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Gull over-travels?

Consequences of diverse migration strategies in a generalist seabird

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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*, Linnaeus 1758).

Lesser black-backed gulls: the study system

1

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 then 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.