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Distributions of the subspecies of Lesser Black-backed Gulls *Larus fuscus* in sub-Saharan Africa

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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* winter in westernmost Africa.

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

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

Results The wintering area of *L. f. fuscus* that is described in standard reference literature (East Africa) is incorrect; 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 leapfrog 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. We hypothesize that climate change will have a larger effect on the distributions of *L. f. intermedius* and *L. f. graellsii* than on *L. f. fuscus* in this region.

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) suggested 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, 2004, Liebers & Helbig 2002, 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 Lesser Black-backed Gulls in Africa are probably equally unclear. Lippens & Wille (1976) suggest that all three subspecies, *fuscus*, *intermedius*, and *graellsii* occur in the Congo

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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 in the Congo we observed only *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

Ringing 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 and so 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) ringing schemes, and from published Norwegian records (Bakken *et al.* 2003, Helberg *et al.* 2009). The subspecies are not registered in the ringing 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. However, as this area is easier to access and, therefore, more studied, we concentrated this study on 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 therefore could not be assigned to subspecies, and 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, and for this reason 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. This dispersion had a maximum of 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, dispersed maps of the individual subspecies are provided (Figs 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 in westernmost Africa from Western Sahara to Senegal, with some distributed further east and south. Figs 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

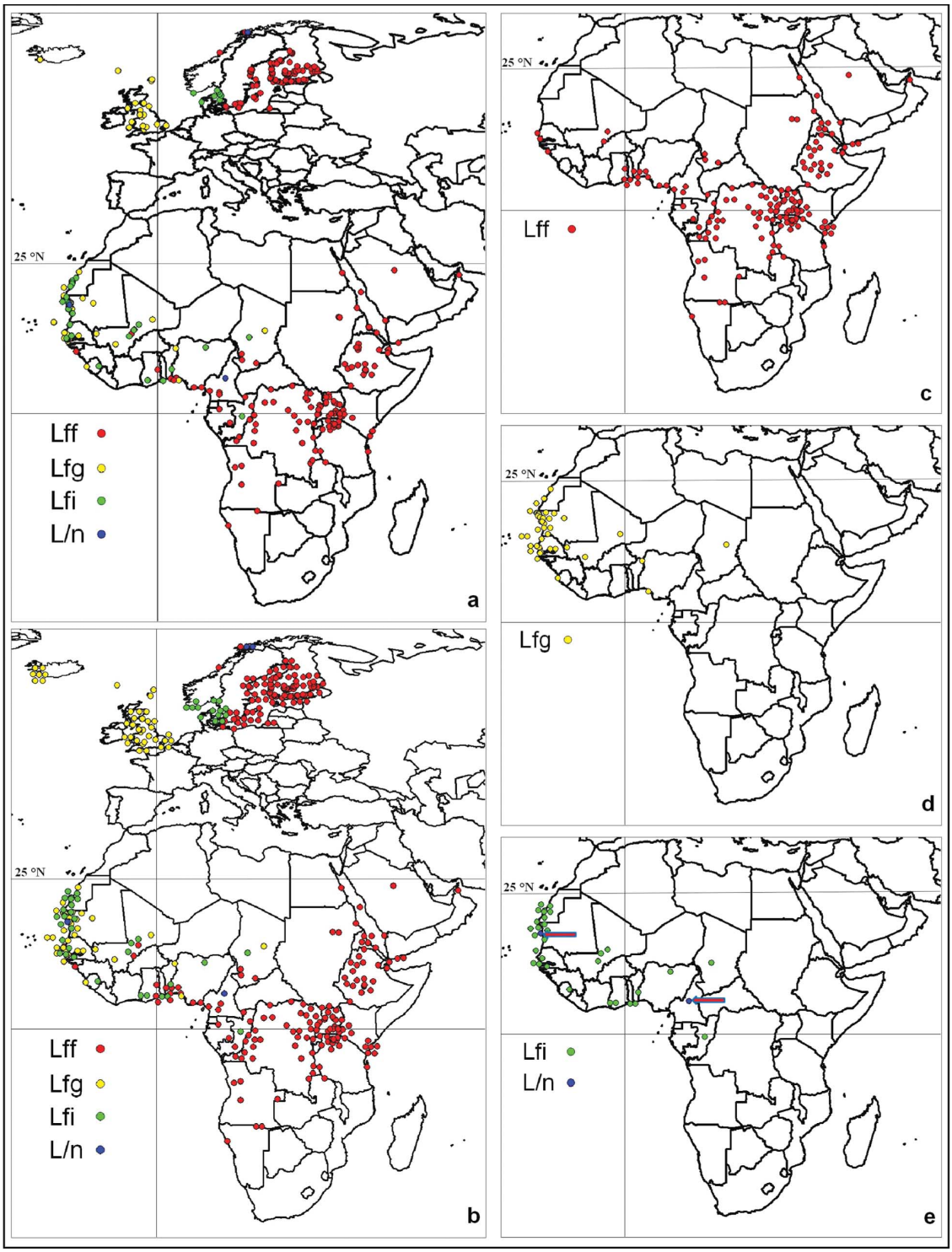

Figure 1. (a) Overview of ringing and recovery locations of the three subspecies of Lesser Black-backed Gulls *Larus fuscus*. The lines indicate the equator and the Greenwich longitude. Lff, *fuscus*; Lfg, *graellsii*; Lfi, *intermedius*; L/n, uncertain *fuscus* or *intermedius*. The data from Norway are 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.

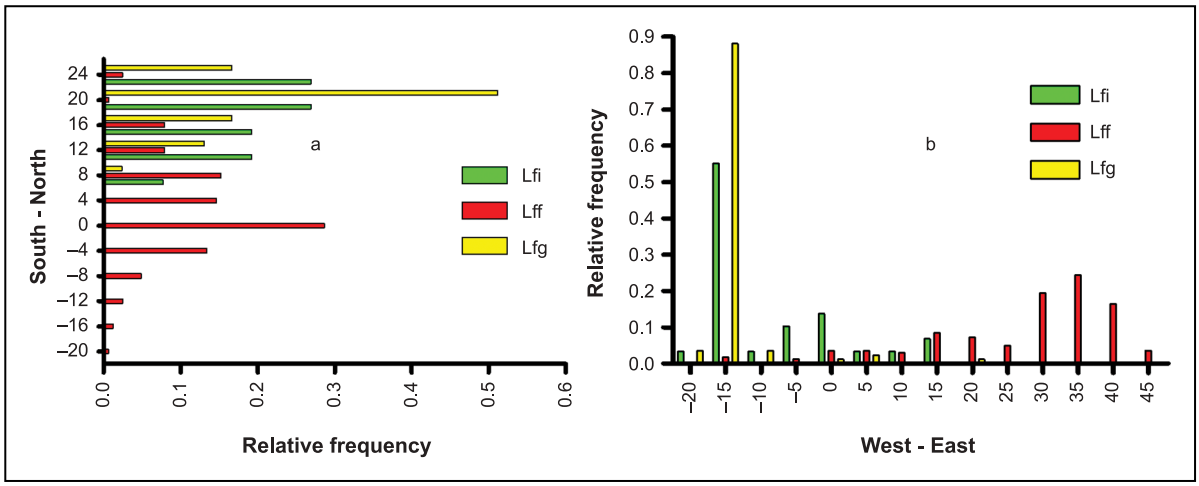

Figure 2. (a) Relative latitudinal distribution of the three subspecies of Lesser Black-backed Gulls *Larus fuscus*. Bin widths are 4°. (b) Relative longitudinal distribution of the three subspecies of Lesser Black-backed Gulls. Bin widths are 5°. Lff, *fuscus*; Lfg, *graellsii*; Lfi, *intermedius*.

(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 19th or early 20th centuries, 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) only partially confirm the conventionally accepted wintering area of this subspecies (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 west to the Atlantic coast up to Nigeria and Ghana. Except for around Lake Victoria (the outline of which is clearly visible in Figs 1a–c), the number of 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).

In the previous study (Kylin *et al.* 2010) we showed that the Congo basin was probably 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 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. Thus it appears that individuals of the *fuscus* subspecies 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 breeds 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 (Figs 2a,b) and significant. Harris (1962) also reported that 86% of *graellsii* ringed in Britain that were found along the west coast of

Africa (down to Mauritania) were first-year birds. We did not analyse our data to look for changes over time or the 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), then 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 (Figs 1d,e, Figs 2a,b). The latitudinal ring recovery distribution (Fig. 2b) indicates that a larger percentage of *intermedius* than of *graellsii* move on, especially further east. However, it must be pointed out, that our material suffers from an incomplete data set 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.

Analysing the ringing localities gives 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 (Figs 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 2 sightings (of a 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,e & 2a). When more ringing and recovery data become 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. However, 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*. The senior author has 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 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 the 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* employ 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 Gulls 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 difficulty finding sufficient food, but allowed *fuscus* to disperse more widely in and beyond the Congo basin (compare distributions Figs 1c–e).

CONCLUSIONS

Although the EURING data set 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 an individual subspecies has been recovered is the whole extent of its wintering range, but that the density of recoveries has substantial indicative value. If a high number of individuals of one subspecies have been recovered in an area, but none 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 in more southern parts of Europe. However, our focus has been to understand the distribution of the subspecies south of the Sahara and for this reason we have excluded any such information here. In addition to Africa, *fuscus* disperses around the Arabian Peninsula south of 25°N (Figs 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*, is concentrated in western Africa, with some inland towards the east and south. The southernmost ring recovery of both of these two subspecies, 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.

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