



Gulls can change their migratory behavior during lifetime

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Migration is a widespread phenomenon among birds and is likely to be subject to strong selective pressures. Birds' annual routines and behaviors might be expected to change during their different life history stages, resulting in different, age-related migration patterns. However, although migration has been the subject of many publications, age-related differences in migration have received little attention. The present study examined age-related changes in individual migration habits in lesser black-backed gulls, *Larus fuscus*. We analyzed data from 10-year (1998–2007) color-ringing project in NW England, comprising more than 10 000 ringed individuals. Our results showed a latitudinal cline in age structure across the wintering range, with adults and gulls in their first breeding year wintering closer to the breeding grounds. Supporting this result we observed that individuals, as they get older, changed the migration behavior and winter closer to the breeding areas. Interestingly, we found no differences in survival rates across the wintering grounds. Thus differences in survival rates can not account for the latitudinal cline in age structure, and the observed findings seem to be best explained by the arrival time hypothesis, based on a mechanism whereby individuals are able to change their migratory behavior as result of the onset of sexual maturity and associated mating pressures.

Migration is a widespread phenomenon that has fascinated mankind for centuries. Natural selection has shaped geographic movements in response to seasonal changes (Greenberg and Marra 2005). In the context of individuals' annual routines, migration results from a critical tradeoff between the need to breed, avoid starvation and balance energy demands.

A considerable amount of research has increased our understanding of many aspects of this extraordinary behavior (Recher 1966, Moreau 1972, Coppack et al. 2008, Hahn et al. 2009), though other aspects remain unexplored (e.g. migration vs life history traits; Bairlein 2003). In this context, differential migration (where individuals of different sexes or ages from the same population or same species migrate different distances or at different times; Ketterson and Nolan 1983, Holberton and Able 2000, Nebel 2007) is of particular interest, as it can help to explain how life history traits may have influenced migratory behavior. Three hypotheses based on breeding or wintering routines have been suggested to explain the origin and evolution of differential migration (Alerstam and Hedenström 1998, Cristol et al. 1999, Greenberg and Marra 2005). The arrival-time hypothesis (Myers 1981) predicts that the class of individual that benefits most from early arrival at the breeding grounds should winter closest (i.e. adults and individuals that will attempt to breed in the next season; year-3 and older). The dominance hypothesis (Gauthreaux 1982) predicts that the

distance travelled during migration is inversely correlated with the individual's social rank (i.e. dominant adults should winter closer to the breeding grounds; year-4 and older). The body-size hypothesis (Ketterson and Nolan 1976) predicts that the distance travelled during migration is inversely related to the individual's body size (i.e. larger individuals should winter closer to the breeding grounds).

The results of empirical studies to test these hypotheses have been largely inconclusive (reviewed by Cristol et al. 1999, Boyle 2008), mostly due to their overlapping predictions (Belthoff and Gauthreaux 1991). For example, sex differential migration has been reported in several species, but the results of studies are usually consistent with more than one hypothesis (Cristol et al. 1999). Age-differential migration is a less well-studied phenomenon (Gromadzka and Serra 1998, Yosef et al. 2003, Markovets et al. 2008) and studies focusing on this process usually suffer from a lack of information. The differences observed between adults and juveniles are not consistent with any particular hypothesis, and the behaviors of different species appear to support different hypotheses (Cristol et al. 1999), possibly because of different life-history traits.

In the present study, we aimed to investigate the presence of age-related migratory patterns in the long-lived lesser black-backed gull *Larus fuscus*. We performed a detailed analysis of their migratory patterns throughout their life cycle, to investigate how it changed during the individuals

lifetime. We also addressed the predictions of the three most common hypotheses and suggest a possible mechanism to explain this phenomenon.

Methods

Species and study area

This study used data from the *Larus fuscus* color-ringing project coordinated by David Sowter (NW Gull Project, Lancashire, England). As part of this project 10 557 individuals were ringed in northwestern England between 1997 and 2007, mainly at the Ribble Estuary (53°42'N, 02°55'W), Tarnbrook Fell (54°01'N, 02°35'W) and South Walney colonies (54°03'N, 3°12'W), all within a radius of approximately 50 km. The birds were ringed as pulli at these locations. The recorded range of these populations extends from their breeding locations in northwestern England to their wintering locations as far afield as Tanji, Gambia, Africa (13°21'N, 16°40'W).

Age structure

Birds sighted during December and January were considered to be in their wintering grounds. The distinction between migration and wintering periods can be difficult to establish and depends on individual differences and environmental conditions. The use of observations only during the core winter period was intended to overcome this difficulty. We assumed that individuals' movements during this period were mostly short-range, and that long-range movements were uncommon and only occurred under unusual circumstances, e.g. persistent inclement weather. A total of 754 sightings were selected from the original dataset. Selection criteria included only one entry per individual; if multiple sightings of an individual were recorded, one sighting was chosen at random. This procedure guaranteed the independence of the analyzed dataset.

To analyze the age structure across the wintering grounds, data were clustered according to distance of the wintering locations from the breeding sites: first distance rank = places located at distances ≤ 1000 km from the breeding grounds, second distance rank = places located between 1000–2000 km from the breeding grounds, third distance rank = places located between 2000–3000 km from the breeding grounds, and fourth distance rank = places located > 3000 km from the breeding grounds. Data were also clustered according to the age of the birds: birds in their first winter were classified as 0 years, in their second winter as 1 year, in their third winter as 2 years, and so on.

The age structure was analyzed using contingency tables of age (0, 1, 2, 3, 4, 5, 6, > 6) versus distance ranks (1, 2, 3, 4). Frequencies of occurrence of gulls (F) in each age class versus each distance rank were tested using a simulation program (ACTUS software, Michigan Univ.), which allowed the significance of the contingency tables to be assessed without the restrictions imposed by a χ^2 distribution, by means of 1000 simulations while simultaneously assessing the significance of individual cells. The significance of the observed counts in each cell was presented in two tables: one

for large counts and one for small counts. Each cell in the large count table recorded the significance of the observed count as a fraction of the simulated tables with counts in that cell greater \geq the count in that cell in the observed table. If for any given cell, very few of the simulated tables had counts \geq the observed count, then the observed count in that cell was atypically large. Similarly, each cell in the small count table recorded the significance of the observed count as a fraction of the simulated tables with counts in that cell \leq the count in that cell in the observed table. If for any given cell, very few of the simulated tables had counts \leq the observed count, then the observed count in that cell was atypically small (Estabrook and Estabrook 1989, Estabrook et al. 2002). According to Manly (1997), the use of 1000 simulations produces a confidence level of 5%. F was then classified as expected (if values were not atypically large or small), or as higher (if values were atypically large) or lower (if values were atypically small) than expected, compared with the simulated scores.

The non-parametric Spearman's rank test was used to test for possible correlations between distance ranks and age classes. Non-parametric tests were used because, even after several attempts to standardize the data, they continuously violated parametric assumptions.

Individual migration dynamics

We used the re-sighting index to test if differential migration could be a by-product of differential survival rates at the distinct wintering grounds. This index was determined as the ratio between the number of individuals from an age class observed during winter (December–January) in a given distance rank and the number of those individuals that were re-sighted at least once, anywhere and at any time in the future. The re-sighting index was then compared across distance ranks for each age class using Fisher's exact test.

We also tested individual winter displacement (i.e. the capacity of individuals to change their wintering-grounds with age) as a possible alternative explanation for differential migration. In addition to the re-sighting index presented above, we calculated differences in individual winter displacements between two given years. Values could be positive, if individuals wintered further from the breeding grounds in the second of two given years; zero, if they kept the same wintering ground both years; or negative, if they wintered closer to the breeding grounds in the second of the two years. To assure the independence of the dataset, only one pair of sightings was used per individual; for gulls that had more than two sightings, one pair of sightings was chosen randomly. A total of 193 displacements were recorded and grouped into five categories, according to the age of the individual. Thus, differences in individual winter displacement between the year 0 and year 1 were grouped in class A (non-adults); differences in displacement between the years 0 or 1, and year 2 were grouped in class B (non-adults/immatures); differences between the years 0 or 1, and ≥ 3 years were grouped in class C (non-adults/adults); differences between year 2 and ≥ 3 years were grouped in class D (immature/adults); differences reporting individual winter displacement between years of birds ≥ 3 years were grouped in class

E (adults). Differences among these classes were then analyzed using the non-parametric Kruskal-Wallis test (data violated parametric assumptions). The multiple comparisons of mean ranks test was run as a post hoc test (Siegel and Castellan 1988).

Results

Color-ringed *Larus fuscus* from NW England were observed in winter (December–January) over a wide range of distances, from NW England in the north to Tanji, Gambia,

in the south, > 4700 km south of the breeding grounds (Fig. 1A). However, most of the individuals (84%) were detected < 2000 km from the breeding grounds.

Age structure

The results showed a differential, age-related migratory pattern ($n = 754$, $\chi^2_{(21)} = 196.36$, $p < 0.001$), with a latitudinal cline in age structure across the wintering grounds (Spearman's rank test, $n = 754$, $R = -0.40$, $p < 0.0001$; Fig. 1B).

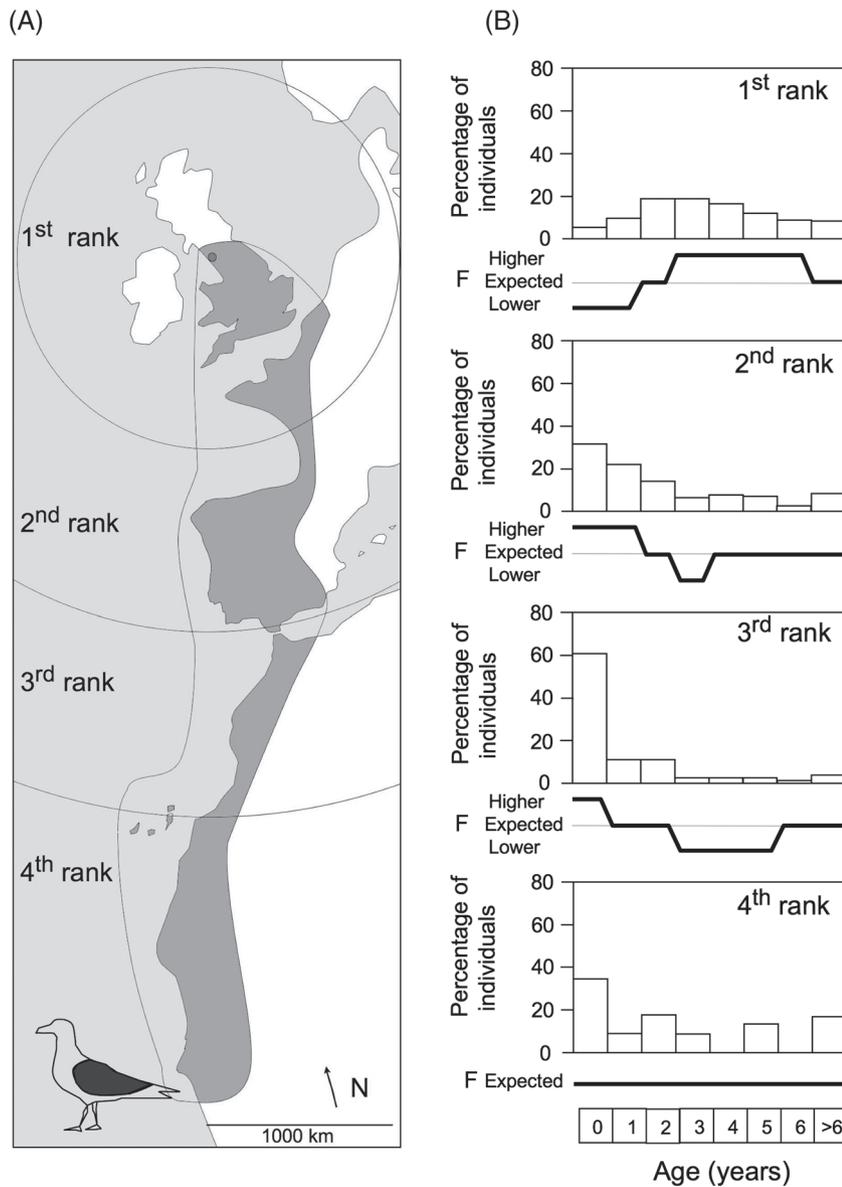


Figure 1. Winter distribution and age structure of lesser black-backed gulls *Larus fuscus* ringed in SW England. (A) Distribution of the color ring recaptures during winter from 1997 to 2007 (December and January); (B) Variation of the age structure across distance ranks, 1st rank, places at ≤ 1000 km ($n = 263$), 2nd rank, places between 1000 km – 2000 km ($n = 369$), 3rd rank, places between 2000 km – 3000 km ($n = 99$) and 4th rank, places at > 3000 km ($n = 23$) from the breeding colonies. F, frequency of occurrence of each age class, represents the comparison of the expected versus the observed frequency of each age class in the different distance ranks (F can be classified as higher, if frequencies were above expectations, lower, if frequencies were below expectations and expected; for further details see Methods).

Table 1. Re-sighting index. Values are discriminated by age class and by wintering distance rank. Survival rates were then calculated based on the total number of individual observed in a given age in a given rank N, divided by the number of those who were re-sighted anywhere in the future N (n).

Age (years)	Winter distance rank (km)			
	1st ≤ 1000	2nd 1000–2000	3rd 2000–3000	4th > 3000
0	12(6)	135(63)	66(29)	8(3)
1	29(17)	91(44)	14(8)	3(3)
2	72(41)	64(41)	12(2)	6(3)
3	82(49)	30(14)	4(0)	3(1)
4	71(36)	37(17)	3(1)	0(0)
5	61(26)	35(14)	2(0)	3(1)

Older gulls tended to winter closer to the breeding grounds, while younger gulls spread further south. Analysis of the frequencies showed that 0- and 1-year gulls wintered preferentially in the second or third distance rank, and avoided wintering in the first wintering range. In contrast, 3–6-year gulls wintered preferentially in the first distance range, and avoided the third wintering range. Gulls in years 2 and 7 demonstrated no preference for wintering areas (Fig. 1B).

Individual migration dynamics

We found no evidence for differential survival rates across the wintering areas (for all combinations of the re-sighting index, Fisher's exact test, $p > 0.05$, Table 1).

Analysis of changes in displacement of individuals to the wintering grounds between two given years clearly showed age-related changes in the use of wintering grounds (Kruskal-Wallis test, $n = 193$, $H_{(4)} = 42.50$, $p < 0.0001$; Fig. 2). Moreover the results showed that differences in displacement were longer during the transition from non-adults to adults (Fig. 2, class C), and shorter between years for adults (Fig. 2, class D), with a tendency towards wintering closer to the breeding grounds (Fig. 2).

Discussion

In a previous study (Marques et al. 2009), we identified the possibility of differential, age-related migratory pattern as a plausible explanation for the observed discrepancies in age structure of migratory and wintering populations along the Portuguese coast line. The results of the present study clearly support the existence of differential, age-related migration, with a cline in age structure across the wintering range (i.e. adults winter closer to the breeding grounds, while non-adults winter further south; Fig. 1). Moreover the findings show that this pattern arises because individuals change their migratory behavior during lifetime (Fig. 2).

A review of this subject classified 23 species of birds as differential, age-related migrants (Cristol et al. 1999). Most studies found that non-adults migrated further (Kerlinger and Lein 1986), which is in agreement with our findings. However, the results of most previous studies were unable to confirm any particular hypothesis (Cristol et al. 1999).

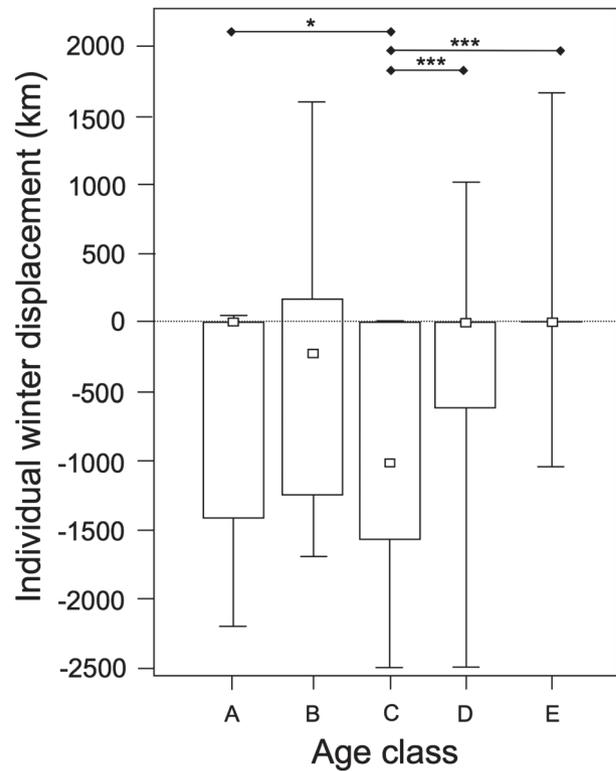


Figure 2. Age-related individual winter displacements. Individual winter displacement, give the differences for an individual in distance traveled to the wintering grounds in two given years. It assumes negative values, if the displacement in the second of the two given years was shorter; zero, if the displacement is the same in the two given years and positive values, if the displacement was longer. (A) displacements between 0- and 1- year ($n = 15$); (B) between 0- or 1-year and the year 2 ($n = 23$); (C) between 0- or 1- year and years ≥ 3 ($n = 37$); (D) between year 2 and years ≥ 3 ($n = 41$); (E) between years ≥ 3 ($n = 77$). Square represent the median, box the 25% quartiles and whiskers the range. Significances are given by the Multiple comparisons of mean ranks test, *, **, *** respectively $p < 0.05$, $p < 0.005$ and $p < 0.001$.

Our use of a long-lived gull allowed us to perform a detailed analysis of its life cycle, and enabled us to determine that, as individuals get older, their wintering grounds get closer to their breeding grounds. Of the three hypotheses put forward to explain differential migration, our findings are best explained in the context of the arrival-time hypothesis. The body-size hypothesis seems unlikely to account for our observations, because differences in body size are minimal in *L. fuscus* (Robinson 2005). In fact, according to Robinson (2005) the biometric measures (body weight and wing length) of juveniles complete overlap with those of adults. The dominance hypothesis predicts that dominant gulls (i.e. year-4 and older) occupy the most favorable areas (i.e. winter closer to the breeding grounds), which is similar to the predictions of the arrival-time hypothesis, which suggests that breeding gulls (i.e. year-3 and older) should winter closer to the breeding grounds. Detailed information on the behavior of different age classes is necessary to distinguish between these two hypotheses. Analysis of the data for year-3 (adult) gulls seems to support the arrival-time hypothesis over the dominance hypothesis; based on their plumage, these gulls

are adults, but they have never bred before. However, because they are approaching their first breeding season, they winter closer to the breeding grounds, in the first distance rank, and avoid the second and third ranks. Although these individuals cannot be classified in the dominant or breeder classes, their motivation to breed in the next season seems to support the arrival time hypothesis, where individuals intending to breed in the following season winter closer to the breeding areas. Nevertheless, a definitive test between these hypotheses must include the study of the dominance relation between age classes. The need of adult gulls to breed, and therefore to arrive early at the breeding grounds and secure the best nest sites, appears to account for the differential, age-related migratory pattern observed. Arriving early at the breeding grounds has been shown to increase the breeding success in species such as American redstarts *Setophaga ruticilla* and white storks *Ciconia ciconia* (Lozano et al. 1996, Vergara et al. 2007). The acceptance of the arrival-time hypothesis requires studies demonstrating that staying at more northerly latitudes ensures earlier arrival at the breeding areas, which in turn contributes to improved reproductive success.

However, the mechanisms behind this behavior remain unclear. Differential survival rates across the wintering range could produce a similar pattern, but we found no evidence for differences in mortality across the distinct distance ranks, so excluding this as a mechanism. Alternatively, our results suggest a mechanism whereby individuals change their wintering grounds with age, in response to physiological adjustments associated with sexual maturation, such that sexual maturation induces gulls to winter closer to their breeding grounds. This novel result proposes the mechanism behind the existence of differential, age-related migration and a cline in age structure across the wintering range within populations. Changes in behaviors like migration, in line with sexual maturation, are known in widely different species, such as salmon and armyworms (McNeil et al. 1996, Carruth et al. 2002). The progressive change in winter displacement of *L. fuscus*, with gulls wintering closer to their breeding grounds as they get older, could also favor pre-breeding visits to the colonies, as in other long-lived species with delayed maturity, where immatures visit the colonies prior to their first breeding attempt (Halley et al. 1995, Jenouvrier et al. 2008). The results of this study, in addition to those of earlier studies, support the importance of interactions between migration and other annual routines (Saino et al. 2004, McNamara and Houston 2008).

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