

## Distribution of the subspecies of the Lesser Black-backed Gull *Larus fuscus* in sub-Saharan Africa

HENRIK KYLIN<sup>1\*</sup>, HENK BOUWMAN<sup>2</sup>, AND MICHEL LOUETTE<sup>3</sup>,

<sup>1</sup>*Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, PO Box 7050, 75007 Uppsala, Sweden;* <sup>2</sup>*School of Environmental Sciences and Development (Zoology), North-West University, P Bag X 6001, Potchefstroom 2520, South Africa;* <sup>3</sup>*Department of African Zoology, Royal Museum for Central Africa, 3080 Tervuren, Belgium*

**Capsule** The wintering area of the nominate subspecies of Lesser Black-backed Gull *Larus fuscus fuscus* is from Ethiopia across Uganda and the Congo basin to the Atlantic, while *L. f. intermedius* and *L. f. graellsii* winters in westernmost Africa.

**Aims** To clarify the wintering distributions of the subspecies of Lesser Black-backed Gull.

**Methods** We compiled, mapped, and analyzed available data on ring recoveries (269) and verified museum specimens (22) south of 25°N.

**Results** The wintering area of *L. f. fuscus* as described in standard reference literature (East Africa) is wrong; more rings have been recovered in the Congo basin and along the Atlantic coast than on the eastern seaboard. *L. f. intermedius* and *L. f. graellsii* winter mainly in westernmost Africa with some ring recoveries south and east of Senegal. There are no verifiable finds of the latter two subspecies south of the equator. Ring recoveries suggest leap-frog migration.

**Conclusions** We have updated the distribution of *L. f. fuscus*, *L. f. intermedius* and *L. f. graellsii* in sub-Saharan Africa and found it to be different from previous authorities.

---

\*Correspondence author. Present address: Department of Thematic Studies - Water and Environmental Studies, Linköping University, 58183 Linköping, Sweden Email [henrik.kylin@liu.se](mailto:henrik.kylin@liu.se)

Climate change may have a larger effect on *L. f. intermedius* and *L. f. graellsii* than on *L. f. fuscus*.

## INTRODUCTION

Recently, Kylin *et al.* (2010) pointed out discrepancies between major reference works regarding the wintering area of the nominate subspecies of Lesser Black-backed Gull (*Larus fuscus fuscus*) (Lippens & Wille 1976, Britton 1986, Malling Olsen & Larsson 2004) and ring recoveries (FMNH 2010, SMNH 2010). Britton (1986) and Malling Olsen & Larsson (2004) suggest that *L. f. fuscus* (henceforth called *fuscus*) winters in the Great Lakes of the Rift Valley and eastward along the eastern Africa seaboard. Ring recoveries clearly confirm that the Rift Valley lakes are important for wintering *fuscus*, but contrary to what the reference literature suggests there are more ring recoveries of *fuscus* in the Congo basin (west of the Rift Valley) than east of the Rift Valley (Kylin *et al.* 2010). Thus, the wintering area of *fuscus* is not well understood. The other subspecies, *L. f. intermedius* and *L. f. graellsii* (henceforth called *intermedius* and *graellsii*, respectively) winter along the African west coast as far south as Cameroon and also along the Niger River (Britton 1986, Malling Olsen & Larsson 2004).

There is much ongoing discussion on the status of the different taxa within the *L. fuscus/argentatus* complex (Crochet *et al.* 2002, Liebers *et al.* 2001, Liebers & Helbig 2002, Liebers *et al.* 2004, Yesou 2002). We do not intend to enter into any detailed discussion of the taxonomic problems here, but maintain the three subspecies *fuscus*, *intermedius*, and *graellsii* as useful in the present discussion of the distribution of *L. fuscus* in sub-Saharan Africa. These taxa breed in distinct areas in Europe (Malling Olsen & Larsson 2004).

While summarizing the occurrence of *fuscus* in the Congo basin (Kylin *et al.* 2010) it became clear that the distributions of all the subspecies of the Lesser Black-backed Gull in Africa are probably equally unclear. Lippens & Wille (1976), suggest that all three subspecies, *fuscus*, *intermedius*, and *graellsii* occur in the Congo basin. Ajonina *et al.* (2007) states that about 50% of the Lesser Black-backed Gulls along the coast of Cameroon are *fuscus* and 50% *graellsii*, but do not mention *intermedius*. Moreover, although *fuscus* supposedly dominates in Angola (Dean 2000), some authors suggest the occurrence of *graellsii* even this far south (Dean 2000, Günther & Feiler 1986).

The apparent confusion in the literature as to the distribution of the different subspecies in sub-Saharan Africa, and the fact that we in the Congo only observed *fuscus* (Kylin *et al.* 2010) led us to further elucidate the distribution of the three subspecies by using verifiable evidence in the form of ring recoveries and museum specimens.

## METHODS

Ringling data of birds recovered south of 25° N were obtained from the EURING database. A complication for the evaluation presented here is that some countries have not fully digitalized their historical records, why the EURING database is not complete (Chris du Feu pers. comm.). Additional data were obtained directly from the Icelandic, Norwegian (partial) and German (old data available only on paper) ringling schemes, and from published Norwegian records (Bakken *et al.* 2003, Helberg *et al.* 2009). The subspecies are not registered in the ringling databases, but was assigned by us, based on where the birds were ringed as pulli in colonies know to contain only one subspecies. In the case of birds ringed in southern Sweden and easternmost Denmark assigned to *fuscus*, all were ringed prior to the recent decline of this subspecies while the colonies in this area were still *fuscus* (Malling Olsen & Larsson 2004). Two birds ringed in northern Norway in colonies in which both *fuscus* and *intermedius* nest were included as uncertain (Helberg *et al.* 2009). A ring recovery (a beach wreck) on the Cocos Keeling Islands in the SE Indian Ocean was excluded as an anomaly. It should be noted that there are many recoveries of Lesser Black-backed Gulls in Saharan Africa north of 25° N (EURING 2010), especially along the Mediterranean coast. But as this area is easier to access and, thus, more studied, we concentrated this study to sub-Saharan Africa where major knowledge gaps exist.

To obtain additional data and check for discrepancies with the ring recoveries, museums likely to have major collections of bird skins from Africa were contacted and skins were examined either by personal visit to the museum or via photographs provided by the museum. Many skins were of juveniles and could therefore not be assigned to subspecies, or occasionally not even to species, with certainty. Only adult or subadult individuals were assigned to subspecies after stringent visual inspection.

Maps were drawn using MAPVIEWER (version 7.4.2986; Golden Software Inc, Colorado, USA). Latitude and longitude relative frequency distributions were generated using PRISM 4.03 (GraphPad Software, La Jolla, CA, USA). Kruskal-Wallis (non-

parametric) tests were used to test the overlaps (separation) of the subspecies for both latitude and longitude. Dunn's multiple post-hoc tests were used to distinguish between subspecies.

## RESULTS

Recoveries of 166 rings for *fuscus*, 82 for *graellsii*, and 19 for *intermedius* were obtained. In addition, 2, 12, and 8 collection localities were obtained for *graellsii*, *intermedius*, and *fuscus* respectively, from verifiable museum skins. For ease of discussion, unless otherwise qualified, we will refer to museum skins and ring recoveries as ‘recoveries’ from here on.

An overview of the 269 ringing and 283 recovery locations of individuals of all three subspecies recovered south of 25° N is given in Fig. 1a. Many birds have been ringed or recovered at locations close together causing overlap of the points on the chosen scale, why additional maps with dispersed points (with reduced overlap) are presented (Fig. 1b) to show the approximate location of each recovered bird. Points were dispersed using the ‘overlap’ feature of the mapping programme. Dispersion was maximum 30 km at the highest latitudes, and 140 km at the equator. Since all three subspecies had overlapping distributions in western Africa and to aid in interpretation of distribution, individual dispersed maps are provided (Fig. 1c-e).

Recoveries of *fuscus* are most dense from Ethiopia down through the African Great Lakes to the Congo basin and to the west coast of Africa from the Gulf of Guinea to Namibia (Fig. 1c). There are also some *fuscus* recovered along the eastern seaboard. Recoveries of both *graellsii* (Fig. 1d) and *intermedius* (Fig. 1e) are concentrated to westernmost Africa from Western Sahara to Senegal, with some distributed further east and south. Fig. 2a-b show the latitudinal and longitudinal distributions, respectively, of all three subspecies in Africa south of 25° N. For both latitude and longitude, the separation was highly significantly different (Kruskal-Wallis  $p < 0.0001$ ) between *fuscus* and the other two subspecies (Dunn’s multiple post-hoc tests  $p < 0.001$ ), but not between *graellsii* and *intermedius* ( $p > 0.05$ ). The nominate distribution was further east and south, centring on Lake Victoria, than *graellsii* and *intermedius*, both centring on southern Mauritania.

The ring recoveries are dispersed over the whole time span of the ringing programmes while many of the museum specimens are from the 19<sup>th</sup> or early 20<sup>th</sup> century, i.e., prior to most ringing programmes. The number of recoveries of *graellsii* and *intermedius* is too low to distinguish any major shift in the wintering area. Although the number of recoveries of *fuscus* is higher, there is no obvious shift in the distribution in sub-Saharan Africa when the data are partitioned into recoveries per decade.

## DISCUSSION

### Geographic distribution

The recoveries of ringed *fuscus* (Fig. 1c) do only partially confirm the conventionally accepted wintering area (Britton 1986, Malling Olsen & Larsson 2004). Based on the density of recoveries (Fig. 1c) we conclude that the core wintering area of *fuscus* in sub-Saharan Africa is from Ethiopia over Uganda to the Congo basin and further to the Atlantic coast up to Nigeria and Ghana. Except for around Lake Victoria (the outline of which is clearly visible in Fig. 1a-c), the recoveries of *fuscus* east of the Albertine Rift (the western arm of the Rift Valley system) and along the eastern seaboard are surprisingly few, considering that this was considered as an important wintering area (Britton 1986, Malling Olsen & Larsson 2004).

Already in the previous study (Kylin *et al.* 2010) we showed that the Congo basin was likely a more important wintering area for *fuscus* than the East African coast, based on ring recoveries from Finland and Sweden. This impression is augmented when also Danish and Norwegian data are included, although a few additional ring recoveries from the eastern seaboard were found among these newly included data. To enhance the picture, there are also a fair number of registered sightings in Namibia, Botswana, and South Africa (ADU 2010a, 2010b, Zest for Birds 2010; locations not indicated in Fig. 1) and a couple of museum specimens from Zimbabwe; individual *fuscus* apparently wander widely over much of the southern part of the continent. Indeed, Donnelly (1974) suggested that Lesser Black-backed Gulls are more common in southern Africa than the literature normally indicates, but that many are mistaken for Kelp Gulls (*L. dominicanus*). The situation on the eastern seaboard of Africa remains unclear due to the presence of a fourth taxon, *L. [fuscus] heuglini*. This taxon nests in Russia and we have not gained access to any relevant ringing data.

The latitudinal and longitudinal separation between *fuscus* on the one hand, and *graellsii* and *intermedius* on the other is pronounced (Fig. 2a-b) and significant. Harris (1962) also reported that 86% of *graellsii* ringed in Britain found along the west coast of Africa (down to Mauritania) were first year birds. We did not analyse for any changes over time or effects of age classes as we do not yet have complete data sets from all of Europe. It does seem from our data that in Africa, *intermedius* and *fuscus* are less constrained latitudinally and longitudinally than *graellsii*. Changes in local conditions as well as climate

change may therefore have a greater negative effect on the wintering range of *graellsii* than the other two, as there may be more scope for exploratory migration in Africa to the south and east.

### Migration routes

Drawing conclusions about migratory routes based on recoveries is complicated, but it is notable that only three *fuscus* rings (Fig. 1c) have been recovered in westernmost Africa in the area where most *graellsii* (Fig. 1d) and *intermedius* (Fig. 1e) have been found while quite a few have been recovered in the inner Gulf of Guinea and along the Niger River. It is difficult to envisage that all the *fuscus* individuals recovered in the Gulf of Guinea and the Niger River have migrated via the western flyway as sometimes suggested (Cramp & Simmons 1983). Rather, it is noteworthy that these recoveries more or less lie within a contiguous area of ring recoveries extending between Lake Victoria, across the Congo basin to Namibia and the Niger River/Gulf of Guinea. This pattern of recoveries makes migration along an eastern flyway (Åkesson 2010), via the Congo basin to the Atlantic likely, although some may also migrate directly across the Sahara (Schmaljohann *et al.* 2008). That migration across deserts does occur is obvious from a ring recovered in central Saudi Arabia. Although this bird was recovered in a farming area with artificial irrigation, it must have flown over desert to reach the location. A low number of *fuscus* will clearly migrate along the western flyway as observed, e.g., in Portugal (Marques *et al.* 2009), but given the great variability of plumage colouring in colonies normally attributed to *intermedius* (Noeske 2008) some of the birds reported as *fuscus* off Portugal may be of another subspecies.

Although the ring recoveries of *graellsii* and *intermedius* are concentrated to westernmost Africa (95% and 62% between 27°30' and 17°30' W for *graellsii* and *intermedius*, respectively), some clearly migrate further east and south from the core wintering area (Fig. 1d-e, Fig. 2a-b). The latitudinal ring recovery distribution (Fig. 2b) indicates that a larger percentage of *intermedius* than of *graellsii* move on, especially further east. It must be pointed out, though, that our material suffers from an incomplete dataset of *intermedius* ringed in Norway pending an ongoing national evaluation. Once these data become available the complete picture may become clearer. Presently, the only ring recovery south of the equator of either of these two subspecies is an *intermedius* recovered at 0°27' S in the Republic of the Congo (Brazzaville; Fig. 1e). Thus, the statement by

Lippens & Wille (1976) that all three subspecies are present in the Congo basin is not supported by recoveries. If subspecies other than *fuscus* are present in the Congo basin this would in all likelihood be low numbers of *intermedius*. Likewise, in contrast to the statements of Ajonina *et al.* (2007) that equal numbers of *fuscus* and *graellsii* occur off Cameroon, the recoveries indicate that *fuscus* and *intermedius* dominate, while the number of *graellsii* should be lower.

Analyzing the ringing localities give additional interesting information on the migration behaviour of the western subspecies of the Lesser Black-backed Gull. All recovered *graellsii* south of 25° N were ringed in Britain, the Shetland and Faeroe Islands, and Iceland, while recoveries of birds ringed in Ireland are absent (Fig. 1a-b). Similarly, all recovered *intermedius* were ringed in Denmark, Norway, and Sweden, while birds ringed further south in continental Europe have not been recovered south of the Sahara, e.g., from 447 colour-ringed nestling birds and 39 breeding adults in the colony in Belgium, only two sightings (on a grand total of 3395) were made in Mauritania, one in Senegal and none further south (Van Waeyenberge *et al.* 2002). Collectively, the sightings and recoveries indicate leapfrog migration where individuals nesting in the north of the nesting area of the respective subspecies migrate further south than those nesting in the south. This can also be seen by comparing Figs. 1b and 2a where *fuscus* that breed further north than the other two subspecies are recovered further south. This pattern could, however, also be due to geography, where birds breeding in European Scandinavia, when flying south, end up in eastern and central Africa as they seemingly skirt the drier Sahel. For *graellsii* and *intermedius*, the Gulf of Guinea limits any movement further south (Figs. 1d, 1e & 2a). When more ringing and recovery data becomes available, these patterns can be studied in more detail.

### **Field observations and museum specimens**

There are published field observations that suggest the occurrence of *graellsii* in Angola. Günther & Feiler (1986) tentatively assigned a flock of 12 foraging Lesser Black-backed Gulls observed just north of Luanda in Angola to *graellsii*. However, when checking the reference given as basis for the determination (Tuck & Heinzel 1978) it contains major errors. We have checked 12 individual copies of both the first (1978) and second (1980) printing of this book and find that the printing quality of the plates varies and in many of them the mantle of *graellsii* is depicted too dark. But, most importantly, the available

distribution maps contain errors showing *graellsii* as the only subspecies wintering in Africa while *fuscus* is shown wintering in the North Atlantic (*intermedius* is not mentioned). It is, therefore, possible, if not likely, that the assignment of the observed birds to *graellsii* is based on faulty information and that they actually were *fuscus*. On direct question, the senior author agreed that this conjecture is plausible (Rainer Günther, pers. comm.), but that it has been too long since the observations were made for him to remember clearly how the discussions then went.

There is also a museum specimen from Angola; a juvenile bird collected in 1900 determined as *graellsii* (Dean 2000). But when inspected even the species determination of the specimen is doubtful. Our conclusion, therefore, is that there is no clear evidence from ring recoveries, verifiable museum specimens or published field observations, that *graellsii* or *intermedius* occur to any great extent south of the equator.

Additional information, especially on past distributions, could be gained from skins of juvenile specimens in museum collections if it was possible to use genetic markers to distinguish the subspecies of Lesser Black-backed Gull. Unfortunately, this does not currently seem to be possible (Liebers *et al.* 2004).

### **Feeding ecology**

Strann & Vader (1992) studied the differences in feeding behaviour between the subspecies of Lesser Black-backed Gull. They suggested that *fuscus* has adapted a feeding behaviour, catching small fish at the water surface, that allow them to avoid competition with both other large gull species (e.g., *L. argentatus* and *L. marinus*) and the other subspecies of Lesser Black-backed Gull that all aggregate around major food sources such as fishing boats and garbage dumps. We observed *fuscus* feeding on small fish between the trees of the flooded forest of the Congo basin (Kylin *et al.* 2010). Most of the fish productivity in this area is in the flooded forest, less so in bodies of open water (Marlier 1958), and it is possible that this feeding adaptation has enabled *fuscus* to utilize the flooded forest in ways that the other subspecies will not. If so, the large tracts of flooded forest in the Congo basin could act as a geographic barrier where *intermedius* and *graellsii* have difficulties finding sufficient food, but allowed *fuscus* to disperse more widely in and beyond the Congo basin (compare distributions Fig 1c-e).

### **CONCLUSIONS**

Although the EURING dataset is incomplete, the number of data is reasonable and the general distribution picture should not change substantially even with complete data from all countries. We are not suggesting that the area where rings have been recovered of an individual subspecies is the whole extent of its wintering range, but that the density of ring recoveries has substantial indicative value. If a high number of rings of one subspecies have been recovered in an area, but no rings of other subspecies, this should give valuable information on the relative abundance of the subspecies over time. For Africa as a whole there are many additional recoveries of Lesser Black-backed Gulls further north (EURING 2010), including birds ringed further south in Europe. But our focus has been to understand the distribution of the subspecies south of the Sahara, why we exclude any such information here. In addition to Africa, *fuscus* disperses around the Arabian Peninsula south of 25° N (Fig. 1a-c).

We have updated the distribution of *fuscus*, *graellsii* and *intermedius* in Africa south of 25° N based on rings recovered from birds ringed as pulli, and visually verified museum specimens. *Fuscus* show a high density of recoveries in an area stretching in an arc from Ethiopia, over Lake Victoria and through the Congo basin to the Gulf of Guinea, with some recoveries south into Angola and Namibia. The previously suggested wintering area along the east coast of Africa for this subspecies seems less important than the Congo basin and the western seaboard. Distribution of the other two subspecies, *graellsii* and *intermedius*, are concentrated in western Africa, with some inland towards the east and south. The southernmost ring recovery of either of these two, an *intermedius*, was on the equator in the Republic of the Congo (Brazzaville). Some museum specimens and field observations of *graellsii* south of the Equator are doubtful, and we have not found any verifiable evidence (either ringed as pulli or visually confirmed museum skins) of any subspecies other than for *fuscus* south of the equator. Climate change might have a greater effect on *graellsii* and *intermedius*, as they seem to be more constrained in available landmass to the south than *fuscus*, but might shift farther southwest along the coast.

## ACKNOWLEDGEMENTS

Particular thanks are due to Chris du Feu at the EURING databank for valuable help and providing most of the ringing data. Klaus Malling Olsen and Hans Larsson gave valuable

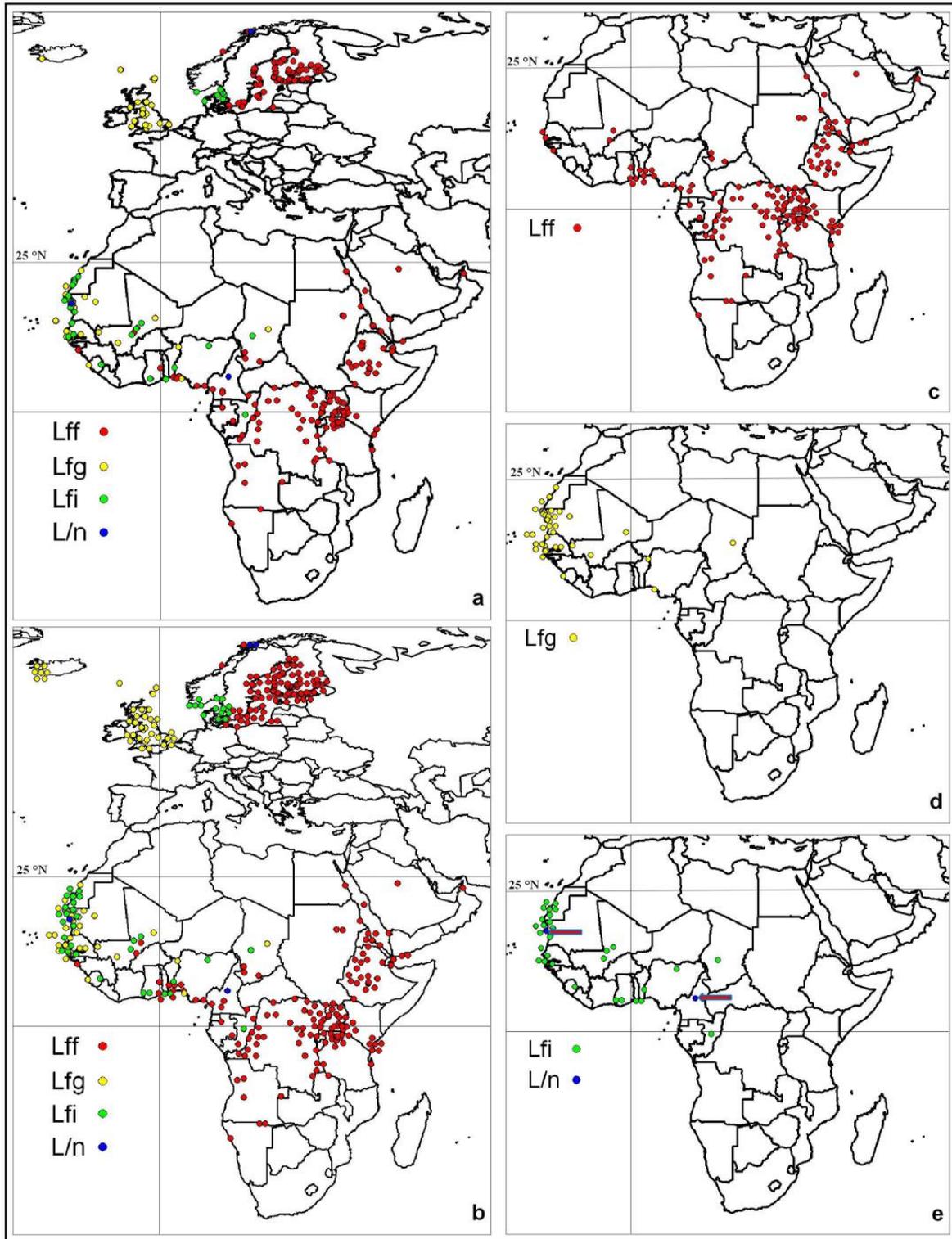
comments on photos of museum specimens. Additional ringing data were provided by Wolfgang Fiedler from the German ringing programme, Morten Helberg and Alf Tore Mjøs from the Norwegian ringing programme, Ævar Petersen from the Icelandic ringing programme, William Velmala from the Finnish ringing programme, and Thomas Wenninger from the Swedish ringing programme. Hein van Grouw, British Museum of Natural History, Alain Reygel, Royal Museum for Central Africa (Belgium), Paul Sweet and Thomas J. Trombone, American Museum of Natural History, Tamar Cassidy from the Transvaal Museum, Pretoria, South Africa, and Peter Mundy, Bulawayo, Zimbabwe, helped locate museum specimens or providing photos thereof. The staff of several other museums also searched their holdings for relevant specimens. Valuable discussion points were provided by Inogwabini Bila-Isai (WWF Congo), Richard Dean, and Rainer Günther. The text was much improved by two reviewers. The authors declare they have no conflict of interest.

## REFERENCES

- ADU 2010a.** Animal Demography Unit, University of Cape Town.  
[http://sabap2.adu.org.za/species\\_maps.php?Spp=4136](http://sabap2.adu.org.za/species_maps.php?Spp=4136). Accessed 20 August 2010
- ADU 2010b.** Animal Demography Unit, University of Cape Town.  
[http://sabap2.adu.org.za/species\\_maps\\_sabap1\\_smoothed.php?Spp=4136](http://sabap2.adu.org.za/species_maps_sabap1_smoothed.php?Spp=4136). Accessed 20 August 2010
- Ajonina, G., Napoleon, C., Skeen, R. & van der Waarde, J.** 2007. *Waterbird Census of Coastal Cameroon and Sanaga River. WIWO Report Series 83.*
- Åkesson, S.** 2010. [http://www.seaturtle.org/tracking/index.shtml?project\\_id=408](http://www.seaturtle.org/tracking/index.shtml?project_id=408) . Accessed 18 July 2010
- Bakken, V., Runde, O. & Tjørve, E.** 2003. *Norsk ringmerkingsatlas*. Vol. 1: 338-346 (in Norwegian with English summary). Stavanger Museum, Stavanger, Norway.
- Britton, P.L.** 1986. Laridae. In Urban EK, Fry CH, Keith S (eds) *The Birds of Africa*. Vol 2: 340-374. Academic Press, London.
- Cramp, S. & Simmons, K.E.L. (eds)** 1983. *Birds of the Western Palaearctic*. Vol 3: 801-815. Oxford University Press, London.
- Crochet, P.-A., Lebreton, J.D. & Bonhomme, F.** 2002. Systematics of Large White-headed Gulls: Patterns of Mitochondrial DNA Variation in Western European Taxa. *Auk* **119**: 603–620.

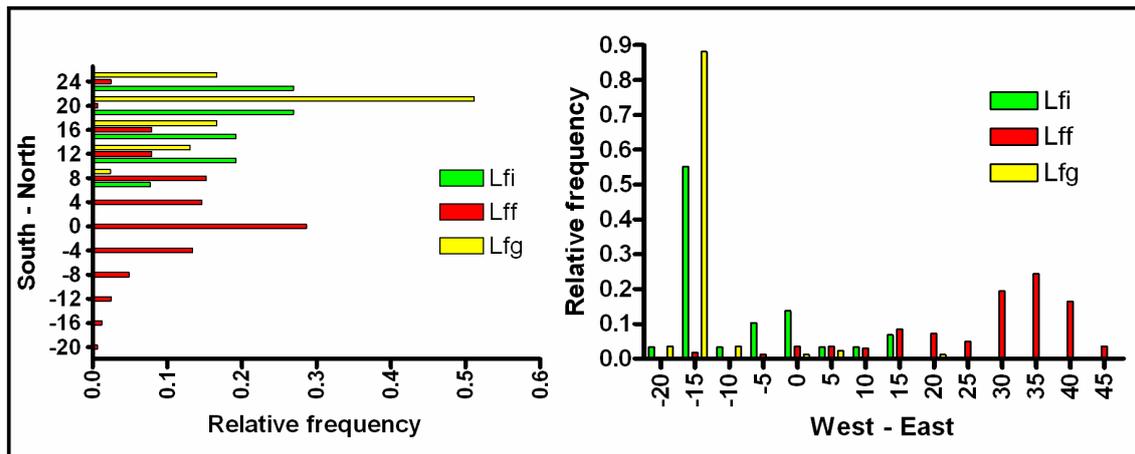
- Dean, W.R.J.** 2000. *The Birds of Angola: An Annotated Checklist*. BOU Checklist 18. British Ornithologists' Union, Tring.
- Donnelly, B.G.** 1974. The Lesser Black-backed Gull *Larus fuscus* in southern and central Africa. *Bull. Brit. Ornith. Club* **94**: 63–68.
- EURING** 2010. <http://www.euring.org/edb/species-maps/sp05910.htm>. Accessed 17 June 2010
- FMNH** 2010. Finnish Museum of Natural History, bird ringing centre, <http://www.fmnh.helsinki.fi/elainmuseo/rengastus/tuloksia/karttoja/selkalokki.gif>. Accessed 15 July 2010
- Günther, R. & Feiler, A.** 1986. Zur Phänologie, Ökologie und Morphologie angolanscher Vögel (Aves). Teil I: Non-Passeriniformes. *Faunist. Abhand. Staat. Mus. Tierk. Dresden* **13**: 189–227 (in German).
- Jonsson, L.** 1998. Baltic Lesser Black-backed Gull *Larus fuscus fuscus* – moult, ageing and identification. *Birding World* **11**: 295–317.
- Harris, M.P.** 1962. Migration of the Lesser Black-backed Gull as shown by ringing data. *Bird Study* **9**: 174–182.
- Helberg, M., Systad, G.H., Birkeland, I., Lorentzen, N.H. & Bustnes, J.O.** 2009. Migration patterns of adult and juvenile Lesser Black-backed Gulls *Larus fuscus* from northern Norway. *Ardea* **97**: 281–286.
- Kylin, H., Louette, M., Herroelen, P. & Bouwman, H.** 2010. Nominate Lesser Black-backed Gulls (*Larus fuscus fuscus*) winter in the Congo basin. *Ornis Fenn.* **87**: 106–113.
- Liebers, D., Helbig, A.J. & de Knijff, P.** 2001. Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadriiformes). *Mol. Ecol.* **10**: 2447–2462.
- Liebers, D. & Helbig, A.J.** 2002. Phylogeography and colonization history of Lesser Black-backed Gulls (*Larus fuscus*) as revealed by mtDNA sequences. *J. Evol. Biol.* **15**: 1021–1033.
- Liebers, D., de Knijff, P. & Helbig, A.J.** 2004. The herring gull complex is not a ring species. *Proc. Roy. Soc. London, Ser. B – Biol. Sci.* **271**: 893–901.
- Lippens, L. & Wille, H.** 1976. *Les Oiseaux du Zaïre*. Lannoo, Tielt, Belgium (in French).
- Malling Olsen, K. & Larsson, H.** 2004. *Gulls of Europe, Asia and North America*. Christopher Helm, London.
- Marlier, G.** 1958. Recherches hydrobiologiques au lac Tumba. *Hydrobiologia* **10**: 352–385.

- Marques, P.A.M., Costa, A.M., Rock, P. & Jorge, P.E.** 2009. Age-related migration patterns in *Larus fuscus* spp. *Acta Ethol.* **12**: 87–92.
- Noeske, A.** 2008. Mantelfärbung und taxonomische Stellung der Heringsmöwen *Larus fuscus* auf Amrum. *Vogelwelt* **129**: 379–394 (in German with English summary).
- Schmaljohann, H., Liechti, F. & Bruderer, B.** 2008. First record of lesser black-backed gulls *Larus fuscus* crossing the Sahara non-stop. *J. Avian. Biol.* **39**: 233-237.
- SMNH** 2010. Swedish Museum of Natural History Bird Ringing Centre.  
<http://www.nrm.se/images/18.1416bda210eb7cf4e7880004711/Silltrut.png>. Accessed 15 July 2010
- Strann, K.-B. & Vader, W.** 1992. The nominate Lesser Black-backed Gull *Larus fuscus fuscus*, a gull with a tern-like feeding biology, and its recent decrease in northern Norway. *Ardea* **80**: 133–142.
- Tuck, G. & Heinzel, H.** 1978. *A Field Guide to the Seabirds of Britain and the World*. William Collins Sons & Co.
- Van Waeyenberge, J., Stienen, E.W.M. & Vercrujse, H.J.P.** 2002. Kleurringproject van Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* aan de Belgische kust: overzicht van algemene resultaten. *Natuur.oriolus* **68**: 146-156 (in Dutch with English summary).
- Yesou, P.** 2002. Systematics of *Larus argentatus-cachinnans-fuscus* complex revisited. *Dutch Birding* **24**: 271–298.
- Zest for Birds** 2010. <http://www.zestforbirds.co.za/> (Rarities page) Accessed 30 May 2010



**Figure 1a.** Overview of ringing and recovery locations of the three subspecies of Lesser Black-backed Gulls. The lines indicate the equator and the Greenwich longitude. Lff – *fuscus*, Lfg – *graellsii*, Lfi – *intermedius*, L/n – uncertain *fuscus* or *intermedius*. The data from Norway is incomplete and all ringing localities in the southern part of the country are

indicated from a single location although ringing occurred in much of western Norway. **b.** Overview map with ringing and recovery data dispersed to reduce overlap of multiple ringings/recoveries at many locations. **c-e.** Detailed maps of the recoveries in sub-Saharan Africa of each subspecies of Lesser Black-backed Gull. **c.** *fuscus*. **d.** *graellsii*. **e.** *intermedius* plus two non-assigned (*intermedius* or *fuscus*) from northern Norway. To help locate the unassigned these dots are indicated by arrows.



**Figure 2.** **a)** Relative latitudinal distribution of the three subspecies of Lesser Black-backed Gulls. Bin widths are 4°. **b)** Relative longitudinal distribution of the three subspecies of Lesser Black-backed Gulls. Bin widths are 5°. Lff – *fuscus*, Lfg – *graellsii*, Lfi – *intermedius*.