island in the mouth of the IJmuiden harbour (‘IJmuiden’, 52°28’N, 04°34’E). Adults were captured during the incubation phase using walk-in traps (May – June), and nearly fledged chicks were hand caught after the chick rearing phase (June – July). Gulls were marked with a numbered steel ring and a green colour ring with an engraved unique four-letter combination. Sex was assessed for adults using head and bill measurements (Coulson et al. 1983). Targeted resighting effort was carried out during the breeding season in both colonies by ourselves and a team of dedicated volunteers, while winter resightings were largely reported by citizen scientists.

Between 2008 – 2020, a subset of adult birds (n = 139) were additionally fitted with solar powered GPS loggers (12.5 - 18 g UvA Bird Tracking System; Bouten et al. 2013) using a backpack harness (Thaxter et al. 2014). GPS loggers were below 3% of body weight, and do not appear to affect early breeding parameters (Kavelaars et al. 2018). See Camphuysen et al. (2015) for more details on capture and tagging methods. Outside the breeding season, GPS locations were generally taken every 20 minutes and stored data was download remotely once birds returned to the colony. GPS-tagged birds were included in reproductive analyses, including the year they were tagged (Kavelaars et al. 2018), though tagged birds were excluded from survival analyses as we do not know whether GPS loggers impact survival probability.

**Reproductive parameters**

We visited the Texel breeding colony every third day throughout the breeding season (April – July) to mark new nests, number and measure length and width of newly laid eggs (in cm, to the mm), and identify parents. Nests were followed until hatching (see Camphuysen and Gronert 2012) for more details). Clutches mostly consist of three eggs, of which the last egg is often smaller than the first two. Lay date refers to the lay date of the first egg in the clutch. Egg volume (cm\(^3\)) was calculated as \((0.5035 \times \text{length} \times \text{width})^3\); Spaans and Spaans 1975). We included reproductive data from individuals from the year...
they were captured and marked (i.e. with colour rings and GPS tags if applicable), as well as any subsequent season where reproductive monitoring was carried out for those individual’s nests. Nests in IJmuiden were not followed in the same detail as in the colony on Texel, so the IJmuiden individuals were not used for analyses of reproductive efforts, only for survival analysis.

**Calculating migration distance**

Individuals were assumed to be at their main wintering locations between January or February, when GPS data indicates that 95% of lesser black-backed gulls are within their winter region (see ‘Determining winter resighting range’ and Fig. S5.1 in supplementary material). Not all birds were resighted every year. However, GPS data indicates that individuals have a high winter area fidelity and thus migratory distance is highly repeatable within individuals (R = 0.81; Chapter 2) so we assume winter area is constant across years. Therefore, the median latitude and longitude of all resightings or GPS data between January and February, pooling across all years, was used as an individual’s winter location. To ensure we do not accidentally include resightings during migration, we divided the wintering range into three regions: Africa, Iberia (Spain and Portugal), and France/UK. If an individual was resighted in multiple regions during January - February, only resightings in the furthest region were used to determine the winter location. Since Africa is the furthest region but had low resighting probabilities, we expanded the resighting period used to determine the winter location to include resightings in December. This added 6 individuals that winter in Africa to the dataset, five of which were resighted in West Africa, and were therefore unlikely to still be migrating. One individual is known to have changed wintering areas during the period of this study, and was removed. Migration distance was calculated as the geodesic between the breeding colony and their winter area (implemented in the geodist package in R; Padgham et al. 2021).

**Data analysis**

To examine parameters linked to reproductive performance, we fit generalized linear mixed-effect models (GLMM) of laying date, mean egg volume, volume ratio between first and third egg, and hatching success (proportion of eggs laid that survived until hatching) as a function of migration distance in R using package lme4 (Bates et al. 2015). Individual and year were included as random effects. Mean egg volume was only calculated for clutches with three or more eggs, and only using the volumes of the first three eggs if number of eggs laid exceeded three (if eggs are predated, females occasionally produce replacement eggs or repeat clutches). Wintering areas of both parents were often unknown. We therefore model reproductive parameters separately for males and females, without
accounting for the partner’s migration strategy. Mean egg volume and ratio between the volume of the first and third egg were only modelled for females, since males should have no influence on egg volumes. Gaussian error distributions were used for all models except proportion of eggs hatched, which was modelled with a binomial distribution with a logit link function. Models were validated visually by plotting histograms of residuals, and scatter plots of residual versus fitted values and migration distance. We used likelihood ratio tests to compare models with and without migration distance.

We estimated adult apparent survival (\( \Phi \)) and resighting probability (\( p \)) from ring-resightings of non-GPS-tagged birds using Cormack-Jolly-Seber mark-recapture models in program MARK (White and Burnham 1999) using RMark (Laake 2013). We used two resighting periods during the year, a breeding period (May – Jul), and a winter period. We increased the sighting period during winter from Jan-Feb to Dec-Feb in order to obtain sufficient sightings, but kept the migration distance based on resightings from the Jan-Feb period. Therefore, the survival probability between winter and summer represents ‘spring survival’ and the survival between summer and winter ‘autumn survival’. We account for unequal time steps in the models, and survival is estimated as a half-yearly survival probability. Individuals marked as fledglings could only enter the dataset as adults (more than five years) to exclude age-dependent effects.

We analysed a set of models where survival probability was constant throughout the year (‘constant’), differed by season (‘season’), differed with migration distance equally across seasons (‘distance’), where migration distance influences spring survival only (‘spring × distance + autumn’), where migration distance influenced autumn survival only (‘spring + autumn × distance’), and where migration distance influenced survival differently per season (‘spring × distance + autumn × distance’). For all models, resighting probability in winter could differ between wintering destinations (France/UK, Iberia, Africa). In summer, resighting probability may depend on whether a bird was marked as an adult in IJmuiden or on Texel, or marked as a fledgling. This is because resighting effort is expected to be higher in IJmuiden than on Texel, while fledglings may disperse from the natal colony as adults, lowering summer resighting probability. We did not let survival or resighting probability vary over time or by sex, due to the relatively small sample size (Table 5.1).

Goodness-of-fit is tested with U-Care (Choquet et al. 2009) called from R with R2Ucare (Gimenez et al. 2017). The overall fit, which was tested separately for birds ringed in IJmuiden, Texel or as fledglings and then summed, was not significant (\( \chi^2 = 151.5, \ df = 159, \ p = 0.65 \)). Model selection was based on Akaike’s information criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2010). We also present model averaged results, where predicted survival from each model in the set are averaged, weighting by the Akaike weights (\( w_i \); Burnham and Anderson 2010).
Chapter 5 - Survival and reproductive parameters

Table 5.1 Summary of migration distances and sample sizes per winter region for reproductive and survival analysis

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</table>

Results

Migration distances between individuals differed by more than 4500 km (Table 5.1), with Iberia being the most common winter region based on both resightings and GPS (Fig. 5.1). We had monitoring data from 275 nests from 155 individuals with a known wintering location (females: 118 nests from 72 individuals, males: 185 nests from 83 individuals; Table 5.1, Fig. 5.1). For 28 nests, both parents had known wintering areas, so were included in both female and male models. Nests from two females and five males were found after eggs were laid, so lay date was unknown. Two nests were missing an egg volume and 17 were incomplete clutches (fewer than three eggs), which were removed from models of egg volume. Nests from one female and four males had eggs with unknown fates and were removed from the models of hatch success. For survival models, we had a dataset of 322 individuals of known wintering area (Table 5.1).

We did not find an effect of migration distance on laying date (Female: \(\chi^2 = 0.270, df = 1, p = 0.603\), Male: \(\chi^2 = 1.350, df = 1, p = 0.245\); Fig. 5.2a), average egg volume (\(\chi^2 = 0.652, df = 1, p = 0.419\); Fig. 5.2b), the ratio between volume (\(\chi^2 = 0.095, df = 1, p = 0.758\); Fig. 5.2c), or proportion of eggs hatched (Female: \(\chi^2 = 0.076, df = 1, p = 0.783\), Male: \(\chi^2 = 0.300, df = 1, p = 0.584\); Fig. 5.2d). See Table 5.2 for model estimates.
Figure 5.1 Map of wintering locations of lesser black-backed gulls breeding in two colonies in the Netherlands (green triangles). Individuals are coloured to show which analysis they were included in, with both colour-ringed and GPS tracked birds from Texel with monitored nests being used for analysis of reproductive effects, and only colour-ringed individuals from both colonies being used in survival analysis. Points were jittered in both directions to increased visibility of overlapping points. Histograms on the right show the latitudinal distribution of winter locations determined from colour-ring resightings and GPS.
Figure 5.2. a) Laying date, b) mean egg volume, c) ratio between 3rd and 1st egg volumes, and d) proportion of eggs hatched by female (purple) and male (green) lesser black-backed gulls in relation to their migration distance. Points were jittered vertically in d) so overlapping values are visible. Effect of migration distance was insignificant for all reproductive parameters (p > 0.05).
The best supported survival model had a constant survival parameter, and thus there was no support for differential apparent survival between seasons with migration distance (Table 5.3). The seasonal 6-month survival probability was estimated as 0.91 (0.90 – 0.92 95% CI). Resighting probability during summer was higher than during winter, and highest for birds marked in IJmuiden. Resighting probability during winter was lowest for birds wintering in Africa (see Table S5.1 in supplementary materials for full model results). Although the model including an effect of distance and the model including an effect of season on survival were within 2 AIC of the top model, considering that both models have one additional parameter and that 95% confidence interval of the these parameters overlap zero (distance: -0.133 – 0.321; autumn: -0.505 – 0.962), we did not consider these models to be competitive (Arnold 2010). Model averaged survival estimates from the entire model set (Table 5.3) also show no effect of migration distance and season on survival probability (Fig. 5.3).

Table 5.2. Parameter estimates (± standard error) of GLMMs estimating the effect of migration distance on laying date, average egg volume, ratio between 3rd and 1st egg volumes, and proportion of eggs hatched. None of the models including migration distance explained significantly more variance than models excluding migration distance (LRT: p > 0.05).

<table>
<thead>
<tr>
<th>Laying date (Julian date)</th>
<th>Mean Egg volume (mm³)</th>
<th>3rd:1st egg volume</th>
<th>Proportion hatched</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed Effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>135.65 ± 1.57</td>
<td>74.68 ± 1.38</td>
<td>0.93 ± 0.01</td>
</tr>
<tr>
<td>Migration distance</td>
<td>-0.35 ± 0.67</td>
<td>-0.61 ± 0.76</td>
<td>-1 x 10⁻³ ± 7 x 10⁻³</td>
</tr>
<tr>
<td>(10³ km)</td>
<td>0.54 ± 0.47</td>
<td>0.76 ± 0.47</td>
<td>0.08 ± 0.30</td>
</tr>
<tr>
<td>Random Effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>12.16 ± 4.98</td>
<td>27.09 ± 1 x 10⁻³</td>
<td>3.38 ± 1.23</td>
</tr>
<tr>
<td>Year</td>
<td>14.67 ± 13.97</td>
<td>1.90 ± 1 x 10⁻⁴</td>
<td>0.45 ± 0.63</td>
</tr>
<tr>
<td>Residual</td>
<td>19.65 ± 19.40</td>
<td>9.48 ± 2 x 10⁻³</td>
<td>-</td>
</tr>
<tr>
<td>Sample Size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. Nests</td>
<td>114 ± 170</td>
<td>99 ± 99</td>
<td>116 ± 172</td>
</tr>
<tr>
<td>N. Individuals</td>
<td>70 ± 78</td>
<td>64 ± 64</td>
<td>71 ± 79</td>
</tr>
<tr>
<td>N. Years</td>
<td>13 ± 15</td>
<td>13 ± 13</td>
<td>13 ± 15</td>
</tr>
</tbody>
</table>
Chapter 5 - Survival and reproductive parameters

Table 5.3. Model selection results of lesser black-backed gull survival probability (Phi), where we examined whether survival probability was influenced by season and migration distance, including different distance effects per season. Models are ordered by ΔAICc, where n. par. is the number of parameters, wi is the Akaike weight, and deviance is the residual deviance. An interaction between two parameters is indicated with ×.

<table>
<thead>
<tr>
<th>Model</th>
<th>n. par.</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi(constant)</td>
<td>7</td>
<td>3208.495</td>
<td>0.000</td>
<td>0.390</td>
<td>2319.050</td>
</tr>
<tr>
<td>Phi(distance)</td>
<td>8</td>
<td>3209.847</td>
<td>1.351</td>
<td>0.199</td>
<td>3193.744</td>
</tr>
<tr>
<td>Phi(season)</td>
<td>8</td>
<td>3210.142</td>
<td>1.646</td>
<td>0.171</td>
<td>2318.673</td>
</tr>
<tr>
<td>Phi(spring × distance + autumn)</td>
<td>9</td>
<td>3210.901</td>
<td>2.406</td>
<td>0.117</td>
<td>3192.773</td>
</tr>
<tr>
<td>Phi(spring + autumn × distance)</td>
<td>9</td>
<td>3212.000</td>
<td>3.504</td>
<td>0.068</td>
<td>3193.872</td>
</tr>
<tr>
<td>Phi(spring × distance + autumn × distance)</td>
<td>10</td>
<td>3212.421</td>
<td>3.926</td>
<td>0.055</td>
<td>3192.265</td>
</tr>
</tbody>
</table>

Figure 5.3. Model-averaged apparent survival estimates with 95% confidence intervals of lesser black-backed gulls by season (autumn = purple, spring = green) and migration distance (based on all models in Table 5.3).
Chapter 5 - Survival and reproductive parameters

Discussion

Quantifying the consequences of different migration strategies on reproductive performance and survival is central to understanding short-term population dynamics and long-term evolution of migratory systems (Pulido 2007a, Taylor and Norris 2010). Contrary to our expectations, we found that migration strategy had no effect on reproductive parameters linked to reproductive success, nor apparent survival in lesser black-backed gulls breeding in the Netherlands where the shortest-distance migrants winter 4500 km closer to the breeding area than the longest-distance migrants.

Reproductive parameters

Arrival date to breeding areas is a metric commonly used to infer reproductive success in avian systems (Kokko 1999, Drent et al. 2003). The long-distance African migrants in our study system return on average more than three weeks later to the breeding colony than European migrants (Shamoun-Baranes et al. 2017), and thus we anticipated negative effects of migration distance on reproductive success. Yet, we found no subsequent effect on laying date, egg volumes, or hatching success, parameters which are expected to influence reproductive outputs and recruitment (Verhulst and Nilsson 2008, Krist 2011). As such, the common assumption that short distance migrants have a reproductive advantage due to benefits of priority access to territories does not hold in this species, breaking an assumption which has major implications on results of theoretical models of partially migratory systems (Kokko 2011).

Lesser black-backed gulls are colonially nesting seabirds and laying synchrony within Laridae is socially induced (Henson et al. 2010), which may explain why late-arriving long-distance migrants did not have later laying dates. Breeding before or after the peak laying date increases mortality of eggs and chicks in gull colonies (Brown 1967, Sydeman et al. 1991), whereas in non-colonial birds typically the earliest breeders have a reproductive advantage (e.g. Dijkstra et al. 1990, Lepage et al. 2000, Brinkhof et al. 2002, Verhulst and Nilsson 2008, Kwon et al. 2018). One consequence of laying synchrony is that late-arriving long-distance migrants will have a shorter interval between completing migration and laying their eggs. If birds return from migration in poor body condition, or if egg production commences during migration for late returning individuals, this could result in females reducing investment in egg production, decreasing the volumes of one or more eggs (Styrsky et al. 2002, Crossin et al. 2010). Individuals could also compensate for poor body condition by increasing foraging effort during the incubation period, potentially increasing the risk of egg predation. However, no effect of migration distance on either egg volumes nor hatching success was found. Overall, this suggests that even in later arriving African
migrants, the three-week interval between arrival and laying (based on average arrival dates in Shamoun-Baranes et al. 2017 and average lay dates in this paper) is sufficiently long to recover from migration and prepare for laying, resulting in no carry-over effect of migration strategy on reproduction (Carneiro et al. 2021).

It is also possible that migrants do not return in a deteriorated condition. Our study on energy expenditure of lesser black-backed gulls demonstrated that gulls limited energy expenditures to similar levels during migration days, regardless of migration distance or season (Chapter 4). Instead, long-distance individuals increased the number of days spent migrating. Limiting energy expended within a day likely helps migrants of all distances maintain energy balance and return to the breeding colony in similar condition. Further, the benefits of wintering in high quality habitat can carry-over to subsequent seasons to increase reproductive success (Norris et al. 2004, Sorensen et al. 2009). In our system, foraging habitat differs with wintering area, with birds wintering in Africa typically spending more time in marine habitats, and short distance migrants using more terrestrial habitats (Chapter 4), which may result in different energy intake rates or nutritional value across winter regions. This could mitigate the effects of late arrival to the breeding colony, particularly if long-distance migrating birds depart winter areas in better body condition, which may enable them to use stored energy reserves for breeding (i.e. capital versus income breeding).

While long distance migrants appear to fully compensate for their delayed arrival to the colony, we cannot account for variation in breeding propensity between strategies. It is possible that if a female’s body condition is poor or if one of the partners returns too late, an individual will forgo breeding in that year. The migration strategy of both parents of a nest was often unknown, so we also cannot account for mitigating effects of partners using different migration strategies (Grist et al. 2017). However, egg volumes are likely only influenced by female (versus male) migration strategy, with no significant effect found.

**Apparent Survival**

We found no support for an effect of migration distance on survival probabilities. Constant survival across migration distances could either indicate that mortality is not elevated during one of the migratory periods (Gauthier et al. 2001, Grüebl et al. 2014, Rakhimberdiev et al. 2015, Ely and Meixell 2016, Pearse et al. 2019), that increased mortality during migratory periods as migration distance increase is balanced by higher winter survival (Zúñiga et al. 2017), or that the migration strategy providing the highest survival probability fluctuates temporally with changing environmental conditions, resulting in balanced long-term survival (Acker et al. 2021b). Constant survival regardless of migration distance corresponds with our study showing that annual energy expenditures do not differ among migration strategies (Chapter 4), though we could not account for potential differences in energy intake rates between winter regions.
We also did not find support for a seasonal effect on survival. In many avian species, spring migration tends to be condensed into a shorter time period (Nilsson et al. 2013), which can be more energetically demanding and thus potentially more risky. Lesser black-backed gulls likewise have a shorter spring migration relative to autumn, though peaks in energy expenditures were similar across migratory seasons in all but the longest distance migrants (Chapter 4). If the migration period has an elevated mortality risk, increased migration effort during spring should lead to elevated mortality relative to autumn (Klaassen et al. 2014, Rushing et al. 2017, reviewed in Robinson et al. 2020), and we would expect this effect to be exacerbated as migration distance increases (Lok et al. 2015). A lack of seasonal effect in our survival model, for even the longest distance migrants, could be indicative that mortality is not greatly increased during migratory stages in our system, at least once an individual has reached adulthood. An interesting next step would be to examine whether survival is also balanced across strategies during immature stages, as young, inexperienced individuals often have higher mortality risk during migration and may be more susceptible to poor environmental conditions in winter than experienced adults (Sanz-Aguilar et al. 2012, Sergio et al. 2019).

Constant survival between different annual cycle stages (winter, breeding, migration), and thus among migration strategies, seems plausible for lesser black-backed gulls. Elevated mortality during migration can be attributed to food limitation at stopover sites (Moore and Yong 1991, Russell et al. 1994), diminished body conditions (Ward et al. 2018), and severe weather (reviewed in Newton 2008), all of which are exacerbated before or during the crossing of geographic barriers where no suitable habitat is available for landing during emergencies (Klaassen et al. 2014, Lok et al. 2015, Senner et al. 2019). Lesser black-backed gulls, being able to rest and forage on both land and at sea, and detouring around arid inland areas (Chapter 2), do not cross any major geographic barrier along their migration routes, and thus may be less susceptible to these hazards typically associated with migration. Further, we have little reason to expect elevated winter mortality in short distance migrants for this species. Modelled thermoregulatory costs throughout the wintering range of lesser black-backed gulls suggest that winter temperatures had little influence on daily energy expenditure even in the shortest distance migrants (Chapter 4), while anthropogenic resources such as refuse sites and livestock feeding stations likely provide stable food resources year-round, relieving the risk of resource instability expected for natural food resources at higher latitudes in winter.

**Co-existence of diverse migration strategies**

Coexistence of different migration strategies within a population are thought to evolve and be maintained either as a result of equal fitness payoffs across strategies, typically
modelled as evolutionarily stable strategies (ESS; Lundberg 1987), or alternatively, that the optimal strategy for an individual is conditional on its phenotype (e.g. dominance; Ketterson and Nolan 1976), where unequal fitness between strategies is often expected (Lundberg 1988, Adriaensen and Dhondt 1990). Most empirical research supports the latter (reviewed in Chapman et al. 2011). However, we found no effect of winter region on either survival or reproductive parameters, suggesting there is no strong selective pressure acting on migration strategy within these populations once individuals reach breeding age. Other systems have likewise found no effects of migration strategy on either survival or reproduction (Pelletier et al. 2007, Carneiro et al. 2021), while others find trade-offs that likely balance selective pressures across strategies (Acker et al. 2021b).

Given that differential migration is a widely spread phenomenon within migratory species (Chapman et al. 2011, Dingle 2014), encompassing species that differ greatly in fundamental aspects of their ecology and physiology such as breeding habits, foraging ecology and habitat requirements, morphology, thermal tolerance, and cognitive abilities, it is perhaps unsurprising that empirical evidence of the fitness consequences of different migration strategies are inconsistent. Thus, the survival and reproductive consequences of migration do not apply universally to all migratory species, likely contributing towards the huge diversity in migration strategies that exist among species, populations and individuals.

Acknowledgments

We thank Fred Cottaar, Maarten van Kleinwee and Jose Verbeek for their substantial ringing and monitoring efforts in the IJmuiden colony, as well as countless people who submitted ring resightings along the flyway. We also thank Susanne van Donk and numerous volunteers and students who have helped collecting data over the years in the Texel colony. RK and JSB were supported by Open Technology Programme, project Interactions between birds and offshore wind farms: drivers, consequences and tools for mitigation (project number 17083), which is financed by NWO Domain Applied and Engineering Sciences, in collaboration with the following private and public partners: Rijkswaterstaat and Gemini Windpark. JMB was supported by NSERC (PGSD3-503551-2017). UvA-BiTS studies are facilitated by infrastructures for e-Ecology, developed with support of NLeSC and LifeWatch and carried out on the Dutch national e-infrastructure with the support of SURF Cooperative. We thank the Staatsbosbeheer and PBN for to access the colonies on Texel and IJmuiden, respectively. The work was done under licence number AVD8020020174225, following the Dutch Animal Welfare Act Articles 9, 10 and 11 of animal experiment documents.
Supplementary Materials for Chapter 5

Methods

Determining winter resighting range

We separated the wintering range into three geographical regions: Africa, Iberia (Spain and Portugal), and France/UK. To determine when the majority of individuals are residing within their wintering region, we began with a set of all GPS tracks from individuals tagged on Texel or IJmuiden, with coverage for more than 75% of the bird-year (start and ending June 1) and no period with missing data exceeding 45 consecutive days. If an individual had tracks from multiple years, we selected the bird-year with the fewest recording gaps. Winter region was determined based on the most southerly latitude obtained. For each date, we then determined what percentage of individuals were within their winter region. The period during which more than 95% of individuals were within their winter region began on December 31 and ended March 2 (Fig. S5.1).

Supplementary tables and figures

Figure S5.1 Latitude by date of migrating lesser black-backed gulls tracked using GPS loggers. Tracks are coloured by wintering region. Vertical black lines show the time frame where 95% of individuals were within their winter regions. Periods with no data are more transparent.
Table S5.1 Parameter estimates (± standard error) and 95% confidence intervals of the most parsimonious model for 6-month apparent survival (Phi) with resighting probability (p) of lesser black-backed gulls.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi (constant)</td>
<td>0.910 (0.007)</td>
<td>0.896 - 0.922</td>
</tr>
<tr>
<td>p (marked as fledgling)*</td>
<td>0.226 (0.032)</td>
<td>0.169 - 0.296</td>
</tr>
<tr>
<td>p (marked on Texel)</td>
<td>0.643 (0.026)</td>
<td>0.591 - 0.692</td>
</tr>
<tr>
<td>p (marked in IJmuiden)</td>
<td>0.880 (0.015)</td>
<td>0.847 - 0.907</td>
</tr>
<tr>
<td>p (FRUK)</td>
<td>0.458 (0.033)</td>
<td>0.394 - 0.523</td>
</tr>
<tr>
<td>p (IB)</td>
<td>0.443 (0.022)</td>
<td>0.3401 - 0.486</td>
</tr>
<tr>
<td>p (AFR)</td>
<td>0.280 (0.050)</td>
<td>0.195 - 0.386</td>
</tr>
</tbody>
</table>

*a marked as fledgling but only entered the dataset as adult
CHAPTER 6

Consequences of diverse migration strategies: A synthesis

J. Morgan Brown
Why do animals migrate? During migration, animals move seasonally between two or more distant ranges. This allows them to exploit temporal fluctuations in resources and weather in seasonal environments, occupying these regions during the season when resources are abundant, and moving away as conditions deteriorate (Alerstam et al. 2003). Animals should benefit by having better access to resources year round, while experiencing more constant temperatures throughout the year (Somveille et al. 2019). Migratory journeys themselves, however, are expected to be costly, and the benefit to be gained by undertaking migration may change with current environmental conditions and how well animals can track them.

Migration is a complex behaviour that impacts the entire annual cycle. Where an individual migrates to spend the nonbreeding season should greatly influence both the environmental conditions they experience throughout much of the year, as well as the time, energy and risk associated with arriving there. While we have assumptions regarding the costs, benefits, and challenges of migrating, many of these consequences have yet to be quantified across different migration strategies. In this thesis I measured several ecological currencies, including energy, time-budgets, survival, and reproductive parameters of lesser black-backed gulls that migrate to different winter regions spanning more than 40 latitudinal degrees, from the UK to West Africa. The primary aim was to examine how these currencies trade off throughout the year, as well as among each other. First we examined whether migratory behaviour becomes less variable as migration distance increases, which may limit how well long-distance migrants can match their behaviour to year-to-year fluctuations and long-term changes in environmental conditions (Chapter 2). We then examined whether migration strategy influenced energy expenditure throughout the year, as well as whether individuals using different migration strategies were able to adjust their behaviour equally to different stages in in their annual cycle (Chapter 4). To do so, we first explored how our previously collected accelerometer data could be best used to estimate daily energy expenditures while revealing potential pitfalls of acceleration-based methods (Chapter 3). We achieved this by deploying heart rate loggers alongside our accelerometer-GPS tracking system, which also allowed us to measure the energetic costs of different movement modes in lesser black-backed gulls. From this we concluded dynamic body acceleration was a reasonable proxy for energy expenditure in this species, including during soaring flight though not while birds were floating on the water. It also could not account for all variation in resting costs among days. Finally, we examined whether migration distance influenced survival probabilities or reproductive success in this study system (Chapter 5).

Our general expectation was that costs of migrating would increase with distance, but that this would be balanced by increasing benefits during the winter. Such a trade-off might
Chapter 6 - Consequences of diverse migration strategies: A synthesis

Consequences of diverse migration strategies: A question of scale

Our environment is in constant flux. Animals can respond to environmental fluctuations by modifying their behaviour on a range of different spatial and temporal scales (Levin 1992). On the finest scale, animals can modify their movement behaviour in response to immediate changes in the landscape as they move through it (Shepard et al. 2013), such as a bird switching from flapping to soaring flight when it encounters rising air (Sage et al. 2019). On hourly to daily scales, animals can make decisions regarding where they go to forage, and how they distribute their time between different activities (Stephens and Krebs 2019). Migration is a response to seasonal environmental fluctuations, acting at broad spatio-temporal scales. Behavioural decisions on finer scales are nested within broad-scale behaviour strategies, mitigating or contributing towards the costs and benefits of broad-scale behaviours. Additionally, broad-scale movement decisions, such as where and when to migrate, influence the landscape within which an individual makes their fine-scale decisions.

Lesser black-backed gulls show immense variability in behaviour across all spatio-temporal scales, from their flexibility in flight mode (Shamoun-Baranes et al. 2016), diverse foraging behaviours (Camphuysen et al. 2015, Spelt et al. 2021), and, of course, different
migration strategies (this thesis). This enables them to respond to environmental change on different scales, simultaneously. In Chapter 2, we found that generally individuals were very repeatable in their migratory behaviours across years (e.g. migration timing and routes). We suggested that flexibility in fine-scale behaviour decisions may buffer gulls from potential consequences of mismatching their movements with current conditions, thus allowing them to repeatedly use the same strategy at a broad scale. Likewise, in Chapter 4, we found similar energy expenditure among strategies, though high variation in energy expenditure among individuals using the same strategy. From this we concluded that the day-to-day decisions of individuals, such as individual differences in foraging behaviour within the same winter region, is likely more influential to an individual’s annual energy budget and time allocation than their migration strategy. If all individuals, regardless of their winter destination, can mitigate their energy expenditures during migration, and change foraging strategies to match the resources available in their winter region so that all individuals have adequate energy intake over the winter, we would anticipate that migration strategy may not have a strong influence on survival nor carry over to influence reproduction, as we found in Chapter 5.

The extensive behavioural flexibility gulls demonstrate across spatio-temporal scales introduces a lot of residual variation to our natural experiment. The advantage of an experimental setup is that the experimenter can manipulate one or two independent variables to observe the response of the system while all other factors that may influence the system are kept constant. This allows the experimenter to isolate the effects of the variables being manipulated from other potentially influential factors. In natural experiments, however, investigators rely on experimental groups that arise naturally, and are unable to control other potentially influential factors. Few natural systems are so simple that you can disentangle all the factors which may be influencing a certain process. The lesser black-backed gulls are an extreme example of this. Within a given region and period of the year, individuals specialise on a range of different foraging strategies (Isaksson et al. 2016), introducing a lot of variation in day-to-day behaviour among individuals which is not accounted for with our definition of a migration strategy. On one hand, this behavioural flexibility may confound our ability to properly isolate the effects of migration distance on the currencies we measured. On the other hand, the gull system puts the effect strength of migration distances versus other daily decisions into perspective, where we ultimately conclude that fine-scale behavioural decisions may be far more influential on an individual’s energy budget, time-allocation, survival probability and reproductive success than how far they migrate during the year.

A more generalisable conclusion is that the conditions on an individual’s wintering and breeding areas, as well as at foraging areas along their migration routes, are likely far
more influential to an individual’s success (whether measured in terms of energy, survival or reproductive outputs) than the distance they have to travel to get to those areas. For lesser black-backed gulls, flexibility in foraging behaviours enables them to find suitable access to resources at a range of latitudes. Other migratory species are more constrained in their diets, and thus the choice of wintering areas (which determines their daily foraging opportunities) may be more consequential for their annual energy budgets or fitness than we found for the gulls. However, while quality of wintering areas may often be correlated with latitude, and thus migration distance, this is not always true. For example, in sanderlings (Calidris alba), wintering conditions in tropical areas (near the equator) provide poorer conditions compared to areas further north (shorter migration distance) or south (longer migration distance), as individuals overwintering in the tropics have both lower annual survival and delayed spring migrations (Reneerkens et al. 2020). This coincides with our conclusion that habitat quality (and thus daily behaviour) may be more important than migration distance. Our conclusion contradicts the idea that to reduce migratory costs animals should stop in the nearest area with suitable habitat (Somveille et al. 2015). The difference likely comes down to the fact that we consider the sum of movement and activity costs throughout the year, including the contribution of non-migratory days towards the annual energy budget, whereas many studies focus only on movement costs which arise during migration (e.g. Alves et al. 2013, Somveille et al. 2019). From our full annual cycle perspective, it seems worthwhile to fly an extra mile to reach an area with superior habitat conditions, versus stopping at the nearest suitable area.

Given that annual energy budgets, survival, and reproductive outputs are indeed likely to be influenced by what animals do at fine-scales on winter, breeding, and stopover areas, this reinforces the importance of increasing habitat quality in winter and stopover areas for the conservation and persistence of many migratory systems (Small-Lorenz et al. 2013). Further, it means that the winter ranges of species which have learned to use anthropogenic food sources are likely to be highly influenced by human behaviour with regards to agricultural practices and waste management. Under current management practices, anthropogenic resources provide suitable foraging opportunities further north, so that there is no longer a benefit of migrating long distances. This has led to a shift in wintering ranges in some species like the lesser black-backed gulls (Baker 1980), while other species are decreasing their migratory distances or have stopped migrating all together (Flack et al. 2016, Teitelbaum et al. 2016). Future changes to our land and waste management practices, such as closures of open landfill sites (Langley et al. 2021), may again constrict the suitable wintering range for these species. Whether or not species which have adapted to using anthropogenic resources during the winter will be able to resume their traditional migration routes if these resources become less readily available will likely depend on how
these routes are inherited. Species who learn migratory routes through social transmission run the risk of losing this knowledge, which may result in species failing to resume their migrations and having to relearn migratory patterns if their environment changes (Fagan et al. 2012, Jesmer et al. 2018).

Generalisability and migration

While we have tried to extend what we have learned from our studies on lesser black-backed gulls to other migratory systems, something else we could take away from this work is the challenge of trying to generalise across migratory species. For the main studies of this thesis, we tried to frame our expectations based on ‘general’ migration theory, versus what we may expect for the lesser black-backed gulls. More often than not, our results did not align with these general expectations. Are gulls an exception to the rule, or do we need a more diverse set of rules? We began this thesis heralding the diversity among migratory species, how it spans all major animal groups and terrestrial, aerial and aquatic environments. In the opening chapter of his taxon-inclusive book, Dingle (2014) expresses concern regarding our ‘ornithocentric’ view of even our most basic definition of what migration is, which he warns may inhibit biologists from drawing more general conclusions across diverse taxa.

Even among avifauna, migration can refer to many different types of seasonal movements. Some avian species are obligate migrants, with migrations occurring every year between fixed destinations, while others are facultative or irruptive, changing whether or not they migrate, and to where, among years (Newton 2012). Some species are nocturnal migrants, whose long flights are fuelled by fat reserves built up at stopover sites during the day. Others migrate during the day, foraging as they migrate (Strandberg and Alerstam 2007, Ward and Raim 2011, Amélineau et al. 2021). A lot of empirical and theoretic research on seasonal migration focuses on obligate, nocturnal migrants with more specialised diets, such as songbirds and waders. This creates a biased impression of what ‘typical’ consequences of migration may be. For example, obligate nocturnal species are expected to minimize the time they spend migrating between breeding and winter areas (Alerstam and Lindström 1990). Gulls, like many other seabird species (Amélineau et al. 2021), are diurnal migrants, and likely use a fly-and-forage migration strategy. This allows them to migrate slower, maintaining activity patterns more similar to non-migratory periods (Amélineau et al. 2021), which reduces the energetic consequences and risks of migrating (this thesis). In this thesis, we also used terminology developed for nocturnal migrants to describe the migratory movements of gulls. For example, while we use the
term stopover for stationary periods during migration (Chapters 2 & 4), the function of these areas in gulls is likely more analogous to secondary wintering areas, compared to how it is applied to nocturnal migrants who use them to rapidly refuel and depart on the next leg of their migration. We used the term stopover to make it more comparable to other migration systems, as have many other studies on seabird migrations (Klaassen et al. 2012, Dias et al. 2013), but perhaps trying to conform to these definitions perpetuates the issue of trying to generalise across groups where we should instead be trying to differentiate. Therefore, instead of broadening our research to a more diverse set of migratory species in order to increase our ability to generalise Dingle (2014), expanding the species we study for migration research may allow us to better identify what properties of migration give rise to certain costs or constraints, or, for which migratory species we may expect migration will have few consequences, as we found with the lesser black-backed gulls.

No consequences of migration strategy?

Before concluding that there are no consequences of migration strategy in lesser black-backed gulls, we must also consider whether our methods may be biasing our results. A drawback to our ‘natural experiment’ is that we cannot assess the consequences of potential migration strategies not observed within our population. For example, none of our GPS tracked gulls stay in the Netherlands year-round. From a climatic standpoint, it is typically only a few degrees colder in the Netherlands compared to the UK. Anecdotally, we know that many gulls in the UK forage at livestock feeding stations in open-air farms, a food source less available in the Netherlands where livestock (e.g. pigs) are kept indoors. The reduced availability of anthropogenic resources may mean that remaining resident within the Netherlands is costly, encouraging individuals to migrate to other wintering areas, whereas some gulls breeding in the UK can stay within 10 km of the colony year-round (Chapter 2).

If we can only observe and quantify the consequences of existing patterns, should we have expected to find any major misbalance between strategies? One advantage of lesser black-backed gulls as a study system is that their wintering range is in the process of shifting further north (Lack 1968, Baker 1980). Anthropogenic changes to the environment now provide food year-round at higher latitudes throughout the winter, presumably reducing the survival costs of wintering further north. Meanwhile, the consequences of long-distance migration have likely remained the same (Lack 1968). Even if the more northerly sites provided similar benefits at a lower cost, it is unreasonable to expect that individuals know
this and always behave in an optimal way. It is likely that individuals will continue to use the same strategies that they previously used, changing their strategy only under extreme circumstances (Chapter 2). For this reason, the population response to current, optimal conditions will be lagged, with many individuals continuing to use more ‘traditional’, if now suboptimal, migration strategies (Lok et al. 2013, Reneerkens et al. 2020). Because of this lag effect, we anticipate we should have observed any misbalance between strategies under current conditions if they existed.

The consequences of using a particular migration strategy may also differ with age, however this thesis only focused on adult individuals which have reached sexual maturation (> 4 years). Migrants can refine their migratory behaviour with experience. For example, black kites (*Milvus migrans*) improved their migratory behaviour throughout the first six years of their lives. Older birds departed and arrived from migrations earlier, were less likely to be delayed by crosswinds, and flew at paces more likely to conserve energy versus time, all traits likely to reduce some of the potential costs of migration (Sergio et al. 2014). The ontogeny of migratory performance may result in different strategies being more beneficial for different age groups. For example, in adult greater flamingos (*Phoenicopterus roseus*), long-distance migrants have higher annual survival than mid-distance or residential individuals. However, for first or second year birds, shorter distance strategies increased annual survival, presumably because migrating is more risky for inexperienced individuals (Sanz-Aguilar et al. 2012). By focusing on only experienced individuals, we cannot address the learning costs associated with different migration strategies.

We also do not account for sex differences in our study. Lesser black-backed gulls do not show sex-differential migration, though sexes can differ in their habitat use during the migratory periods (Baert et al. 2018). Males are also larger than females, which can increase the energetic cost of flight while reducing the thermoregulatory costs of cold weather. Differences in activity costs and foraging strategy within a region between sexes could explain some of the high intra-strategy variation within our studies, and may also mean that within a sex there are some trade-offs between strategies that were undetected when the data were pooled. We do not, however, anticipate that our results would change drastically if we analysed the sexes separately. If sexes were more successful with different strategies, we would also expect differences between sexes in the migration strategies they use (Ketterson and Nolan 1976).
Chapter 6 - Consequences of diverse migration strategies: A synthesis

Future directions: Initiating data collection on wintering areas

If gulls are using finer-scale behavioural adjustments to respond to environmental variation, we need higher-resolution analyses of their daily behaviour during winter. To provide a more mechanistic understanding of how individuals using different migrations strategies are able to adjust time-budget and regulate energy expenditure throughout their wintering range, more detailed studies on the foraging options and habitat use of over-wintering gulls are required to build upon the coarse-scale exploration initiated in Chapter 4. For this I recommend locally-based projects, versus relying on data from individuals migrating away from the breeding colony, to provide sufficient sample sizes per region, as well as obtaining local insights into the landscape and resource utilization in these areas. Excellent work in this regard is already ongoing in the Iberian Peninsula (Martín-Vélez et al. 2020), which has revealed the complexity of inter-individual variation in foraging and movement behaviour during the winter. Setting up research programs based within winter regions, including dedicated resighting efforts such as we carry out in the breeding colony, would also potentially enable us to estimate survival probability over the winter period in each region. Integration of winter and breeding survival estimates may allow more detailed separation of survival probability among winter, breeding and migratory periods (Sillett and Holmes 2002, Rushing et al. 2017, Schaub and Kéry 2021), which could be used to evaluate our speculation that survival in lesser black-backed gulls is likely to be constant across these four seasons (Chapter 5).

Another potential outcome from these winter-based projects would be to try to quantify population densities in these areas and relate that to foraging effort or energy intake. If resources in winter areas are potentially limiting, intra-specific competition will likely be an additional influential factor determining the cost-benefit trade-off between different migration strategies (Chapman et al. 2011). Density-dependant processes should play an important role in the evolution and maintenance of partial migratory systems (Taylor and Norris 2007, Lundberg 2013). For example, if too many individuals begin to use a given migration strategy, leading to a population density that exceeds the carrying capacity of that wintering area while creating a surplus in another wintering area, this should make the other strategies more favourable. I believe winter energy intake rates and identifying the roll of density dependence within these areas are our largest knowledge gaps with regards to understanding the consequences of diverse migration strategies in lesser black-backed gulls.
Future directions: Control of diverse migration strategies

By quantifying the costs, benefits and challenges of different migration strategies, we gain understanding into the drivers underlying migration life-histories (Cresswell et al. 2011, Shaw 2016). Yet an important objective in evolutionary ecology is to understand how animals respond to short and long-term changes to their environment (Reid et al. 2018). This in turn may help us predict how animal populations may be effected by the widespread and rapid changes to our planet’s environment. I believe our ability to forecast changes in migratory behaviour is limited by our understanding of how migratory animals, and gulls in particular, make migratory decisions.

Behavioural decisions result from the processing of information (or cues) that inform how an animal should behave (McFarland 1977, Schmidt et al. 2010). How an animal processes information could, on one extreme, be entirely under genetic control (including genetically programmed reaction norms; van Noordwijk et al. 2006, Bonamour et al. 2019). On the other end of the spectrum, animals can use exploration and learning to create new decisions rules about how they respond to information (Sol et al. 2013, Mueller et al. 2013, Jesmer et al. 2018). Research in different migratory systems has supported both of these extremes. For example, re-introduced populations of ungulates do not immediately resume historical migration patterns, although they do eventually relearn how to migrate, suggesting migration routes are socially transmitted (Jesmer et al. 2018). Similarly, captive raised whooping cranes (Grus americana) must be trained to migrate, and genetic relatedness has no effect on migratory behaviour (Mueller et al. 2013). However, experiments on songbird species have found that the timing of migratory readiness and migratory orientation is heritable and under endogenous control (Berthold 1996, Gwinner 1996), though it is increasingly recognised that there is ‘residual variation’ around genetic programs arising from response to environmental conditions and individual state (Pulido 2007b, Åkesson and Helm 2020).

Currently, we do not know how the migration strategy of individual lesser black-backed gulls is determined. Tracking of juveniles has provided some initial insights, suggesting orientation may be broadly genetically programmed but use of stopover and wintering areas may be influenced by social learning (Borrmann et al. 2021). Joint tracking of adults with their offspring would enable us to determine whether offspring use the same migration strategies as their parents. If offspring do show similar migratory behaviour, translocating eggs among nests and between populations would help separate whether similarities arise due to genetic inheritance (where offspring behaviour should match the behaviour of their genetic parent and colony) versus being socially learned (where behaviour of translocated
fledglings should match that of their adopted parents and colony). Joint tracking of parents and their offspring is currently being attempted, though logistically hampered by the need to capture adults during their incubation phase combined with over all low survival of chicks until fledgling, making the successful pairing of tracked adults with surviving chicks difficult.

Beyond determining how broad-scale migration strategies arise, it could also be fruitful to examine the regulation of finer-scale migratory decisions, such as the timing of movements in relationship to current environmental conditions or other stages in the annual cycle (e.g. moult; Watts et al. 2018) in systems with differential migration. This is particularly worth considering in the case of migration strategies that develop through learning (as we suspect may at least partially be the case for lesser black-backed gulls; Borrmann et al. 2021), as the regulation of these fine-scale traits may set limits on how successfully animals can change or adopt certain migration strategies. Plastic reaction norms, where the information used to inform decisions depends on spatial location, could be one mechanism for genetically controlled behaviours to be optimised regardless of the migration strategy adopted by an individual. For example, animals can change how they evaluate different information sources (e.g. photoperiod versus weather) based on their latitude or distance to their destination (Duriez et al. 2009, Bauer et al. 2020), which should function regardless of migration strategy. Magnetic cues (providing spatial location information to the migrant) have already been shown to control other migratory traits, such as fuel deposition rates (Fransson et al. 2001), so it is plausible that similar control mechanisms could be extended to behavioural decisions.

While it is conceivable that individuals that have adopted different migration strategies can learn to adjust other behavioural decisions alongside their migration strategy, other important traits, such as the timing of moult, must be physiologically controlled. The optimal time to moult in the annual cycle may depend on migration strategy, which determines the relative resource abundance between breeding and winter areas (Barta et al. 2008). Moult timing has been shown to be controlled endogenously in several species (i.e. expressed in the absence of external cues, though endogenous oscillators are often entrained by photoperiod cues; Gwinner 2003, Helm 2006, Karagicheva et al. 2016). Observations of moult patterns have however shown that individuals can adjust the speed of moult, or suspend moult, to avoid overlap with breeding or migration (Piersma and Jukema 1993, Hall and Fransson 2000, 2001, van Bemmelen et al. 2018). Some of this plasticity has been related to food availability, temperature, body condition, or photoperiod (Piersma and Jukema 1993, Mulder and Magrath 1994, Hall and Fransson 2000, Danner et al. 2015). In lesser black-backed gulls, it has been suggested that individuals can suspend moult while they migrate (Harris 1971), and onset of flight feather moult was hypothesised
to relate to migration strategy, where residents initiate moult earlier and long-distance migrants have a delayed onset of moult (Verbeek 1977). We saw behavioural patterns in Chapter 4 which would coincide with this, and it would be interesting to determine how difference in moult timing could be regulated if these strategies are learned as opposed to genetically determined. The first step would be to confirm whether or not gulls using different migration strategies indeed moult in different regions. One possible approach would be to analyse stable isotopes from clippings of the first and last feathers to be grown in the moult sequence, to determine in what regions moult is initiated and terminated. These clippings could then be related to that individual’s winter area, determined by either GPS tracking or colour ring resighting.

Conclusions

The aim of this thesis was to compare the consequences of diverse migration strategies among lesser black-backed gulls migrating a wide range of distances. In Chapter 3 we compared heart rate and acceleration-based methods as proxies for measuring energy expenditure, concluding that dynamic body acceleration is a reasonable proxy in this species. In Chapters 2, 4, and 5, we quantified several potential consequences of migrating in individuals using a range of different migration strategies. Throughout these studies we found no strong effect of migration strategy on behavioural variability (Chapter 2), energy requirements (Chapter 4), activity patterns (Chapter 4), survival probability (Chapter 5) or reproductive parameters (Chapter 5). However, we also found high inter-individual variation in these patterns within a given strategy. From this we conclude that individual behavioural strategies acting on finer spatio-temporal scales may be more influential for determining annual energy budgets, and possibly by extension fitness, than migration distance. Such inter-individual variation in fine-scale behaviours is emphasised by our study system, due to the wide behavioural repertoires gulls exhibit as a result of being foraging generalists. Given the numerous currencies that can be influenced by a migration strategy, and the various scales on which individual can adjust their behaviour, we anticipate that the existence of multiple successful migration strategies is likely to be the norm for most migratory species.
References

Author Contributions

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Summary

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References


References


Berthold, P. 1996. Control of bird migration. - Chapman & Hall.


References


References


Magnan, A. 1922. Les caractéristiques des oiseaux suivant le mode de vol; leur application à la construction des avions. - Annales des sciences naturelles: Zoologie 10(5).


References


Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total
   speed of migration increases with migration distance in migratory songbirds: a cross-
   continental analysis. - Mov Ecol 7: 25.
   overview on the ecological significance of making informed decisions. - Oikos 119:
   304–316.
   migratory survival and highly variable migratory behavior in black-tailed godwits. -
   Frontiers in Ecology and Evolution 7: 96.
Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L. L., Blas, J., Tavecchia, G., Pretoni,
   D. and Hiraldo, F. 2014. Individual improvements and selective mortality shape lifelong
Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G. and Hiraldo, F. 2019. When and
   where mortality occurs throughout the annual cycle changes with age in a migratory
Shamoun-Baranes, J., Bouten, W., Camphuysen, C. J. and Baaij, E. 2011. Riding the tide:
Shamoun-Baranes, J., Bouten, W., van Loon, E. E., Meijer, C. and Camphuysen, C. J.
   2016. Flap or soar? How a flight generalist responds to its aerial environment. - Phil.
   Trans. R. Soc. B 371: 20150395.
   Short distance migrants travel as far as long distance migrants in lesser black-backed
Shaw, A. K. and Couzin, I. D. 2013. Migration or Residency? The Evolution of Movement
   Behavior and Information Usage in Seasonal Environments. - The American Naturalist
   181: 114–124.
   182: 298–312.
Sillett, T. S. and Holmes, R. T. 2002. Variation in survivorship of a migratory songbird


van den Bosch, M., Baert, J. M., Müller, W., Lens, L. and Stienen, E. W. M. 2019. Specialization reduces foraging effort and improves breeding performance in a generalist bird. - Behav Ecol 30: 792–800.


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Chapter 2. Long-distance migrants vary migratory behaviour as much as short-distance migrants: an individual-level comparison from a seabird species with diverse migration strategies

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JMB, JSB and WB conceived the idea for this study. CJC, LL, WM, CT, and JSB led the tracking projects. JMB analysed the data under consultation with EvL. JMB wrote the manuscript. All authors provided comments on the manuscript.

Chapter 3. Acceleration as a proxy for energy expenditure in a facultative-soaring bird: comparing dynamic body acceleration and time-energy budgets to heart rate

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JMB, JSB and WB conceived and led the study. CJC helped design and facilitated data collection in the field. BAN facilitated data collection in captivity and advised on data analysis. JMB analysed the data and wrote the manuscript. All authors provided comments on the manuscript.

Chapter 4. Migrating further does not affect annual energy expenditure but increases variation in daily energy expenditure in lesser black-backed gulls

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JMB, JSB and WB conceived the idea for this study. CJC and JSB led the tracking projects. JMB analysed the data and wrote the manuscript. All authors provided comments on the manuscript.

Chapter 5. Equal survival and reproductive parameters between short- and long-distance migrating lesser black-backed gulls

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All authors conceived the idea for this study. CJC leads the ongoing monitoring work on Texel. CJC and RK conducted field work, CJC managed the colour-ring database. JSB assisted with GPS tracking. RK led the analysis, with contributions from JMB. JMB led the manuscript writing, with contributions from RK. All authors provided comments on the manuscript. * JMB and RK contributed equally to this work and share co-first authorship.
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Summary

Geese honking overhead, filling the sky with their characteristic chevron flight formations. A river turned pink with salmon on their terminal trip to their freshwater spawning grounds. The thunder of hooves from a line of wildebeest crossing the savanna, looking for greener pastures. Migration, the directed movements of animals between two or more distant habitats or regions, is a widespread phenomenon within the natural world. The distances animals cover by walking, flying or swimming during migration can be great, and they often move in large numbers, either together or separately. Animal migrations herald the change of seasons, they are beautiful, they are epic.

Why do animals migrate? Many animal migrations are linked with seasonal changes in weather, which in turn causes predictable increases and decreases in food availability. Seasonal migrations allow animals to move into areas with seasonally fluctuating environments during the part of the year when food is plentiful and the weather is nice. Animals often breed in these areas, which provide abundant food, potentially allowing a parent to raise and feed more young. The return migration journey then allows animals to retreat when weather deteriorates and food becomes scarce, conditions which may decrease their chances of surviving if they remained.

While animals can clearly benefit by following these seasonal changes in food and weather, there are also disadvantages to migrating. Animals must use a lot of energy to travel between distant areas. Migrating takes time away from other tasks they need to carry out. These journeys can also be dangerous. Animals may run out of energy. Predators congregate along migration corridors. Storms may interrupt birds trying to cross water or deserts, while roadways or dams may block the pathways of animals that walk or swim. These so-called costs are likely to increase the further an animal migrates.

How far then, and to where, should an animal migrate? Ideally, animals should move between areas that maximize the benefits they receive by migrating while minimizing the costs. Calculating how much an animal may gain or lose by migrating between two areas is, however, not a simple task, and the results may be difficult to predict. This is because these costs and benefits can interact with each other and change throughout the year. For example, while an animal may use a lot of energy migrating, this could be offset by not having to use as much energy to stay warm during the winter. Or, the increased chance of surviving the winter gained by migrating may come at the cost of fewer breeding opportunities if migrants are delayed when returning to their summer breeding areas.

The main aim of this thesis is to understand how the decision of where to migrate (which I call a ‘migration strategy’), influences the costs, benefits, and challenges an animal faces while migrating. One way of calculating the costs, benefits and challenges of
using different migration strategies is to measure and compare them between individuals from a single population that migrate to different areas. One species which has a lot of variation among individuals in their migration strategies is the lesser black-backed gull (Latin name: Larus fuscus). Within breeding colonies in the Netherlands, you can find lesser black-backed gulls nesting side-by-side that range from short-distance migrants traveling 250 km to winter in the UK, to individuals that migrate over 4500 km to West Africa. For 15 years we have been following the migratory journeys of lesser black-backed gulls by attaching GPS loggers to their backs, as well as monitoring their survival and breeding attempts. This creates an opportunity to measure the consequences of different migration strategies in the natural world.

To begin, it is useful to know whether an individual always migrates to the same place, or whether they can change their strategy year-to-year. We answer this question in Chapter 2, using GPS tracking data from gulls that have been followed for multiple years. As well as looking at whether gulls can change their migration strategies, we examine how much they change their behaviour within a migratory journey across years, such as when they depart and arrive on migrations, the routes they follow, and whether they roost and forage in the same areas within their winter region. These are important decisions to make, because the better an animal can match their migratory movements to patterns of food and weather in a given year, the more they can benefit from their migration journeys.

The information animals use to make these decisions may depend on how far they migrate. Because short-distance migrants have winter ranges near to their breeding range, these areas are likely to be influenced by similar weather systems. This means short-distance migrants can use information in their current area to predict what conditions may be like at their destination, resulting in behaviour that changes among years. Long-distance migrants, on the other hand, being further from their destination, are more likely to experience separate weather systems. Disjunct weather between breeding and wintering areas makes predicting future and distant conditions unreliable, and instead it may be safer for long-distance migrants to move based on averages of past weather conditions. This would result in long-distance migrants having very little variation in their migratory behaviour across years. Concern has therefore been raised regarding whether long-distance migrants will be able to change their migratory behaviour alongside our rapidly changing climate.

In Chapter 2 we found that over-all gulls were inclined to behave similarly across years, with an individual tending to migrate around the same time, using a similar route, and moving to the same area. However, we also found a few exceptions for each trait we examined. This included a handful of individuals that completely changed their migration strategy. Importantly, behavioural variability was not linked with migration distance, and
different individuals were often among the most variable for each of the different traits we
examined. This leads us to believe that any individual could behave flexibly if required,
though their preference is to use strategies that they have used in the past.

Next we wanted to examine the energy and time costs of using different migration
strategies. Alongside taking GPS positions, our trackers also measure body movement
patterns in three dimensions (forwards, sideways, and vertically), using accelerometers.
These patterns can be used to identify whether a gull is flapping, soaring, walking,
floating on water, or resting. Because it takes energy to make these movements, adding
up the acceleration over a recording segment, called dynamic body acceleration, might
also enable us to estimate how much energy the gull was using at that time. First, we
needed to figure out how much energy expenditure increases for every increase in dynamic
body acceleration. We also needed to determine whether this conversion is the same
across the different types of movement modes gulls use. We study this in Chapter 3,
by measuring acceleration alongside heart rate, a more familiar method of estimating energy
expenditure. We found that both heart rate and acceleration showed similar increases and
decreases across most movement types. However, acceleration while floating was higher
than while resting, whereas heart rate indicated energy expenditure was similar among
these behaviours. However, this is likely because acceleration also detects movement from
waves (which does not cost a gull any extra energy). We also compared different ways of
estimating daily energy expenditure using accelerometers, by either averaging patterns of
acceleration over the day, or by creating a time-energy budget, where the proportion of
time an animal spends in a behaviour is multiplied by the average energetic cost of that
movement type and summed over the day. Both methods produced similar results, though
each underestimated daily energy expenditure on days with higher resting heart rates, and
overestimated on days with lower resting heart rates. This shows that acceleration methods
may miss some changes in daily energy expenditure that are the result of changes in resting
metabolic rate (such as energy needed to maintain body temperature, digest food, fight an
infection, or grow new feathers), which cannot be detected by movement alone.

In Chapter 4, we applied the acceleration method to tracking data of migrating gulls,
to estimate how much energy they spend on movement-related activity throughout the
year. We combined the acceleration estimates of energy expenditure with a heat-exchange
model that estimates the energy needed to stay warm based on the weather the individual
was experiencing in its location. We found that the total amount of energy used by gulls
during the year was on average equal across different migration strategies. However,
individuals within the same strategy could differ a lot from each other in how much energy
they used. We also found that, for short-distance migrants, energy expenditure was rather
constant through time, whereas long-distance migrants had periods of the year where
they had high energy expenditures, while during other periods they had below-average energy expenditure. Next, we divided the year into different stages, including breeding, migrating, stopover (days during the migration period when birds aren’t actively moving towards their destination), and winter. Energy use was highest during late breeding and on migration flights, and lowest during winter, as well as on long-autumn stopover where gulls are likely replacing their body feathers (an extra energy costs we didn’t account for). Gulls changed their behaviour in similar ways during each of these stages, regardless of their migration strategy. For example, they increased their time in flight while breeding, spent more time walking during autumn, and reduced movement activity during winter.

Energy expenditure and time allocation may contribute towards an individual’s survival and reproductive outputs. Combined, these traits determine the contribution of an individual’s genes to the next generation, and determine the growth rate of a population. In Chapter 5 we examine whether a gull’s migration distance influences when they lay their eggs, the size of their eggs, and the probability of those eggs hatching, all traits which can influence their reproductive output. We also looked at whether migration distance influences survival probability, using reported observations of colour-coded rings on winter areas as well as in the breeding colony. We found no effect of migration distance on reproductive traits or survival, suggesting migration strategy does not result in any fitness consequences or trade-offs.

It is remarkable that a 20-fold increase in migration distance, as well as spending the winter in regions that range from cold Britain, where birds forage at garbage dumps and on pig feed, to the rice field and cities of Spain, versus the sunny beaches of Africa where surface-feeding fish can be caught throughout the winter, seemed to have little influence on any of the properties we studied. Most of our understanding and assumptions relating to the costs, benefits and challenges of migrating stems from work on smaller avian migrants, which have specific food preferences and are more susceptible to harsh weather. Gulls, however, are a very different type of animal. They have learned to forage on a variety of different food types, including fish (often from fisheries), insects (often in agricultural fields), and human waste. This provides them with many foraging alternatives in the face of unexpected changes to their landscape. They are large, well-insulated birds, making them more robust in the face of winter weather. Gulls can also rest on both water or land, which may lessen the survival risks of migrating. What we can take away from this is that migration does not always present a cost. Through their behavioural flexibility, gulls could adjust to the different challenges presented by their respective migration strategies, allowing them to manage their time and energy budgets throughout the year, and providing them with equal chances of surviving and reproducing when they return to their colonies. By carrying out research on less ‘traditional’ migratory species, we obtain broader insights into the limits posed by migrating as well as how animals can overcome them.

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Samenvatting

Translated by Dr. Marwa Kavelaars

Ganzen vliegen gakkend over, de lucht vullend met hun typerende V-formatie. Een rivier kleurt roze door de zalmen die op weg zijn naar het paagebied, hun laatste bestemming. Hoeven klinken donderend door de Savanne, van gnoes op zoek naar groener land. De trek van dieren tussen twee of meer verre habitats, oftewel migratie, is een wijdverspreid fenomeen in de dierenwereld. De afstanden die dieren vliegend, zwemmend of lopend afleggen kunnen enorm zijn, en ze bewegen zich vaak in grote aantallen voort, samen of alleen. Migratie kondigt op een mooie en epische manier de verandering van de seizoenen aan.

De vraag is waarom dieren migreren. Migratie is vaak gelinkt aan seizoensgebonden veranderingen in het weer, die op een voorspelbare manier invloed hebben op de voedselbeschikbaarheid. Door migratie kunnen dieren verkassen naar gebieden waar de weersomstandigheden op dat moment beter zijn en er genoeg voedsel is. Vaak planten ze zich in die gebieden voort omdat de grote beschikbaarheid aan voedsel de ouders in staat stelt om meer jongen groot te brengen. Wanneer de (weers-)omstandigheden vervolgens verslechteren en er minder voedsel te vinden is, kunnen ze weer verder trekken of terug migreren, daarmee hun overlevingskansen vergroten.

Dieren hebben duidelijk profijt van het meebewegen met de seizoensgebonden veranderingen in het weer en de voedselbeschikbaarheid, maar er zijn ook nadelen aan migratie. Van het ene naar het andere gebied trekken kost veel energie, met eventueel uitputting tot gevolg. Bovendien kunnen tijdens deze lange reis andere belangrijke taken niet uitgevoerd worden en ligt er veel gevaar op de loer. Zo komen roofdieren samen op belangrijke knooppunten van trekroutes en bemoeilijken stormen de oversteek van vogels over de zee of woestijn, terwijl wegen of dammen de paden van lopende of zwemmende dieren blokkeren. De kosten die met al deze hindernissen gepaard gaan zullen waarschijnlijk toenemen naarmate de afstand groter wordt.

Hoe ver en waarheen moeten dieren dan migreren? Idealiter zouden ze tussen gebieden trekken die zo voordeling mogelijk voor hun zijn, terwijl ze de kosten zo laag mogelijk proberen te houden. Berekenen hoeveel voordeel er uit trek gehaald kan worden, is echter geen gemakkelijke taak en het is vooraf moeilijk te voorzien wat het resultaat zal zijn. Er is namelijk een wisselwerking tussen de kosten en de baten, die ook nog eens verandert door het jaar heen. Migreren vereist bijvoorbeeld veel energie, maar waarschijnlijk minder dan de hoeveelheid die nodig is om in de winter warm te blijven in een koud gebied. De kans om de winter te overleven is groter in een gebied met een milder klimaat, maar de
afstand naar het broedgebied is dan soms zo groot dat er in geval van vertraging onderweg bij aankomst minder broedplekken over zijn.

Het doel van dit proefschrift is om te begrijpen hoe de keuze van een dier om naar een bepaald gebied te migreren (vanaf nu ‘migratiestrategie’) invloed heeft op de kosten en baten van migratie en de uitdagingen die daarmee gepaard gaan. Een manier om de kosten, baten en uitdagingen van verschillende migratiestrategieën te bepalen is om deze te berekenen en te vergelijken tussen individuen die naar verschillende gebieden migreren. De Kleine Mantelmeeuw (Larus fuscus) is daar uitermate geschikt voor door de grote variatie aan migratiestrategieën tussen individuen. In de broedkolonies van Nederland kun je individuen vinden die korte afstanden afleggen, bijvoorbeeld 250 km naar het Verenigd Koninkrijk, maar ook vogels die 4500 km naar West-Afrika vliegen. Gedurende 15 jaar hebben we deze Kleine Mantelmeeuwen gevolgd met behulp van GPS trackers, terwijl we ook hun overleving en broedpogingen volgden. Dit stelde ons in staat om de consequenties van de verschillende migratiestrategieën te bepalen.

Om te beginnen is het nuttig om te weten of individuen altijd naar dezelfde plek migreren of dat ze hun strategie van jaar tot jaar kunnen aanpassen. Dit wordt uitgezocht in hoofdstuk 2 met behulp van GPS data van meeuwen die meerdere jaren gevolgd zijn. Naast dat we bestuderen of meeuwen hun migratiestrategie kunnen aanpassen, onderzoeken we ook hoeveel hun migratiegedrag verandert tussen verschillende jaren, bijvoorbeeld de timing (wanneer ze vertrekken en aankomen), de routes die ze volgen en of ze op dezelfde plek slapen en foerageren in het overwinteringsgebied. Dit zijn belangrijke keuzes, want hoe beter dieren hun verplaatsingen kunnen aanpassen aan de weersomstandigheden en de voedselbeschikbaarheid, hoe meer voordeel ze uit hun migratie halen.

De informatie die dieren gebruiken om deze keuzes te maken hebben mogelijk te maken met de afstand die ze moeten afleggen. Korte-afstandsmigranten blijven in de winter in de buurt van hun broedgebied, waar de omstandigheden waarschijnlijk door hetzelfde weersysteem beïnvloed worden, terwijl dit bij lange-afstandsmigranten niet het geval is. Als de weersomstandigheden in het broed- en overwinteringsgebied niet aan dezelfde veranderingen onderhevig zijn, is het moeilijk om op afstand een inschatting te maken van de situatie op de bestemming. Voor dieren die ver migreren zou het daarom veiliger kunnen zijn om uit te gaan van de gemiddelde weersomstandigheden in het verleden, met als resultaat geringe variatie in migratiegedrag tussen verschillende jaren. Dit zou echter kunnen betekenen dat lange-afstandsmigranten zich onvoldoende kunnen aanpassen aan snelle veranderingen in het klimaat.

In hoofdstuk 2 vonden we dat meeuwen over het algemeen elk jaar hetzelfde gedrag vertonen. Individuen migreerden rond dezelfde tijd, gebruikten dezelfde route en hadden dezelfde bestemming. Er waren echter ook een paar uitzonderingen. Enkele individuen
veranderden hun migratiestrategie zelfs compleet. Variabiliteit in gedrag was niet gerelateerd aan de migratieafstand, en voor ieder gedrag dat we onderzochten, waren het weer andere individuen die het meest variabel waren. We kwamen daarom tot de slotsom dat individuen zich flexibel kunnen gedragen wanneer dat nodig is, maar dat ze de voorkeur geven aan een strategie die ze in het verleden hebben gebruikt.

Vervolgens wilden we onderzoeken hoeveel energie en tijd de verschillende migratiestrategieën kosten. Naast GPS posities, leggen de trackers die de meeuwen bij zich dragen met behulp van een versnellingsopnemer ook hun bewegingen in drie richtingen vast (voorwaarts, zijwaarts en verticaal). Deze bewegingspatronen kunnen gebruikt worden om een indruk te krijgen wat de meeuw doet: met de vleugels slaan, zweven, lopen, dobberen of rusten. Al deze bewegingen kosten energie, en door de versnellingen in de drie richtingen tijdens zo’n opnamemoment bij elkaar op te tellen (vanaf nu ‘dynamische lichaamsversnelling’) kunnen we een inschatting maken hoeveel energie een meeuw op dat moment verbruikt. Daarvoor is het belangrijk om er eerst achter te komen hoe het energieverbruik verhoogd wordt met iedere verhoging in dynamische lichaamsversnelling en of dit hetzelfde is voor alle verschillende bewegingen die een meeuw maakt. We bestuderen dit in **hoofdstuk 3** door naast versnelling ook de hartslag van meeuwen te meten, een veel gebruikte methode om een inschatting te maken van het energieverbruik. Tijdens de meeste bewegingen hadden de hartslag en versnelling dezelfde toename. Echter, tijdens het dobberen op zee had de versnelling hoger dan tijdens het rusten, terwijl de hartslag op hetzelfde energieverbruik wees. Dit kan verklaard worden doordat de versnellingsopnemer de bewegingen vastlegt die door de golven van het water worden gemaakt, terwijl dat deel geen extra energie kost. We vergeleken ook verschillende manieren om met de versnellingsopnemer een inschatting te maken van het dagelijkse energieverbruik. Ten eerste kan dit bepaald worden door het gemiddelde te nemen van alle versnellingen over een dag. De tweede manier is door een tijd-energie budget te berekenen, waarbij het aandeel van de tijd waarin een bepaald gedrag vertoond wordt, wordt vermenigvuldigd met de gemiddelde energetische kosten van dat gedrag, en dat vervolgens voor de gehele dag bij elkaar op te tellen. Beide manieren kwamen uit op hetzelfde energieverbruik, maar ze geven allebei een onderschatting van het dagelijkse energieverbruik, omdat ze geen allebei een onderschatting van het dagelijkse energieverbruik op dagen met een hogere rusthartslag, en een overschatting op dagen met een lage rusthartslag. Dit toont aan dat de berekeningen op basis van versnelling misschien kleine veranderingen missen in het dagelijkse energieverbruik die we maken hebben met het rustmetabolisme (bijvoorbeeld het warm houden van het lichaam, ruien, afweersysteem of voedselvertering) en dus niet met bewegingen gedetecteerd kunnen worden.

In **hoofdstuk 4** hebben we de versnellingsmethode toegepast op de tracking data van de migrerende meeuwen om te bepalen hoeveel energie ze spendeerden tijdens activiteiten...
Samenvatting gedurende het hele jaar. We combineerden de schattingen van het energieverbruik, die bepaald werden door middel van versnelling, met een heat-exchange model dat een schatting geeft van de energie die nodig is om warm te blijven bij de weersomstandigheden waarin de meeuw zich bevindt. Het totale energiegebruik was over het algemeen vergelijkbaar tussen meeuwen met verschillende migratiestrategieën. Onderling kon er echter een groot verschil zijn tussen individuen met dezelfde strategie. Daarnaast vonden we dat korte-afstandsmigranten een redelijk constant energieverbruik hadden, terwijl lange-afstandsmigranten tijdens sommige periodes een hoger energieverbruik hadden en op andere momenten juist een lager dan gemiddeld energieverbruik. Vervolgens verdeelden we het jaar in verschillende fases: broedperiode, migratie, stopover (dagen tijdens de migratieperiode waarop individuen zich niet actief verplaatsen naar hun bestemming) en overwintering. Meeuwen gebruikten de meeste energie aan het einde van het broedseizoen en tijdens de migratievluchten, en het minste tijdens de winter en de lange stopovers in de herfst wanneer ze hun veren ruien (de energie die ze hiervoor gebruiken hebben we niet meegerekend). Ongeacht welke migratiestrategie meeuwen hadden, veranderden ze hun gedrag op dezelfde manier in al deze fases. Zo spendeerden ze allemaal meer tijd vliegend tijdens de broedperiode, liepen ze meer in de herfst en hadden ze minder bewegingsactiviteit in de winter.

Hoeveel energie verbruikt wordt en hoeveel tijd een individu besteedt aan bepaalde gedragingen kan invloed hebben op de overlevings- en voortplantingskansen. Samen bepalen ze hoeveel van hun genen individuen aan hun nakomelingen kunnen doorgeven en hoe snel een populatie groeit. In hoofdstuk 5 hebben we bestudeerd of migratieafstand invloed heeft op factoren die te maken hebben met de voortplanting van de meeuwen: wanneer ze hun eieren leggen, de grootte van de eieren en de waarschijnlijkheid dat deze eieren uitkomen. Ook keken we of de afstand een invloed heeft op de overlevingskansen met behulp van ringaflezingen in het overwinteringsgebied en de broedkolonie. Er was geen effect van migratieafstand op elk van deze eigenschappen, wat suggereert dat migratiestrategieën geen consequenties hebben voor het voortplantingssucces.

Naast de enorme verschillen in migratieafstand, zijn er ook uiteenlopende omstandigheden tijdens de winterperiode, zoals in het koude Verenigd Koninkrijk waar de meeuwen op vuilnisbelten foerageren of varkensvoer eten, in Spanje waar ze vooral in de stad of op rijstvelden te vinden zijn, of de zonnige stranden van West-Afrika waar ze gemakkelijk aan vis kunnen komen. Het is dus opmerkelijk dat deze verschillen maar weinig invloed hebben op de factoren die we hebben bestudeerd. Onze voorkennis en veronderstellingen over de kosten, baten en uitdagingen van migratie zijn voornamelijk gebaseerd op onderzoek aan kleinere trekvogels, die specifieker voedselseisen hebben en kwetsbaarder zijn voor slechte weersomstandigheden. Meeuwen zijn echter heel anders.
Ze kunnen allerlei verschillende voedselbronnen gebruiken, van vis (meestal bijvangst van vissers) tot insecten (vaak op akkers) en afval. Dit zorgt ervor dat ze veel alternatieven hebben wanneer ze geconfronteerd worden met onverwachte veranderingen in het landschap. Het zijn grote vogels die beschikken over een dik verenkleed, waardoor ze bestand zijn tegen koud winterweer. Daarnaast kunnen ze rusten op land en water, wat ervoor zorgt dat migratie minder risicovol is. Wat we hier dus uit mee kunnen nemen is dat migratie niet altijd kosten met zich meebrengt. Door hun flexibiliteit in gedrag kunnen meeuwen zich aanpassen aan de verschillende uitdagingen die horen bij hun migratiestrategie. Daardoor zijn ze in staat om het hele jaar rond hun energie- en tijdsbudget goed af te stemmen en hebben ze dezelfde kansen op overleving en voortplanting wanneer ze terugkeren naar hun broedkolonies. Door onderzoek te doen naar een minder ‘traditionele’ trekkende soort, hebben we bredere inzichten gekregen in de beperkingen die zich voordoen tijdens migratie en hoe dieren deze te boven kunnen komen.
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