Gull over-travels?

Consequences of diverse migration strategies in a generalist seabird

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CHAPTER 5

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

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To be submitted
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 allow 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, Rakhamberdiev 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 ($0.5035 \times$ length $\times$ width$^2$; 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 \( \times \) distance + autumn’), where migration distance influenced autumn survival only (‘spring + autumn \( \times \) distance’), and where migration distance influenced survival differently per season (‘spring \( \times \) distance + autumn \( \times \) 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).
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.

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

<table>
<thead>
<tr>
<th>Winter region</th>
<th>Mean migration distance [min. – max.]</th>
<th>N. individuals (N. nests) in Reproductive analysis</th>
<th>N. individuals in survival analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Africa</td>
<td>2894 [1912 – 4898]</td>
<td>10 (13)</td>
<td>13 (27)</td>
</tr>
<tr>
<td>Iberia</td>
<td>1686 [1234 – 2043]</td>
<td>32 (55)</td>
<td>50 (102)</td>
</tr>
<tr>
<td>France/UK</td>
<td>627 [279 – 1113]</td>
<td>30 (50)</td>
<td>20 (54)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>72 (118)</td>
<td>83 (185)</td>
</tr>
</tbody>
</table>
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).
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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 \( \Delta AIC_c \), where n. par. is the number of parameters, \( w_i \) is the Akaike weight, and deviance is the residual deviance. An interaction between two parameters is indicated with \( \times \).

<table>
<thead>
<tr>
<th>Model</th>
<th>n. par.</th>
<th>AICc</th>
<th>( \Delta AIC_c )</th>
<th>( w_i )</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 ( \times ) 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 ( \times ) 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 ( \times ) distance + autumn ( \times ) 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).
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, Grüebler 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.

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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>

*marked as fledgling but only entered the dataset as adult