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ORIGINAL ARTICLE

Migration pattern of Icelandic Lesser Black-backed Gulls *Larus fuscus graellsii*: indications of a leap-frog system

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Abstract On the species level, the non-breeding distribution and the migration patterns of most European birds are well known. In contrast, the knowledge of the contribution of different breeding populations to particular non-breeding sites (migratory connectivity) is far more limited. We studied the non-breeding distribution of individually colour-ringed Lesser Black-backed Gulls (*Larus fuscus graellsii*) from Iceland and sought information on their migration pattern in respect to other populations (leap-frog, chain migration, random mix). Most winter resightings (94%) were from the southern part of the known winter range (Iberian Peninsula and northwest Africa). No statistical difference was found according to age on the latitudinal winter distribution, although 1st winter birds were on average 2° further south. Both 2nd and 3rd calendar year (cy) birds performed a northward spring migration,but spent the summer at lower latitudes than adults. The autumn migration for adults was earlier compared with 1st cy birds. A comparison of resightings of birds ringed in Iceland and in two projects from the Netherlands showed that these populations are not likely to contribute much to the wintering population in the UK. The proportion of winter resightings from Icelandic and Dutch populations showed that 44–65% were from the Iberian Peninsula. However, Dutch birds were much more likely to be seen in France (18–48 vs. 0.4%), but Icelandic birds were more likely to be seen in Africa (29 vs. 6–16%). These results indicate that Icelandic birds to some extent leap-frog more southerly populations.

Keywords Age segregation · Colour-ringing project · Differential migration · Migratory connectivity · Non-breeding distribution

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Zusammenfassung

Zugmuster der Isländischen Heringsmöwe (*Larus fuscus graellsii*): Hinweise auf ein Übersprungs-System

Auf Art-Niveau sind das Vorkommen und die Zugmuster der meisten europäischen Vögel gut bekannt. Deutlich weniger weiß man hingegen über die Präsenz der unterschiedlichen Brut-Populationen in Gebieten, in denen nicht gebrütet wird (migratory connectivity). Wir untersuchten das Vorkommen einzelner beringter, isländischer Heringsmöwen (*Larus fuscus graellsii*), um Informationen über ihre Zugmuster in Zusammenhang mit anderen Populationen zu sammeln (Überspringen, Kettenwanderung, Zufalls-Mix). Die meisten (94%) Ringfunde und

Sichtungen lagen im südlichen Teil der bekannten Überwinterungsgebiete (Iberische Halbinsel, Nordwest-Afrika), und es gab keine statistischen Unterschiede bezüglich des Alters der geographischen Winter-Verteilung, obwohl erstmals überwinternde Vögel im Schnitt 2 Grad weiter südlich zu finden waren. Vögel, die zum zweiten und dritten Mal überwinterten, zeigten eine mehr nördlich ausgerichtete Frühlingswanderung, verbrachten den Sommer aber auf südlicheren Breiten als die adulten Tiere. Die Herbstwanderung adulter Tiere ist früher schon mit der von Erstziehern verglichen worden. Ein Vergleich von in Island beringten Wiederfunden wie auch zwei Projekte in den Niederlanden zeigten, dass diese Populationen höchstwahrscheinlich nicht viel zu den im U.K. überwinternden Populationen beitragen. Ein Teil der Winter-Wiederfunde isländischer und niederländischer Populationen zeigte, dass 44–65% von diesen von der Iberischen Halbinsel stammten. Aber niederländische Vögel wurden mit größerer Wahrscheinlichkeit in Frankreich gesichtet (14–48 vs. 0.4%) und isländische Vögel eher in Afrika (29 vs. 6–16%). Diese Ergebnisse sind ein Hinweis darauf, dass isländische Vögel in gewissem Ausmaß südlichere Populationen überspringen.

Introduction

On the species level, there is, in many cases, good knowledge on migration patterns and routes of migratory birds (Alerstam 1990; Berthold 2001). However, existing knowledge is much less extensive for the migratory connectivity and differential migration between age and sex groups (Bairlein 2001, 2003).

Migratory bird species show various patterns of partial and differential migrations, as well as segregations between migratory populations. A population that breeds north and winters south of a conspecific population at the same longitudinal range must migrate through the latitudinal distribution of the more southerly breeding population. This migration system has been called a leap-frog migration (Alerstam and Högstedt 1980; Lundberg and Alerstam 1986). In other cases, a northerly breeding population winters within the breeding range of another population that migrates further south—a system generally termed chain migration (Kelly et al. 2002; Smith et al. 2003).

However, within a population, not all individuals necessarily have the same migratory behaviour. Partial migration, where only a part of the population migrates, is well known among various species (Terrill and Able 1988). Furthermore, some populations have shown spatial segregation of the sexes (Phillips et al. 2004, 2009) and segregation of birds at different ages (Payevsky 1994). Such systems are referred to as differential migrations (Münster 1996; Holberton and Able 2000; Nebel 2006).

Among seabirds, the chain migration pattern has been found in several species, e.g. Brunnich's Guillemot (*Uria lomvia*), Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*Larus marinus*), in which northerly birds replace more southerly breeders during winter (e.g. Petersen 1998; Wernham et al. 2002). On the other hand, it seems that examples of leap-frog migration in seabirds are scarce or lacking, suggesting that this migration pattern is uncommon in this group of birds.

The Lesser Black-backed Gull (*Larus fuscus*) increased in number and distribution over its world range during the twentieth century (Snow and Perrins 1998; Calladine 2004). Lesser Black-backed Gulls differ from other large European gulls in performing long-distance migration. Even though the global wintering grounds of the Lesser Black-backed Gulls are well known, our understanding on the migratory connectivity of different populations is poor.

The light mantled subspecies of the Lesser Black-backed Gull, *Larus fuscus graellsii*, breeds in Greenland and northwest Europe from Iceland to France. It winters in western Europe from the UK and along the Atlantic coast south to northwest Africa (Rock 2002; Malling Olsen and Larsson 2004; Marques et al. 2010).

Ringing studies on British and Irish Lesser Black-backed Gulls have shown that most winter records are from the Iberian Peninsula, although the winter distribution ranges from the UK to Africa (Rock 2002; Marques et al. 2010). Young birds have been reported to go further south than adults (Baker 1980; Rock 2002). Interestingly, a study on the migration of British Lesser Black-backed Gulls showed a tendency for adult and younger birds to migrate shorter distances, and they were more likely to winter in the UK during the period 1969–1975 compared with the period 1962–1968 (Baker 1980). The number of wintering Lesser Black-backed Gulls in the UK has been increasing during recent decades (Barnes 1961; Rock 2002), but the contribution of foreign populations to local birds is still unclear.

The aims of this study were to describe the non-breeding distribution and migration pattern of Icelandic Lesser Black-backed Gulls, as reflected by sightings of colour-ringed individuals. We asked the main following questions:

(1) Where do Icelandic birds stay during the non-breeding season and what is their migratory connectivity?
(2) Are there any signs of differential migration according to age?
(3) When do they migrate?
(4) Do Icelandic birds leap-frog, chain migrate or mix randomly with conspecifics in other populations?

Methods

Ringing and data collection

We captured and individually colour-ringed 1,200 birds in southwest Iceland from 1996 to 2007. Full-grown birds were caught in nest-traps and with cannon-nets, but most juveniles were caught and ringed before fledging. The colour rings enable reading in the field with a telescope at up to a few hundred metres distance. Recoveries of birds from this project were reported to the Icelandic Bird Ringing Scheme or directly to us. All resightings up to April 2008 are included in this study.

Non-breeding distribution and age groups

We divided the recoveries into three periods; summer (1 May–31 August), migration (1 February–30 April and 1 September–31 October) and winter (1 November–31 January). For birds seen during the summer, we distinguished between three age groups; (1) 2nd calendar year (cy), (2) 3rd cy and (3) adults. For winter sightings, we distinguished between birds at four ages; (1) 1st winter (1st and 2nd cy), (2) 2nd winter (2nd and 3rd cy), (3) 3rd winter (3rd and 4th cy) and (4) adults (4th cy and older). We used a one-way ANOVA for comparing the difference in latitudinal positions between age-groups during different seasons. If a significant difference was found, a Scheffe test was used post hoc to compare the groups.

Migration pattern

To access the timing of migration, all latitudinal positions of resighted birds in the study were plotted against ordinal dates within a frame of 1 year. This was done separately for birds in four age groups; (1) 1st cy, (2) 2nd cy, (3) 3rd cy and (4) adults. A smoother line (based on the average of 10% of sample size) was drawn through all points to view the periods of latitudinal movements.

Resightings of Lesser Black-backed Gulls throughout the non-breeding range are presumably largely reflecting the distribution of birdwatchers looking for ringed gulls. Therefore, the relative number of resightings from different areas should not be considered representative for the numbers wintering in those areas. This well-known problem can be dealt with by different approaches. Here, we use the technique of comparing groups of birds assumed to have equal re-encounter probabilities (Korner-Nievergelt et al. 2010). We compared resightings of Icelandic-ringed birds with two colour-ringing projects from the Netherlands. The project NET 1 was carried out from 2003 to the present time in the south Netherlands, and the project NET 2 was carried out in the north of the Netherlands between 1986 and 1988 (Camphuysen 2008). We collected all winter resightings from NET 1 and NET 2 up to and including winter 2007/2008.

Locations of birds from those three projects resighted in the UK, France, Iberian Peninsula and northwest Africa during winter were compared. The Azores were categorized with the Iberian Peninsula, but the Canary Islands and Madeira were categorized with northwest Africa. We assumed that if Icelandic and Dutch birds mixed randomly during winter they would show similar proportion of resightings from these four areas.

Statistical analyses and graphs were performed in SPSS 12 (SPSS 1998).

Results

Migration routes and wintering grounds

A total of 712 resightings of 307 Icelandic individuals were obtained. Wintering Lesser Black-backed Gulls from Iceland were seen throughout the known winter range of subspecies *greallsii*. However, the vast majority of winter resightings ($n = 241$) were from the Iberian Peninsula (65%) and northwest Africa (29%) with much lower number found in the UK (6%). A single individual was seen in France (adult) and another one in Puerto Rico (1st winter). No birds remained in Iceland during winter.

The wintering grounds of Icelandic birds are not separate from that of other breeding populations, even though majority of the birds winter on the southern part of the winter distribution, and therefore show an example of a moderate or weak migratory connectivity.

In contrast with winter resightings many of the resightings from the migration period ($n = 253$) were reported from the UK and Ireland (18%) but low numbers were reported from France (3%). As for the winter resightings most birds during migration were reported from the Iberian Peninsula (64%). Thus, the migration route of the Icelandic birds as reflected by the resightings seems to be from northwest Africa and Iberian Peninsula directly to Iceland or through UK and Ireland with negligible stopover in France.

Differential migration

Birds of all ages were seen between latitudes 13°21′N and 52°41′N (mean 36°42′N, SD = 8°01′, $n = 241$) during winter and no significant difference was found according to age (one-way ANOVA, $F = 1.016$, $P = 0.386$) (Fig. 1). First winter birds were on average resighted at 35°09′N (SD = 6°26′, $n = 43$) and therefore close to the mean latitudinal distribution of adults, which was at 37°11′N (SD = 7°44′, $n = 152$). Those individuals that were seen

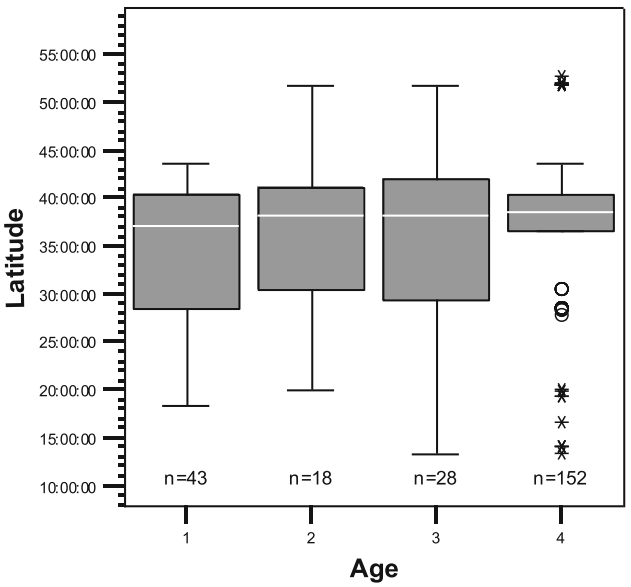

Fig. 1 Latitudinal winter distribution of Icelandic Lesser Black-backed Gulls (*Larus fuscus graellsii*). *1* 1st winter, *2* 2nd winter, *3* 3rd winter, *4* 4th winter and older

at the northernmost and southernmost locations during winter were adults. Sightings of 2nd and 3rd winter birds were on average at 37°59′N (SD = 8°45′, $n = 18$) and 35°43′N (SD = 10°50′, $n = 28$), respectively.

Interestingly, both 2nd cy and 3rd cy birds showed a clear northward migration during summer, although they did usually not go all the way to the breeding grounds (Fig. 2b, c). However, one 2nd cy and seven 3rd cy birds were reported in Iceland during summer, although most immature birds reported abroad ($n = 82$) mainly spent the summer in the UK and Ireland (46%) and France (35%). A significant difference was found between the latitudinal position of 2nd cy, 3rd cy and adult birds during summer (one-way ANOVA, $F = 39.615$, $P < 0.05$). The 2nd cy birds stayed on average further south (mean 48°55′N, SD = 4°37′, $n = 51$) compared with 3rd cy (mean 52°10′N, SD = 5°53′, $n = 39$), but the difference was not significant (Scheffe test, $P = 1.26$). Adult birds showed a significantly more northerly summer distribution (mean 59°32′N, SD = 0.35°, $n = 128$) compared to both subadult groups (Scheffe test, $P < 0.05$).

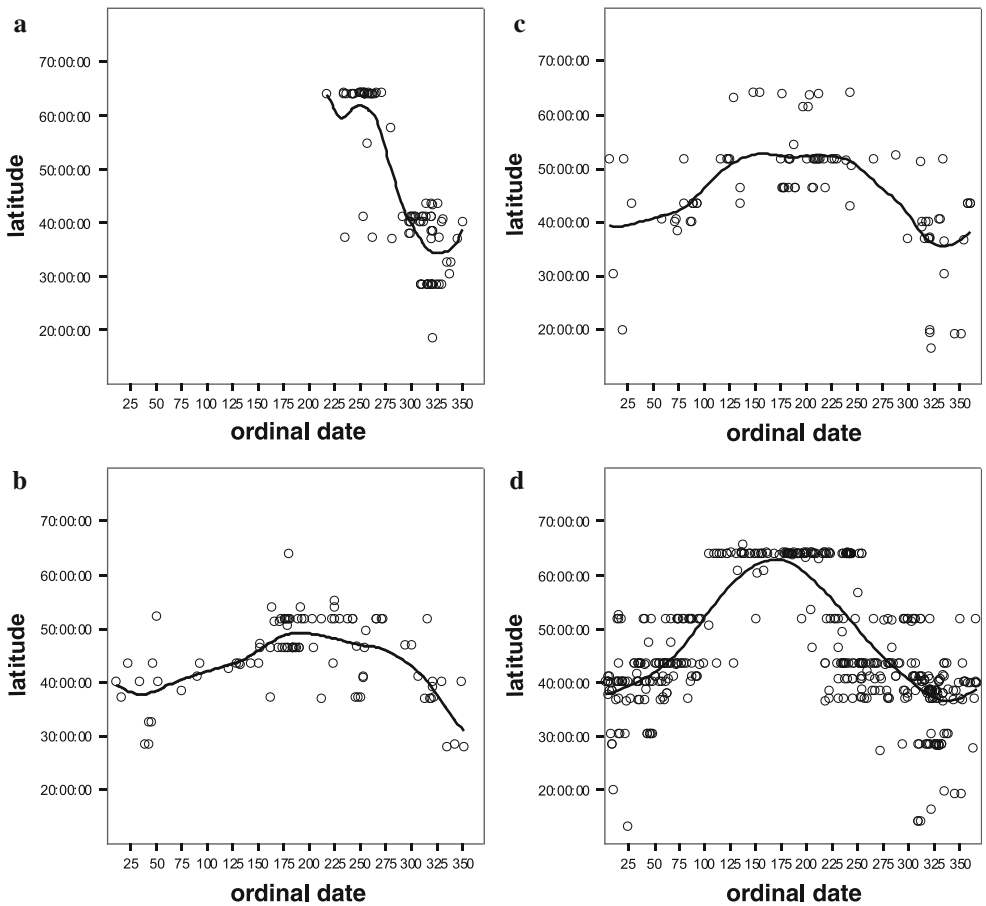

Fig. 2 The latitudinal distribution of Icelandic Lesser Black-backed Gulls over time period of 1 year in four age groups; **a** 1st cy, **b** 2nd cy, **c** 3rd cy and **d** 4th cy and older

Migration pattern

Timing

Adult birds initiated southward migration around mid-August (ordinal date 225) and the main migration period lasted roughly 1 month or until around mid-September (ordinal date 260) (Fig. 2d). Birds in their first autumn showed a later migration, usually starting around mid-September until the last week of October (ordinal dates 260–300) (Fig. 2a). However, a few 1st year birds started their migration earlier or by mid August (ordinal dates around 230). Spring migration of adult birds appears to start early in the year, with a rapid increase in higher latitudinal resightings from mid-February (ordinal dates 45–50), and until birds reach Iceland in the second week of April (ordinal date around 100). Only five adult birds were seen outside Iceland from 5 May until 8 August (ordinal dates 125–220) (Fig. 2d). The spring migration of 2nd and 3rd cy birds was later and less pronounced compared with adults, especially amongst 2nd cy birds that showed gradual northward movements from February until late July (ordinal dates 50–175) (Fig. 2b, c).

Comparison of resightings between populations

A comparison of winter resightings (from the UK, France, Iberian Peninsula and northwest Africa) in the three colour-ringing projects showed that projects ICE and NET 1 had the same proportion of reported colour rings from the Iberian Peninsula (65%) compared to 44% for NET 2. However, when comparing resightings from France, a much higher proportion of Dutch birds was seen (18% for NET 1 and 48% for NET 2) compared to only one Icelandic individual (0.4%). The opposite was apparent when comparing resightings from northwest Africa, as 29% of winter resightings of Icelandic birds were from this area compared to 6–16% of the Dutch resightings. All three projects had few resightings from the UK (1–6%) (Table 1).

On the Iberian Peninsula, there was higher proportion of adults (68%) than younger birds (56–61%) for the Icelandic birds, but this was equal or the opposite for the Dutch birds. A more pronounced age difference was found in northwest Africa. For all three projects 1st winter birds were most likely to be seen (24–43%), followed by subadults (12–32%), and adults were proportionally less likely to be resighted 0–25% (Table 1). In France, adult birds from the Netherlands were more likely to be sighted (24–60%) than younger birds (5–35%) (Table 1).

Discussion

Wintering grounds and migration routes

Our results indicate that the contribution of Icelandic birds to wintering birds in the UK and France must be considered small, as the majority of winter resightings (94%) were from the southern part of the distribution (Iberian Peninsula and northwest Africa). Marques et al. (2010) showed that 35% of all winter resightings of birds ringed in northwest England were less than 1,000 km from the breeding grounds (England, the Netherlands, Belgium and northern France). Furthermore, in the same study, 49% of winter resightings were 1,000–2,000 km distant (southern France and Iberian Peninsula) and 16% from Africa (Marques et al. 2010). This indicates that birds from the UK have a tendency to winter in the northern part of the winter range, the opposite of Icelandic birds that mainly winter in the southern part. Birds belonging to the Icelandic, British and Dutch populations, however, use the whole winter range to some extent. Therefore, existing data suggest that the subspecies *L. f. graellsii* has a moderate to weak migratory connectivity.

Table 1 A comparison of winter resightings (1 Nov–31 Jan) of colour-ringed Icelandic Lesser Black-backed Gulls (*Larus fuscus graellsii*) from Iceland (*ICE*) and two projects from the Netherlands (*NET 1* and *NET 2*) in four different areas

Age	Resightings from three projects														
	Totals			% UK			% France			% Iberia			% NW Africa		
	ICE	NET 1	NET 2	ICE	NET 1	NET 2	ICE	NET 1	NET 2	ICE	NET 1	NET 2	ICE	NET 1	NET 2
1st winter	42	152	50	0	0	6	0	5	8	57	65	62	43	30	24
2nd winter	18	42	60	17	0	2	0	10	35	56	69	51	28	21	12
3rd winter	28	19		11	0		0	5		61	63		29	32	
Adults	146	493	223	6	2	2	1	24	60	68	64	38	25	10	0
Total	234	706	333	6	1	2	0	18	48	65	65	44	29	16	6

Resightings for 2nd and 3rd winter birds from the NET 2 project are lumped

During migration, resightings of Icelandic birds from the UK and Ireland increased, indicating that at least some birds migrate through this area. Others might fly directly from more southern latitudes to Iceland, but resightings of colour-ringed birds are not likely to give a comprehensive picture on this because of observation biases. More unbiased techniques, such as the use of satellite transmitters or GPS loggers, are required to get a better understanding of their flyways.

Differential migration

Young Lesser Black-backed Gulls have been claimed to winter further south than adults (Baker 1980; Rock 2002). We found no statistical difference between the latitudinal winter ranges in birds of different ages, although 1st winter birds were on average 2° further south compared with adults. On the other hand, there was a difference in the latitudinal range during summer. It was not a surprise that adult birds went further north than 2nd cy birds because 1-year-old birds are very rare on the breeding grounds in Iceland. It was less expected that a small difference was observed between 2nd and 3rd cy birds during summer, and also how little spread there was in the latitudinal range during these life stages. Immature birds from the UK seem to show much more latitudinal spread during summer (Rock 2002).

Northward movements of immature Lesser Black-backed Gulls during summer have been reported before (Baker 1980). Helberg et al. (2009) reported sightings of 13 2nd cy Norwegian birds seen during summer between Belgium in the south and Finland in the north. Birds from the same project had mainly been seen further south during winter. Similar movements of immature birds have been observed among other seabirds, e.g. Common Terns (*Sterna hirundo*) (Bairlein 2001). We did not have the possibility to study whether the sexes showed differences in migration or in distribution on the wintering grounds, because few of the birds ringed up to 2004 were of a known sex. This aspect in the migration of Lesser Black-backed Gulls still awaits further attention.

Timing of migration

Assuming an observer bias within the annual range of Lesser Black-backed Gulls, the use of resightings for studies on migration phenology might be problematic (Strandberg et al. 2009). The potential pitfalls in this study are overestimation of birds migrating late from the breeding/ringing area in Iceland and underestimation of the occurrence of birds at the southern limit of the winter range. However, a comparison between age groups is assumed to be more robust. During autumn, the adult birds left earlier (mid-August to mid-September) than 1st cy birds (mid-September to late October). In the UK, adult birds start migrating southwards in late July, but the migration period is not well known. Many 1st cy birds in the UK start migrating in late August, and most have left by the end of October (Rock 2002). Therefore, it seems that the onset of autumn migration in these populations differs, with UK birds departing earlier. Lesser Black-backed Gulls in southwest Iceland (where the bulk of the population breeds) usually start egg laying in the last week of May (Petersen 1998), while the first birds in the UK start breeding much earlier, in late April and early May. This might explain the difference in autumn departure times.

Spring migration of adults in this study seemed to start early in the year and was most prominent from February until April. This migration period seems to be fairly close to or slightly later than for UK birds, which are arriving at the breeding colonies from mid-February until April (Rock 2002). It was more difficult to assign the migration period for 2nd and 3rd cy birds, but the former migrated northward much later than adults. Studying the timing of migration using resightings of a small proportion of colour-ringed birds within a population is likely to give approximate results. This is, however, a convenient way to get information on this aspect, as in many cases the only existing information on the timing of bird migration are the dates of arrival and departure.

Winter distribution of Icelandic Lesser Black-backed Gulls in comparison with other European populations

A comparison of winter resightings of Icelandic and Dutch birds shows that birds from both populations have a high proportion of resightings from the Iberian Peninsula (44–65%). However, Dutch birds were more likely to be seen in France (18–48 vs. 0.4%), while Icelandic birds were more likely to be seen in Africa (29 vs. 6–16%). A colour-ringing project in northwest England (Marques et al. 2010) allows a further comparison. Of all winter resightings from 1997 to 2007, 35% of the birds were seen in the latitudinal range from England to northern France. Proportion of resightings from southern France and the Iberian Peninsula was 49%, and thus lower than for both Icelandic and Dutch birds. Proportion of resightings from Africa was 16%, and thus similar or higher compared to Dutch birds but much lower than for Icelandic birds.

This rough comparison, assuming that the re-encounter probability is the same for all colour-ringing projects, indicates that Icelandic birds do have a tendency to migrate further south than birds from the Netherlands and UK. Therefore, Icelandic birds seem to leap-frog more southerly populations of the subspecies *L. f. graellsii*. The reason for this is not obvious, but assuming that numbers on the

wintering grounds are regulated in a density-dependent manner, the late autumn departure of Icelandic birds might play a role.

Furthermore, a direct comparison of the distance between breeding and wintering grounds shows that 84% of resightings of British birds are within 2,000 km (Marques et al. 2010), while 94% of resightings of Icelandic birds are more than 2,000 km from the breeding grounds (i.e. not in UK). The arrival time hypothesis (Myers 1981), predicting that birds that benefit from arriving early on the breeding grounds should winter the closest, therefore does not seem to apply to Icelandic breeders.

The contribution of the quality of wintering areas to the increase of breeding birds in Iceland or other areas is not known, because hardly any studies have been carried out on the ecology of this species outside the breeding season. Linking wintering grounds, migratory routes and breeding grounds of different populations is essential for future studies of this aspect.

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