

Why are the wings of *Larus f. fuscus* so dark?

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The Scandinavian Lesser Black-backed Gull *Larus f. fuscus* has a much darker mantle and less white and grey on the primaries than other gulls of the *Larus argentatus-fuscus* group. These characteristics of *L. f. fuscus* are adaptations to wintering in tropical regions with a sunny climate and to long distance migration. Such migration demands efficient wings, but wintering in areas with high solar UV radiation makes exposed unpigmented parts of the wing feathers sensitive to wear, which reduces the efficiency of the wings. Selection has therefore preferred darkening of the mantle and increase of the black areas of the wing feathers, especially in the wing tips subject to the strongest wear.

Illumination of primaries of *L. a. argentatus* with UV radiation (amount corresponding to 6-month illumination at the equator) made white and pale grey areas much more sensitive to wear, but did not decrease the resistance of the blackish parts. Even after UV irradiation, the black primaries of *L. f. fuscus* resist wear better than the darkest parts of the primaries of *L. argentatus*. The inner primaries of *L. f. fuscus*, covered by other feathers in resting birds, retain their white tips, but the small white tips of the four longest primaries become worn off before the breeding time. Their loss evidently does not affect the aerodynamics of the wing. Large gulls of the North Atlantic region wintering in less sunny climate have larger white tips on the long primaries and retain them until the moult. The blackish primaries and dark mantle of *L. crassirostris*, *L. pacificus* and *L. heermanni* may have partly the same explanation as the black wings of *L. f. fuscus*.

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Introduction

The systematics and taxonomy of the large gulls, especially the *Larus argentatus-fuscus* group and its relatives, have been discussed by many zoologists, but little attention has been paid to the question why the colouration of the Scandinavian Lesser Black-backed Gull *Larus f. fuscus* differs so much from that of related species. However, the fact that one member of a generally pale-coloured group has developed a very dark wing pigmentation seems to call for an explanation.

In *L. f. fuscus* the white at the wing tips is greatly reduced and the mantle colour is slightly brownish black (colour analysed by Barth 1966). This gull evidently never interbreeds with *L. argentatus* in nature (these species have interbred successfully in captivity in the Helsinki Zoo). However, interbreeding has sometimes been recorded in Holland and England between *L. argentatus* and the race *L. fuscus graellsii*, which is more similar in colouration to *L. argentatus* (Stegmann 1934, Tinbergen 1953). Although there is thus indirect evidence that a very dark mantle and wing

colouration may contribute to separate *L. fuscus* and *L. argentatus*, it seems highly unlikely that the colouration of *L. f. fuscus* should have developed mainly as a character enhancing the separating effects of slight differences in behaviour (Goethe 1955, 1975) and the at least nowadays more obvious differences in breeding time and choice of breeding locality (e.g. Bergman 1939, 1982, Paludan 1951, Goethe 1955, 1960). The main reasons for the development of dark colouring in *L. f. fuscus* are more likely to lie in the fact that this gull is much more migratory than the other large gulls breeding in the NW Palearctic, and winters in tropical and subtropical regions.

Winter range and wing colouration

L. f. fuscus migrates further and is a more completely transcontinental traveller than the other large northern gulls. The climate of its winter range is subtropical or tropical and mainly very sunny. The other large gulls — other members of the *L. argentatus*-*fuscus* group, *L. marinus*, *L. hyperboreus* and *L. canus* — winter in more northern regions with a marine climate and far less insolation. Recoveries of Finnish gulls show, that the winter range of *L. f. fuscus* consists of the coasts, lakes and rivers within a large area from the eastern Mediterranean and Black Sea to Central Africa and the northern part of the Indian Ocean (P. Saurola, manuscript). One recovery was made as far away as the Coco Island. *L. fuscus graellsii*, intermediate between *L. f. fuscus* and *L. argentatus* in migration and many other respects, winters along the coasts between S England and NW Africa (Salomonsen 1967).

Voitkevich (1961) points out that "feathers and parts of feathers which contain melanin are more resilient and less subject to wear than unpigmented feathers". Though he does not explain in which way the pigmentation improves the resistance of the feathers, Voitkevich's statement is readily confirmed by studying primaries dropped from *L. canus*, *L. argentatus* and *L. marinus*. When these lie at the high water line subjected to the wearing effect of the waves and the shore, it is the white parts of the tips that first become damaged. The hamuli and the edges of the second-order barbs are partly worn away and lose the ability to keep the surface of the white web intact, it becomes transparent and the barbs break. The black parts of the feathers remain intact much longer.

The primaries of *L. f. fuscus* have to resist the wear of the long migration. The four longest primaries have a really black or very dark grey pigment even in most of those parts that are pale in *L. argentatus* (cf. Fig. 1 A, B), and their white tips are much shorter (only 0—1 mm, c. 3 mm, 4—5 mm and 5—6 mm, respectively). There is only a small white "speculum spot" beyond the tip of the first primary, or in some old birds on the two first primaries, but the outer web of the primary is mostly black even at this spot.

In the collections of the Zoological Museum of the University of Helsinki, two of the 46 adult *L. f. fuscus* specimens have a speculum spot on the second primary as well, and in three additional individuals this second spot is present merely as a 3—15 mm long white zone on the rachis. Two otherwise adult-coloured specimens have still not developed any speculum spot at all.

In most *L. f. fuscus* individuals arriving in Finland in April, the white terminal tips of the four longest primaries are almost completely worn away. During the breeding season the rest of the white on these tips is lost and

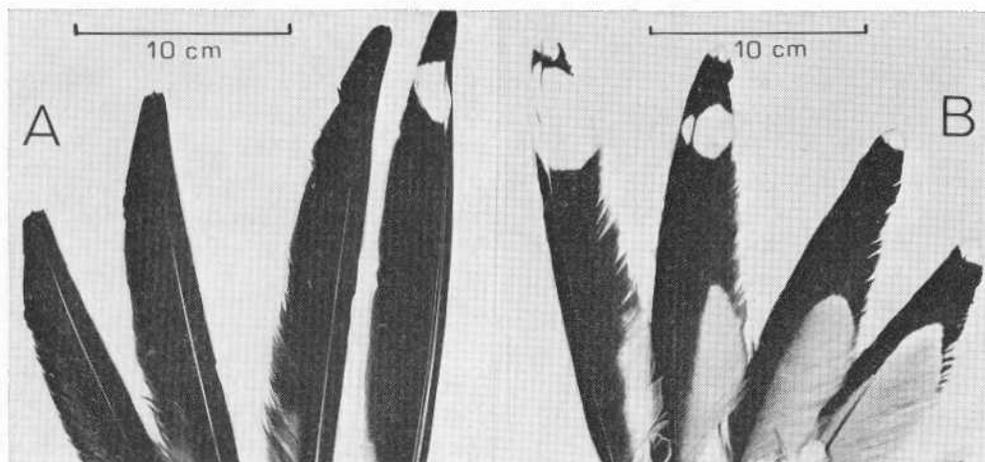


FIG. 1. Primaries 1—4 of (A) a Lesser Black-backed Gull *Larus f. fuscus* (Gulf of Bothnia, 10.7.1948) and (B) a Herring Gull *L. a. argentatus* (Gulf of Finland, 20.5.1971). Note the difference in the wear of the white tips and the reduction of all the white and grey areas in *L. f. fuscus*.

even the innermost secondaries and scapulars may lose much of the white terminal bar. However, the rather large white tips of the inner primaries and outer secondaries remain more or less intact until the moult. A specimen of *L. f. fuscus* shot 35 km SW of Helsinki on about 1 May 1982 has lost most of the white on the tips of the primaries 1—4 (Fig. 2A), and even the tips of the inner primaries show signs of wear. A specimen shot off Helsinki on 5 August 1905 has lost so much of the white tips that the wings, when closed, appear totally blackish, but the white tips of the inner primaries and outer secondaries are intact. They are also intact in most of the other specimens in the collection of the museum.

From this we can conclude that the wing feathers which are exposed to light and wear in the resting bird lose their white tips, but the sheltered wing feathers retain their white tips. The sheltering effect of the closed wing on the primary tips in *L. f. fuscus* and the large white primary tips of *L. argentatus* can be seen in Fig. 2.

All races of *L. argentatus* have a wing tip colouration that could be characterized as a blackish subterminal

bar with different kinds of white terminal spots. This general type is also found in *L. fuscus graellsii*, *L. marinus* and *L. canus*; in *L. glaucescens* the bar is greyish and there are pale traces of it in *L. hyperboreus*. Photographs published in numerous studies show clearly that the pronounced white tips of all the primaries in these gulls are still intact or almost intact during the breeding season (e.g. Berg 1918, Goethe 1937, Tinbergen 1953) and at least in *L. argentatus* the white terminal spots are not badly worn even in August. This is also evident from the collections in the Zoological Museum of Helsinki. Only in *L. marinus* do the broad white tips of the primaries 1—3 become so worn during the breeding season that the shape of the wing tip becomes much more rounded than in the spring (my own field records).

In *L. f. fuscus* the short white tips of the long primaries are already almost completely worn off about 6—8

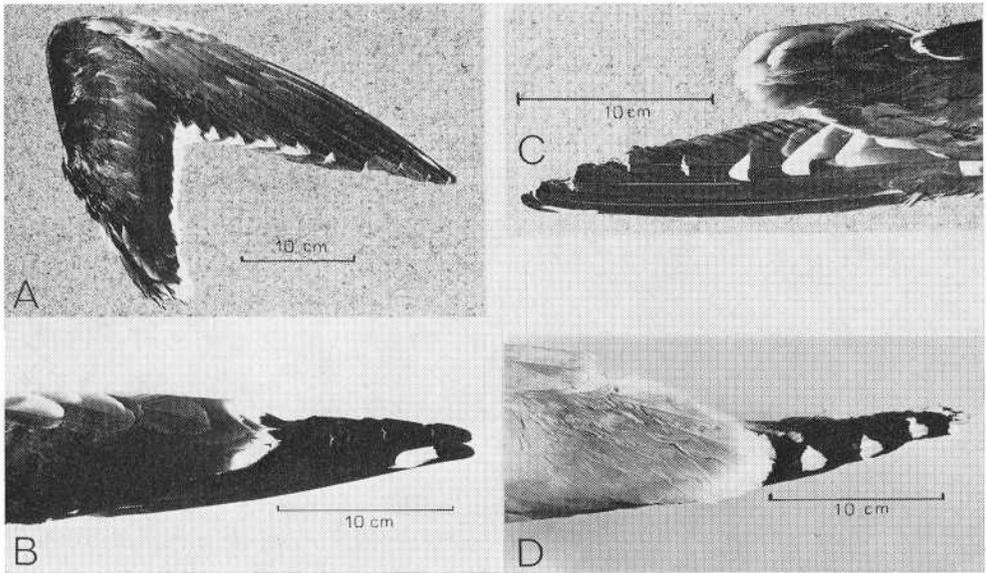


FIG. 2. A. Wing of *Larus f. fuscus* (Gulf of Finland, c. 1.5.1982). Note the strong wear of the white tips of the long primaries and the much slighter wear of the tips of the inner primaries. — B. *Larus f. fuscus* (Gulf of Bothnia, 10.7.1948). The white tips of the long primaries completely worn off. — C. *Larus f. fuscus* (Gulf of Finland, 4.5.1971). No wear of the tips of the inner primaries, in resting birds sheltered by the secondaries. — D. *Larus a. argentatus* (Gulf of Finland, 20.5.1971). The large white tips of the primaries are intact, some signs of wear on the scapulars and wing coverts.

months after the moult (starting during and after the autumn migration, details in Barth 1975). The primary tips of the other large northern gulls resist wear for nearly a year (their moult begins during breeding and ends mostly before the autumn migration). Differences in physical factors in the wintering areas evidently cause this difference in the preservation of the feather tips. There are considerable differences in light (especially in the UV radiation), temperature and humidity. The fact that only those tips which are exposed to light become strongly worn shows that differences in light play a greater role than other factors. There may also be some differences in the habits of the different species, but these are probably of

minor importance for the wear of the feather tips.

L. f. fuscus is the only large northern gull with very little white on the tips of the long primaries, the only one which loses the exposed parts of the white primary tips completely, and the only one with a really dark mantle and wing feather colouration. Therefore it seems very likely that in *L. f. fuscus* the reduction of the white tips and replacement of the greyish colour of the wing feathers with black or dark grey, and also the brownish black mantle colour, are adaptations that reduce the wear of the wing feathers caused by long distance migration and wintering in the tropics, especially the latter.

The long and narrow wings (high

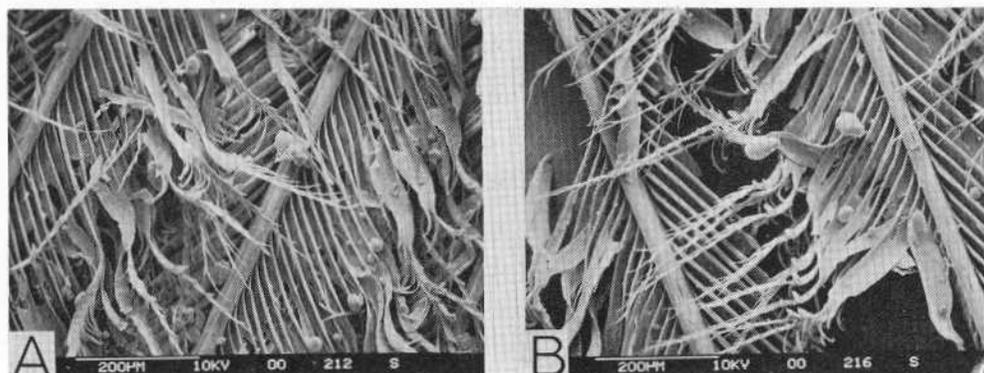


FIG. 3. The effect of 30 light scrapings on the grey part of the inner web of the 3rd primary of *L. a. argentatus*. A. no UV irradiation, B. UV irradiation. Note break-up of the surface in B. Scanning electron micrograph by The Finnish Pulp and Paper Research Institute.

wing index, Kipp 1959) are no doubt an adaptation to long-distance migration (Stegmann 1934), but this type of wings also influences the mode of feeding considerably (Goethe 1975, Bergman 1982), which, in its turn, increases the need for good flight ability and intact wing tips, perhaps even more than the long-distance migration itself. The reduction of the size of the white tips of the outer primaries diminishes the area sensitive to wear and thus also the unfavourable influence of wear on the aerodynamics of the wing tip.

Pigmentation and UV radiation

Does the dark pigmentation protect the wing feathers against the destructive effects of the UV radiation of the sunlight? This would agree with the strong wear of the unsheltered primary tips in *L. f. fuscus* and the less pronounced wear of the same feathers in other gulls of almost the same size but wintering in less sunny regions.

To obtain information on this point, primaries of an adult *L. f. fuscus* (collected on 14 May 1970 25 km SE of Helsinki, no. 15064 Zool Museum Helsinki) and an adult *L. a. argentatus* (collected on 26 May 1971 at the same place, no. 15768, Zool. Museum Helsinki) were illuminated with UV radiation and their resistance to wear compared with the resistance of corresponding unirradiated feathers from the other wing of the same specimens. The amount of UV radiation used corresponded to the theoretical UV radiation at sea level at the equator during half a year.

The resistance of the feathers to mechanical wear was studied as follows. About 4 cm² of the upper surface of the feather was scraped with a knife blade of somewhat rounded shape, held against the feather with a pressure of 20 g (radius of the knife sector 3 cm). The knife was kept perpendicular to the feather surface and moved repeatedly with a speed of c. 2 cm/s in the direction of the first-order barbs towards the edge of the feather. Three samples of each category were scraped.

The feathers were irradiated and the scanning electron micrographs taken at The Finnish Pulp and Paper Research Institute, Espoo.

In the white and pale grey areas of unirradiated primaries of *L. argentatus* damage became visible in the centre of the scraped area after 25–30 scrapings; after 40–50 scrapings the web became highly transparent. In UV-irradiated primaries of the same grey web colour signs of damage appeared after 10–15 scrapings and transparency of the web after 25–35 scrapings (see Fig. 3). The

blackish web in the primaries of *L. argentatus* showed much better resistance whether irradiated or not: damage first became visible after 45—55 scrapings and transparency at 70—80 scrapings. But the best resistance to scraping was offered by the really black primaries of *L. f. fuscus*, including those which had been irradiated: visible signs of destruction appeared only after 50—60 scrapings and transparency after 80—100 scrapings.

The results thus prove that light parts of primaries of gulls are more sensitive to the destructive effect of UV radiation than dark-pigmented parts of the web. Being a long-distance migrant, *L. f. fuscus* has developed wing pigmentation that makes the feathers less sensitive to deleterious effects of UV radiation and thus also to the wear occurring during the migration.

Concluding remarks

Larus f. fuscus shows at least the following adaptations to long-distance migration and to wintering in tropical areas: (1) long, narrow and highly pointed wings, (2) early autumn migration, (3) moult of the primaries mainly after the autumn migration (not before as in other large northern gulls), and (4) wings with good resistance to wear. This resistance is achieved by darker pigmentation and a larger black area in the primaries, which protect the feathers, especially the most exposed parts of the longest primaries, against the destructive effect of UV radiation during the winter spent in regions with high insolation. The white area on the very exposed tips of the primaries has been reduced so much that it can be worn away without greatly affecting the aerodynamics of the wing tip.

In three other coastal gull species

the long primaries are dark without any white spots: *Larus pacificus* breeding in S Australia, *L. crassirostris* breeding in NE Asia, and *L. heermanni* breeding in Mexico. The wing colouration of these species could possibly be explained as protection against wear, just as in *L. f. fuscus*. However, a dark mantle may also develop as a species character, contributing to separate different species in the same region. This may be the main reason for the rather dark mantle of some other gulls: *L. marinus*, *L. fuscus graellsii* and some other members of the *L. argentatus-fuscus* group. They all have pronounced white tips on all primaries. In *L. f. fuscus* the tropical winter range has caused further darkening of the mantle and primaries and reduction of the white of the wing tips. A gull of the southernmost Atlantic, *L. dominicanus*, is very like *L. f. fuscus* but lacks the brownish colouring of the mantle and has pronounced white tips on all the primaries. Could this species perhaps have been isolated from an ancient *L. fuscus* before the Scandinavian *L. fuscus* had developed its brownish black mantle colour and still had much of the white wing marking left?

It may also be mentioned that *L. ridibundus*, a regular migrant earlier wintering chiefly in the Mediterranean region (now also commonly in Central and W Europe, because favoured by human settlement) has black on the outermost tips of the long primaries, a black bar along their inner web from the tip to the base of the feather, and a thin black stripe along the outer web of the first primary. Thus even in this species those parts of the primaries that are most exposed to wear are black. It is a widespread phenomenon that long-distance migrants and species spending much of

their life on the wing have dark wing feathers. This agrees well with Voitkevich's statement, but naturally the colouration of the wings is the result of many different factors.

Selostus: Miksi selkälökki on Pohjolan lokeista tummasiipisin?

Selkälökki on pitkänmatkan muuttaja, joka talvehtii aurinkoisessa trooppisessa ilmastossa. Muut pohjoisten seutujen isot lokit viettävät talvensa pohjoisempana merellisessä ilmastossa. Pitkä muutto vaatii tehokkaita siipiä. Selkälökin pisimpien käsisulkien pienet valkoiset kärjet ovat jo toukokuussa kuluneet pois, vaikka sulkasato on vasta syysmuuton jälkeen. Muilla lokeillamme vastaavien sulkien paljon isommat valkoiset kärjet säilyvät sulkasatoon asti. Selkälökin puvussa säilyvät vain ne valkoiset sulankärjet, jotka siiven lepoasennossa peittyvät muiden sulkien alle. Ilmeisesti valolla on suuri osuus vaaleiden sulanosien haurastumiseen. Koska pitkien valkoisten kärkien poiskuluminen vaikuttaisi kielteisesti siiven aerodynamiikkaan, valinta on selkälökilla edistänyt näiden kärkien pienenemistä nimenomaan pisimmissä käsisulissa. Myös siiven yleisvärin muuttuminen ruskehtavan mustaksi on tehnyt sulat kestävämmiksi.

Suuritetut kokeet, joissa harmaalokin ja selkälökin käsisulkiä valotettiin UV-valolla (määrä vastasi puolen vuoden säteilyä päivän-tasaajalla), osoittivat, että UV-valo tekee sulkien vaaleat osat hauraammiksi, mutta ei vaikuta mainittavasti sulan mustien osien kestävyteen. Sulan kulutuskestävyyttä kokeiltiin raaputtamalla sen pintaa, jolloin se vähitellen muuttui läpikuultavaksi. Pohjoisemmilla seuduilla talvehtivilla lokeilla UV-säteilyn aiheuttamaa tummenemispainetta ei ole, mutta tumman värin syntyminen voi aiheutua myös lajituntomerkin "tarpeesta". Selkälökki-harmaalokki-ryhmässä on muutama tummanharmaaselkäinen laji tai rotu; merilökki on hyvin tummanharmaa ja Etelä-Atlantin *Larus dominicanus* on mustaselkäinen. Näillä kaikilla on paljon valkoista siivenkärjissä eikä lainkaan ruskeaa sävyä. Selkälökilla kehitys on kulkenut astetta pitemmälle, koska sen pitkien käsisulkien on kestettävä aurinkoisien ilmastoinen vaikutus. Myös *Larus pacificus*, *L. crassirostris* ja *L. heermanni*-lokeilla valkoisten käsisulkakuvien puuttuminen voinee johtua tummien sulkien paremmasta auringonkestävyydestä.

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