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Age-related migration patterns in *Larus fuscus* spp.

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Abstract Migration is a critical period in a bird's life that can affect the fitness of individuals. Intra-population migratory patterns and the way different sex and/or age classes within a population differ in timing and/or distance of migration are not completely understood. The present study aims to observe inter- and intra-population migratory patterns in the western population of Lesser Black-backed Gulls (*Larus fuscus* spp.), shedding light on age-related differences of temporal patterns of occurrence in the Portuguese coastal areas during migration and winter. One thousand seven hundred and fifty-four colour ring records were analysed matching a 30-year period of observations on the Portuguese coast between 1975 and 2005. During migration, the *graellsii* population represents 90% of the migratory flow of *L. fuscus* through Portugal with the *intermedius* accounting for 9% and the *fuscus* population, being vestigial in this period, accounting for 1%. Nevertheless, interesting significant differences were observed between the age classes of the three populations during this period, the *graellsii* population having a large number of first winters (40% of the migratory contingent of this population) followed by immatures and adults whilst in the *intermedius* and *fuscus* populations, the largest age class is the adults. During winter, no inter-population differences were found. When comparing migration and winter periods, intra-population differences were found in the *graellsii* and *fuscus* populations regarding distribution and age classes. These results indicate different migratory routes amongst different populations suggesting a leapfrog migration in L. fuscus and also a differential age-related migration pattern that might result from first winters migrating further south in search of a wintering place since adults heavily occupy the closest wintering quarters in their attempt to arrive earlier at their breeding ground.

Keywords Migration · Wintering quarters · Breeding areas · Migratory patterns · Western Lesser Black-backed Gulls

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Introduction

The seasonal migration of birds is a complex phenomenon (Gauthreaux 1982; Alerstam and Hedenstrom 1998), and, although records of bird migrations are centuries old, the diversity of avian migration observed between species, populations and individuals is still poorly understood (Greenberg and Marra 2005). Theories about migration patterns attempt to explain why, in migrant species, birds from different populations, sex and/or age classes respond differently to ecological factors in their migration behaviour (Ketterson and Nolan 1983; Bell 2005). These variations might affect the timing or average length of migration and thus give rise to both inter- or intra-

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population patterns (Greenberg and Marra 2005). Several causal factors have been put forward to explain the origin of migration patterns and are mostly based on social dominance and competition, such as the competition on wintering grounds or on breeding grounds (Alerstam and Hedenstrom 1998; Greenberg and Marra 2005). Between populations, the patterns frequently take the form of "leapfrog" migration in which the winter distribution of the breeding population forms a mirror image of their position in the breeding season (Boland 1990) or the form of "chain" migration, where the populations are shunted along the axis of migration and retain the same spatial relationship as in the breeding season (Bell 2005). The migration patterns may also vary within populations (Ueta and Higuchi 2002) namely associated with age and/or sex differences and which can occur in a temporal or geographical dimension (Gauthreaux 1982).

Recently, Bell (2005) pointed out three areas of work requiring particular attention: to improve our understanding of migration patterns, to improve the structure of multifactor models and to improve the empirical base available and increase the tests of model predictions. Thus, to improve our understanding of the major questions about migration patterns, the need to increase the empirical base is acknowledged. Characterising the diversity of the migration patterns will allow refining of the theoretical models by providing information to constrain parameter values (Bell 2005) and to assess the models' theoretical assumptions.

The Lesser Black-backed Gull (*Larus fuscus*) presents some characteristics that make it a suitable model for the study of migration. It is, namely, a common migratory species with a wide geographical spread, occurring from Scandinavia to northwest Africa (Rock 2002; BirdLife International 2004) with several long-term colour ring projects across Europe that provide useful information on the movements of individuals. The species presents two major migration routes, southwest and southeast routes that are mostly used by the western and eastern breeding populations, respectively, to their winter quarters (Cramp and Simmons 1982), with the western populations following a coastal route moving south on their movements to the wintering quarters (Galván et al. 2003). Recently, Schmaljohann et al. (2008) suggested that the gulls can perform long non-stop flights between the eastern Atlantic coast of sub-Saharan Africa and the Mediterranean Sea. Eastern populations move south to southeast overland across Europe (e.g. Pütz et al. 2008) towards the eastern Mediterranean and Black Sea, wintering there or continuing further south (Cramp and Simmons 1982; Kilpi and Saurola 1984).

In this study, we aim to assess the existence of age-related differential migration patterns amongst and within populations of Lesser Black-backed Gulls occurring in Portugal. Theoretically, we should expect that, in the absence of a differential migration pattern amongst populations, they should present a similar age structure in both periods (migration and winter). Extending this idea to an intra-population level, in the absence of migratory patterns, we also expected a similar age structure between migration and winter periods. Studying the species in this region can contribute to understanding its migration patterns since Portugal is an important winter quarter (Cramp and Simmons 1982) and is also an important stopover for birds migrating further south. This will be done using colour ring records from 30 years of observations of gulls in Portugal during migration and wintering periods.

Methods

This study examined colour ring records of Lesser Black-backed Gull ringed as chicks from the Portuguese Ringing Centre (CNA) database between 1975 and 2005 (n=1,754 records). When multiple sightings of an individual existed, only one, randomly selected, was used. Based on colour ring information, birds were categorised by age: first winters, immatures (second and third winters) and adults (fourth winter on) and by breeding population: *fuscus* (recoveries from Finland and Sweden), *intermedius* (recoveries from Germany and Norway) and *graellsii* (recoveries from UK, Faroe Isles, Republic of Ireland, Iceland, France, Belgium, Netherlands and Denmark). The assignment of a specific country to each one of the three populations considered here was done based on an analysis of mitochondrial DNA (Liebers and Helbig 2002).

Analyses were carried out considering two periods of time: one period from August to November where birds typically perform large-range movements, matching the migratory season (629 sightings), and another period from December to February where birds perform typically short-range movements, matching the wintering season (141 sightings). This is an operational definition that broadly encompasses most of the observations in the correct period and does not aim to determine the precise temporal definition of the two periods.

Data were analysed using contingency tables. Hypotheses were tested using a simulation programme (ACTUS software) which allowed us to assess the significance of a contingency table without the restrictions imposed using a chi-squared distribution whilst allowing simultaneous assessment of the significance of the deviations between expected and observed frequencies of individual cells by means of 1,000 simulations (Estabrook and Estabrook 1989). The significance of observed counts per cell is given in two tables: one for large counts and one for small counts. Each cell in the table for large counts reports the significance of the observed count as the fraction of simulated tables with counts in that cell greater than or equal to the count in that cell of the observed table. If for a cell very few of the simulated tables have counts equal to or greater than the observed count, then the observed count in that cell is atypically large. Similarly, each cell in the table for small counts reports the significance of the observed count as the fraction of simulated tables with counts in that cell less than or equal to the count in that cell of the observed table. If for a cell very few of the simulated tables have counts less than or equal to the observed count, then the observed count in that cell is atypically small (Estabrook and Estabrook 1989; Estabrook et al. 2002). According to Manly (1997), the use of 1,000 simulations produces a confidence level of 5%.

Results

The Lesser Black-backed Gulls observed in the two periods in Portugal had their origins in 12 countries, Finland, Sweden, Norway, Denmark, Germany, Netherlands, Belgium, France, Iceland, Faroe Islands, Ireland and UK.

During migration, we detected gulls from all of the major breeding areas including the Baltic Sea, the North Sea and the northeast Atlantic coast with the *graellsii* population dominating with 90% of the individuals (1% *fuscus* and 9% *intermedius*). Similar to migration, the *graellsii* population is largely the most abundant, with 94% of the wintering individuals (3% *fuscus* and 3% *intermedius*).

Gulls occur along the Portuguese coastal areas during migration, long-range movement period, and winter, short-range movement period (Fig. 1). In migration, all subspecies were detected in the three regions of Portugal; contrarily, in winter, individuals of the *intermedius* and *fuscus* populations were not detected in the central region and in the southern region, respectively (Fig. 1).

Overall, we found that the three populations differ in their distributions along the Portuguese coastal area during the migration period (n=629, $\chi^2_{(4)}$=45.33, p<0.001) with the *graellsii* population showing lower counts in the southern region (ACTUS$_{(small\ counts)}$, 28 out of 1,000 simulations) and the *intermedius* population with lower counts in the northern region and higher counts in the southern region (ACTUS$_{(small\ counts)}$, three out of 1,000 simulations; ACTUS$_{(large\ counts)}$, one out of 1,000 simulations, respectively; see Fig. 1). A detailed analysis

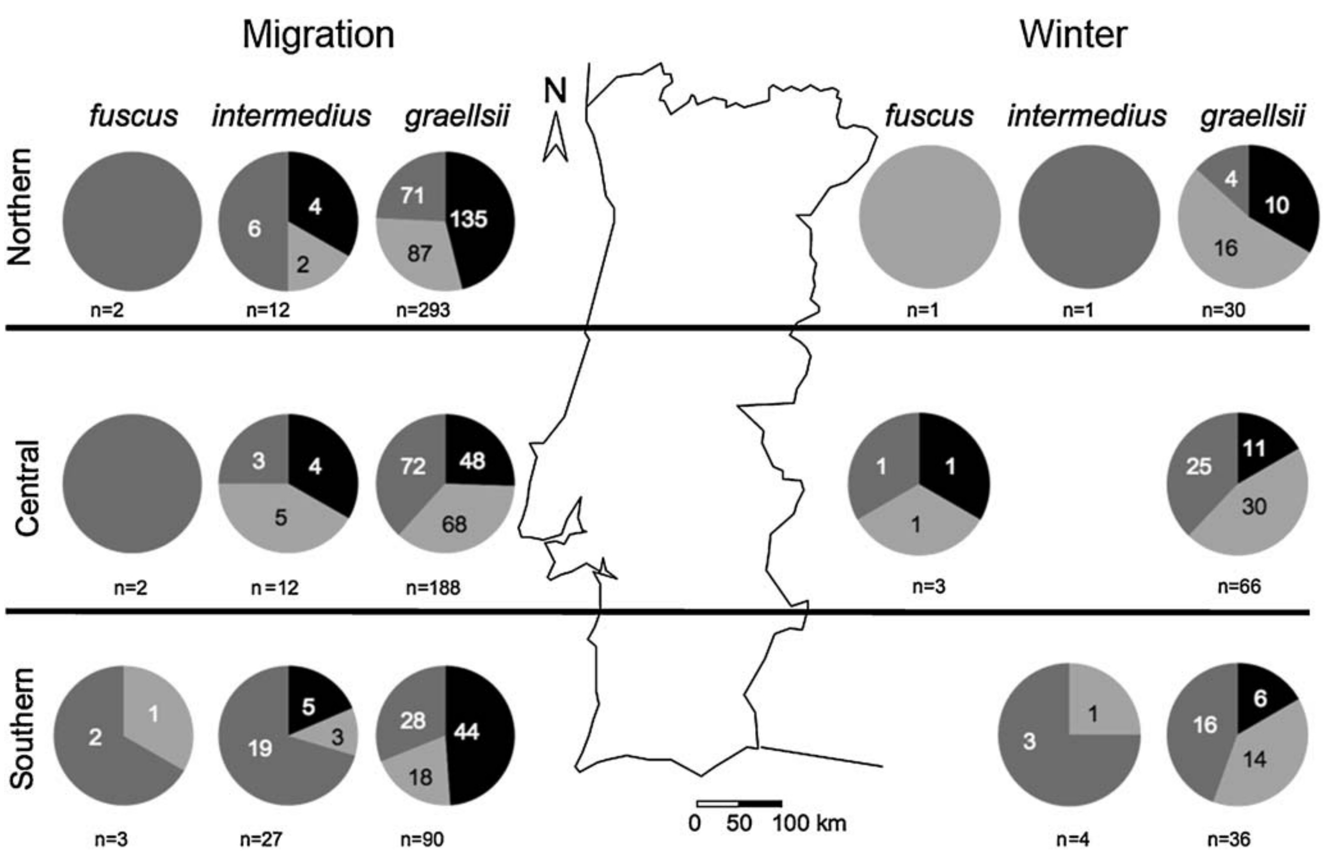

Fig. 1 Migration and winter distribution of *L. fucus* spp individuals of the groups *fuscus*, *intermedius* and *graellsii* in the northern, central and southern Portuguese coastal areas (*black*, 1st winters; *light grey*, immatures; *dark grey*, adults)

considering the age structure of each one of these populations showed differences for the *graellsii* distribution ($n=571$, $\chi^2_{(4)}=27.34$, $p<0.001$). Comparing the three regions, the first winters showed low counts in the central region (ACTUS$_{\text{(small counts)}}$, two out of 1,000 simulations) and high counts in the northern region (ACTUS$_{\text{(large counts)}}$ 32 out of 1,000 simulations) in contrast to adults which showed high counts in the central region (ACTUS$_{\text{(large counts)}}$, 22 out of 1,000 simulations) and low counts in the northern region (ACTUS$_{\text{(small counts)}}$, 30 out of 1,000 simulations). The immatures, in turn, showed low counts in the southern region (ACTUS$_{\text{(small counts)}}$, 35 out of 1,000 simulations).

At the winter period, the three populations once more showed distinct distributions along the Portuguese coastal area ($n=141$, $\chi^2_{(4)}=8.95$, $p<0.034$) with *intermedius* population showing high counts in the southern region (ACTUS$_{\text{(large counts)}}$, 34 out of 1,000 simulations). Considering the age structure of each one of these populations, although we had previously reported a difference for the *intermedius* population, we did not find significant differences.

Comparisons between the distributions of each population in migration and winter showed differences for the *graellsii* population ($n=703$, $\chi^2_{(2)}=35.65$, $p<0.0001$) which presented high counts during the winter period in the centre (ACTUS$_{\text{(large counts)}}$, six out of 1,000 simulations) and south regions (ACTUS$_{\text{(large counts)}}$, six out of 1,000 simulations) and low counts in the north region (ACTUS $_{\text{(small counts)}}$, one out of 1,000 simulations). During the migration period, a high count was recorded at the northern region (ACTUS$_{\text{(large counts)}}$, one out of 1,000 simulations).

Overall, the age structure of individuals occurring in the Portuguese coastal area differed between migration and winter ($n=770$, $\chi^2_{(2)}=19.91$, $p<0.0001$); this is clear for the *graellsii* population in Fig. 2. During the migration, the most abundant age class was the first winters followed by the immatures and the adults with the same percentage (Fig. 2A). Surprisingly, in winter, the most abundant age class was immatures, with a significantly large number of individuals (ACTUS$_{\text{(large counts)}}$, four out of 1,000 simulations), followed by adults and then first winters, with a significantly smaller number of individuals (ACTUS$_{\text{(small counts)}}$, one out of 1,000 simulations; Fig. 2B).

Discussion

Lesser Black-backed Gull *L. fuscus* occurs along the Portuguese coast during migration, long-range movement period, and winter, short-range movement period. Within the different breeding populations, this study confirms *graellsii* as the most abundant both in migration and winter, with results in line with what was previously thought. The abundance of *graellsii* contrasts with the low occurrence of individuals from the *intermedius* population and the vestigial presence of the *fuscus* population, corresponding to a decrease in the size of the populations according to their distance from the Portuguese coast. This is in agreement with the current view of the species migratory behaviour that considers two major migration routes: a western route along the Atlantic coast in a direction towards west Africa and an eastern route through central and eastern Europe in a direction towards east Africa (Cramp and Simmons 1982; Kilpi and Saurola 1984). In support of this finding is the difference in age structure between these populations, with only the *graellsii* presenting an age structure typical of a postbreeding period with a boom of first winters (Fig. 2A). In contrast, in the *intermedius* and *fuscus* populations, adults are the largest age class.

In this study, we found that the considered populations differed in their distribution along the Portuguese coastal area. In migration, the long-range movement period, the *graellsii* population had lower counts in the southern region, and the *intermedius* population had lower counts

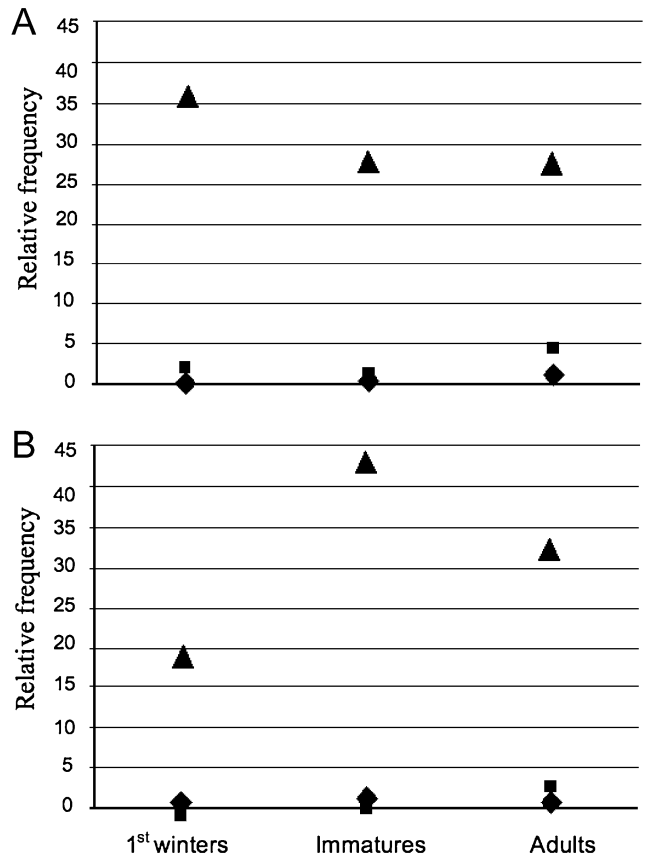

Fig. 2 Relative frequencies of the age classes in the different populations of *L. fuscus*. *Symbols* represent the different populations: *filled diamond*, *fuscus*; *filled square*, *intermedius*; *filled triangle*, *graellsii*. **A** Age frequencies relative to the migratory population ($n=629$). **B** Age frequencies relative to the wintering population ($n=141$)

in the northern region and higher counts in the southern region. This result seems to support the leapfrog hypothesis (Boland 1990; Bell 2005); however, since migration is a period of long-range movements, this result needs confirmation by a similar effect in winter. In winter, the short-range movement period, the differences found do not support either the leapfrog hypothesis with *fuscus* absent from the south or the chain hypothesis with *graellsii* having higher density in the central area. The comparison between migration and winter revealed an increase of the relative abundance of *graellsii* (from 90% to 94%) and a decrease of *intermedius* (from 9% to 3%), consistent with a leapfrog migration. Moreover, the result for the *graellsii* geographical variation in abundance between migration and winter suggests a shift towards the southern regions in Portugal with time, although, overall, our results suggest the possibility of a leapfrog migration at a larger scale.

It is common to find different migratory patterns between the different populations, i.e. different geographic locations may lead birds to choose alternative routes; however, the same is not true with different migratory patterns within the same population mainly because all individuals share the same geographical area, and only 53 species clearly present differential migration (Cristol et al. 1999). Interestingly, when considering all birds, we found significant differences in the age structure between the migration and winter periods. Our data highlighted a significant reduction of first winters between migration and winter, suggesting that they might migrate further south in their search for a wintering ground (Cramp and Simmons 1982). Alternatively, first winters could also move to the central Iberian Peninsula in their migration movement; however, the age structure observed in the central Iberian Peninsula population (Galván et al. 2003), similar to the one presented in this study, rejects this possibility. On the other hand, immatures present an inverse trend, increasing their relative abundance during the winter. Furthermore, this difference could also be interpreted as a result of the high mortality rate of the first winters. Although mortality rates of 22% over a period of 2 months can occur, it is uncommon, and even if it happened the long time span of this study would attenuate its effect on the average. Thus, this mortality hypothesis seems very unlikely.

Overall, these results seem to support the existence of a differential migration pattern between age classes. In the face of the currently accepted model, our data fit both the dominance and the arrival time hypotheses (Alerstam 1998; Greenberg and Marra 2005). The dominance hypothesis predicts that socially dominant individuals (older) can obtain enough resources close to the breeding range whilst subordinate individuals will be forced to leave and migrate to survival habitats further away (Alerstam 1998; Greenberg and Marra 2005). In the case of the arrival time hypothesis, the reproductive individuals, subject to a more intense competition for breeding resources, should winter near the breeding grounds to benefit by returning earlier (Greenberg and Marra 2005). To clarify this issue in Lesser Black-backed Gulls, additional research is needed, assessing which hypothesis better explains the mechanism underlying the existence of the differential migration patterns, that is, if the distribution in the winter quarters is an outcome of competition for winter or breeding resources.

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