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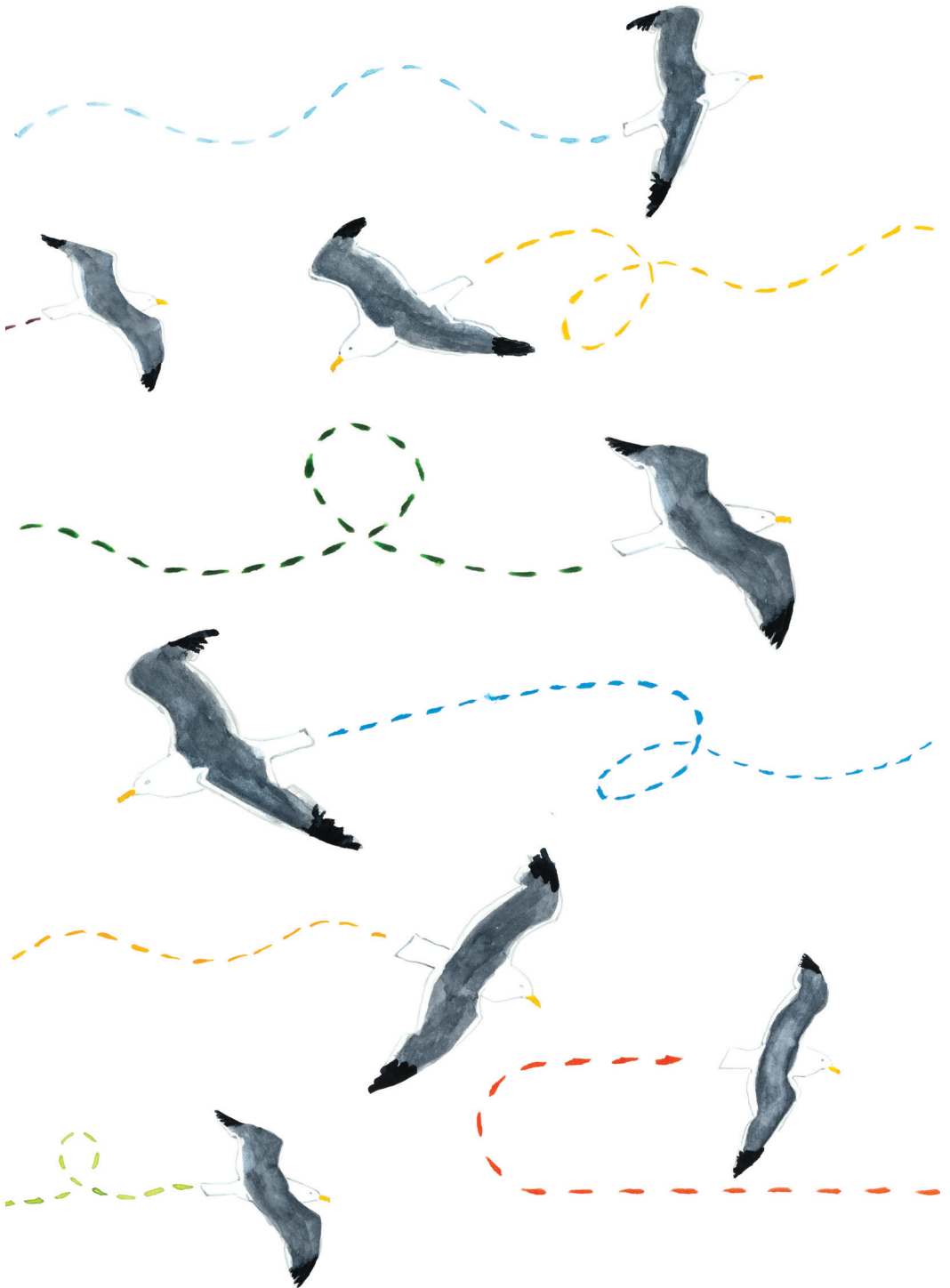
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CHAPTER 6

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 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

occur within a single currency, for example, long distance migrants were expected to allocate more of their annual energy expenditure to migrating, while spending less energy on thermoregulatory costs during the winter. The costs and benefits of different currencies could also trade-off with each other, for example if short-distance migrants have lower annual survival, but higher reproductive outputs. However, instead of observing trade-offs among strategies, we instead found that migration strategy had very little influence on the consequences we examined, including behavioural variability, energy expenditure, time-budgets, apparent survival and reproductive parameters. We did, however, find high variability in these traits among individuals deploying similar migration strategies. While these results are surprising within the context of how we understand migration, they are less surprising when we consider them in the context of what we know about gulls and their extensive behavioural repertoire. In this final chapter, I discuss more generally what our results contribute to the general understanding of migratory life-histories. I also consider attributes of our study species and approach that may influence our general conclusions, and suggest some future research directions.

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

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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).

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 overwintering 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.