

THE NOMINATE LESSER BLACK-BACKED GULL *Larus fuscus fuscus*, A GULL WITH A TERN-LIKE FEEDING BIOLOGY, AND ITS RECENT DECREASE IN NORTHERN NORWAY

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ABSTRACT In northern Norway, *Larus fuscus fuscus* feeds mainly offshore on the wing on pelagic fish and fishery discards. It avoids competition with other large gulls for concentrated stationary food sources such as garbage dumps and fish-factories. It is also inferior to the Herring Gull *L. argentatus* and the Great Black-backed Gull *L. marinus* when competing for large food items behind stationary or slow-moving fishing boats. However it is superior in obtaining small items from fast-moving boats. Nominate *fuscus* is clearly more specialised in its feeding biology than *L. f. graellsii* and *L. f. intermedius*. It also shows clear differences in morphology, migration route, moulting cycle, population parameters and population development, and may be specifically different from *graellsii* and *intermedius*. During the last decades the breeding population of nominate *fuscus* in northern Norway has decreased alarmingly. Food shortage is thought to be the main reason for this decrease.

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INTRODUCTION

The systematics of the large *Larus* gulls is highly complex. Most recent authorities agree that the Lesser Black-backed Gull *Larus fuscus* is a distinct species (Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983). In both modern hand-books *L. fuscus* is sub-divided into five subspecies: the small, dark-mantled and very long-winged nominate *L. f. fuscus* of northern and eastern Scandinavia, the somewhat heavier and lighter-mantled west European *L. f. intermedius* and *L. f. graellsii*, and the still larger and also lighter-mantled *L. f. heuglini* and *L. f. taimyrensis* of northern Russia.

Most Lesser Black-backed Gulls are highly migratory, although increasing numbers of *graellsii* are wintering in Britain (Baker 1980, Cramp & Simmons 1983). The two south-western subspecies migrate to the south-west to winter in the Iberian peninsula and north-west Africa, the other three subspecies migrate to the south-east towards wintering areas in east Africa and along the Arabian

coasts (Glutz von Blotzheim & Bauer 1982, Urban *et al.* 1986).

In northern Norway, nominate *fuscus* is decreasing alarmingly in number (Fig. 1). Earlier breeding colonies on the Kola peninsula (Biancki 1967) and in eastern Finnmark (Wessel 1904) apparently disappeared at the beginning of this century, and at present *fuscus* is virtually absent from Finnmark (Røv 1986, Strann & Vader 1986). At the end of the nineteenth century it was still numerous in Troms, particularly in its southern parts. Numbers then underwent a drastic decline to about 450 pairs in the 1930s (Soot-Ryen 1941) and 300 pairs in the early 1980s (Strann & Vader 1986). Few early records exist for the counties of Nordland and Trøndelag, the main stronghold of nominate *fuscus* in Norway, but the breeding population is estimated to have decreased by 50-90% during 1970-85. At present there are about 3500 breeding pairs in Trøndelag and southern Nordland (Røv 1986, Thingstad 1986). A similar, though less severe numerical decrease has been noted in Finland (Kilpi 1983).

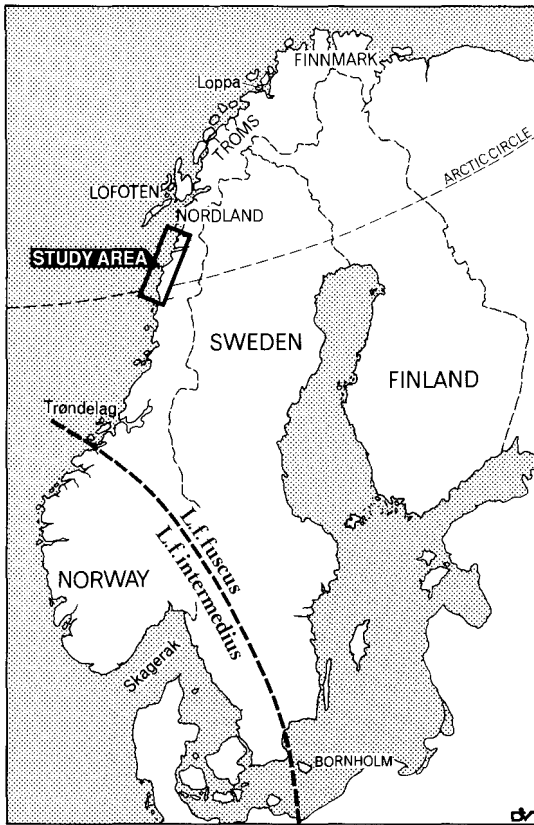


Fig. 1. Map of Norway and adjacent countries showing the location of the study area and the geographical names outside that area mentioned in the text.

Populations of *intermedius* in southern Norway, on the other hand, have steadily increased in number throughout this century. This has been particularly well marked along the Skagerak coast (see Røv 1986). In the northern part of west Norway some local declines have been noted in earlier years, but at present the overall population appears to be stable or increasing (see Røv 1986, Thingstad 1986, Lorentsen 1990). A similar trend has been noticed elsewhere (Cramp & Simmons 1983).

The breeding success of nominate *fuscus* in northern Norway has been very low during the last 10-20 years (Table 1, see also Røv 1986, Thingstad 1986). Chicks found dead had all died within one week of hatching. None of the 13 newly dead chicks dissected in Troms colonies in 1981 and 1982 had food remains in their stomach or oesophagus.

The present paper presents data on the feeding biology of nominate *fuscus* and sympatric populations of Herring *L. argentatus*, Great Black-backed Gull *L. marinus* and Common Gull *L. canus* during the breeding season in northern Norway. The results are compared with earlier studies of nominate *fuscus* in Finland and those of *intermedius* and *graellsii*, in an effort to explain the very different recent population developments of these taxa. The systematic position of nominate *fuscus* will also be discussed.

STUDY AREA AND METHODS

Feeding biology of nominate *fuscus* and of sympatric *argentatus*, *canus* and *marinus* was studied in the Varggård archipelago and around the village of Ørnes, Nordland, close to the Arctic Circle (Fig. 1). Varggård consists of about 30 islands of different sizes. The main island is flat, with rocky shores and a mosaic of small ponds, vegetated areas, and bare rock. There are a large number of breeding seabirds on the island, particularly gulls, and during the study period there were 120 pairs of Great Black-backed Gulls, 450 pairs of Herring Gulls, 110 pairs of Lesser Black-backed Gulls, and 40 pairs of Common Gulls. The Ørnes area on the mainland is dominated by rocky shores: 70% of the

Table 1. Proportion of chicks found dead in three colonies of *Larus f. fuscus* in northern Norway during 1980-84. Numbers in parentheses indicate number of nests checked.

Colony	Date	% dead	N
Varggård	June 1980	95	43 (25)
66° 52'N, 13° 15'E	June 1981	92	27 (19)
Hakstein	July 1981	100	7 (7)
70° 01'N, 21° 05'E	July 1982	100	11 (9)
Spilderøy	July 1981	93	15 (11)
69° 25'N, 18° 29'E	July 1984	72	7 (5)

coastline are rocky, 20% are a mixture of rocky and muddy shores, and 10% are muddy or sandy shores. There are two fish-factories, one garbage dump, and several farms with large fields (Strann 1985).

Most of the fieldwork was carried out during 1978-80. Counts of total number of gulls of each species present in the two study areas were made every second or third day throughout the study, and the gulls' habitat choice (sea, rocky shore, sandy or muddy shore, dumps, fish-factories, and other terrestrial habitats, also including towns) recorded. Randomly chosen gulls were followed for 10 min each, and time spent sleeping (head under wing), sitting (head up), preening, displaying, flying, walking, swimming, and feeding were noted. Feeding methods used by the gulls were subdivided into nine categories: pecking from surface, digging (strong pecks in order to remove sand or mud), searching among seaweed, moving stones or seaweed, robbing, shell-dropping, plunge-diving, foot-paddling, and up-ending.

In order to investigate competition between gulls when feeding on fish offal in multispecies flocks, the number of gulls of each species attracted to about 10 l of fish offal thrown overboard from a stationary or slow-moving fishing boat was recorded every minute for five min. Offal was subdivided into three categories: small (fish liver cut into pieces of 1x1 cm each), medium (fish guts from small fish, 6-8x4 cm each), and large (fish guts from

large fish, 14-40x8-20 cm each). To study the gulls' ability of feeding on the wing we threw pieces of bread and fish guts overboard from boats moving at a speed of about 7.2 m·s⁻¹ and registered the number of gulls of each species attracted to the bait and the number succeeding in obtaining it. Comparisons between species were made using a goodness of fit χ^2 -test (Sokal & Rolph 1969).

RESULTS

In northern Norway, nominate *fuscus* spends most of its time feeding over deep water, either on the fiords or offshore, and it feeds on the shore to a lesser extent (Fig. 2, Table 2). We never found nominate *fuscus* feeding on farmland, as Common Gulls regularly did. It was never found feeding at dumps or fish-factories on the mainland either, as was the case in the Herring, Great Black-backed and the Common Gull. On the seashore nominate *fuscus* fed primarily by pecking food from the surface. We did not see birds digging, searching for food under seaweed or removing small stones and clumps of seaweed, as Herring Gulls in particular did (Table 3).

Throughout the study nominate *fuscus* was regularly observed plunge-diving for sea urchins *Strongylocentrotus droebachiensis*, blue mussels *Mytilus edulis*, and other marine invertebrates in shallow water (less than about 1 m deep). Great Black-backed and Herring Gulls used this method

Table 2. Habitat preference (% of specific species seen in habitats) in four species of *Larus* gulls feeding in northern Norway. Numbers in parentheses indicate number of feeding birds observed.

Species	Deep water		Shallow water		Rocky shores	Muddy shores	Inland
	Swimming	Flying	Swimming	Flying			
<i>L. f. fuscus</i> (470)	19.2	60.0	8.9	5.7	2.1	4.1	0
<i>L. marinus</i> (690)	8.2 ²	13.2 ²	16.6 ¹	10.2 ¹	40.2 ²	11.6 ²	0
<i>L. argentatus</i> (94)	2.3 ²	10.4 ²	12.8 ¹	9.4	55.3 ²	9.8 ¹	0
<i>L. canus</i> (632)	3.2 ²	24.4 ²	7.0	10.3 ¹	1.8	12.7 ²	40.5 ²

^{1,2}differences between species and nominate *fuscus* significant at 0.05 and 0.01 level, respectively (goodness of fit χ^2 -test, *df* = 1).

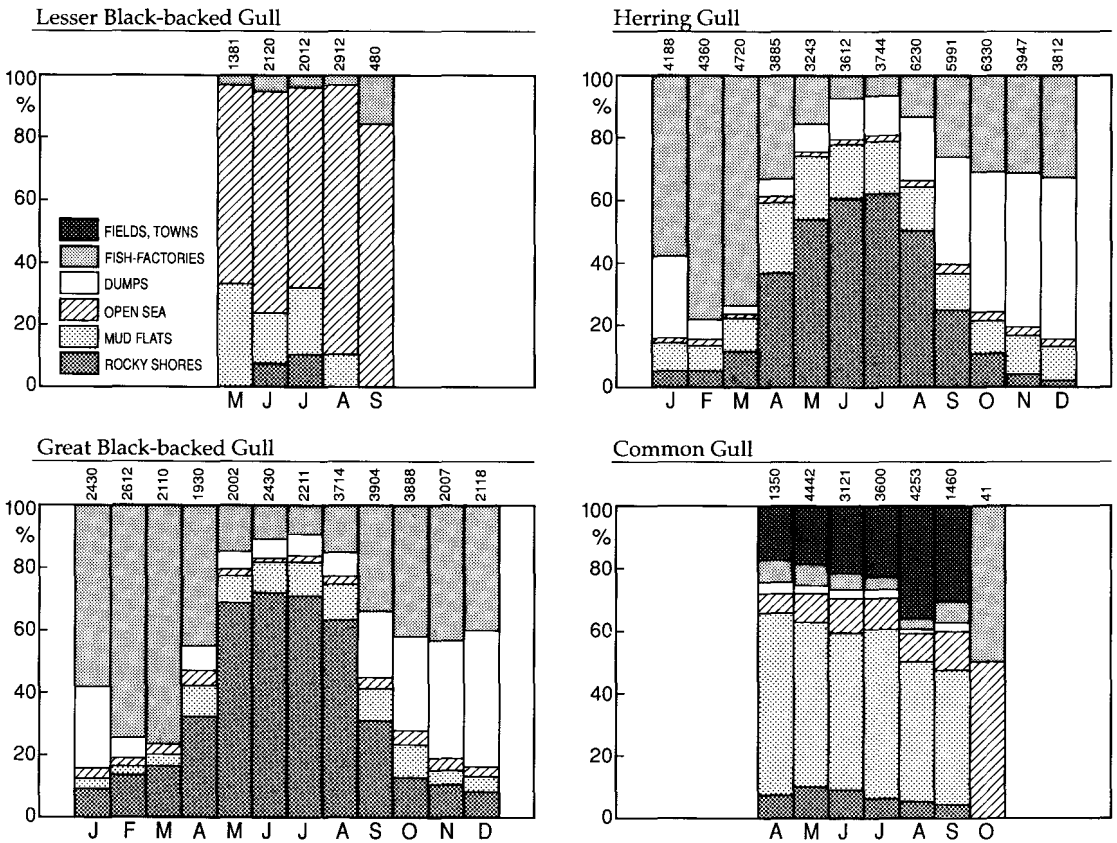


Fig. 2. Habitat choices in four species of gulls in northern Norway (loafing and feeding birds combined). Numbers above bars give total number of gulls observed each month.

significantly less often than nominate *fuscus* (Table 4). When feeding on shoaling fish in deep water the difference between nominate *fuscus* and the two other species was even more clear-cut (Table 4). Nominat*e fuscus* was often seen plunge-diving, Herring and Great Black-backed Gulls did so only seldom.

We have very little information about the feeding methods used by nominate *fuscus* offshore, but 67 observations of multispecies gull flocks feeding on shoaling fish off Ørnes show that *fuscus* was overrepresented when compared with the number of gulls of each species breeding in the area (Table 5).

Nominat*e fuscus* took small pieces of offal more than twice as often as did the Herring Gull and Great Black-backed Gull in the test series from stationary

and slow-moving fishing boats (Table 6). There was little difference between *fuscus* and the two other species for the medium-sized pieces of bait. However, *fuscus* took significantly fewer pieces of the larger pieces of offal than the other two species.

When feeding on small pieces Great Black-backed Gulls were never seen attempting to rob nominate *fuscus*, while Herring Gulls were only seldom seen doing so. Also when feeding on medium-sized and large-sized offal it seldom occurred that these species attempted to rob nominate *fuscus* (Table 7), mainly because *fuscus* avoided the tight flocks of Great Black-backed and Herring Gulls fighting for the larger pieces of offal. Instead *fuscus* flew around picking up smaller pieces of offal floating away from the 'battlefield', a behav-

Table 3. Frequency of various feeding methods (in % of total time that species was observed feeding) in three species of *Larus* gulls foraging on rocky and muddy shores in northern Norway. Numbers in parentheses indicate number of 10 min periods that species was observed.

Species	Feeding method			
	Pecking from surface	Searching between seaweed	Moving stones, seaweed etc.	Digging
Rocky shores:				
<i>L. f. fuscus</i> (191)	94.7	5.3	0	-
<i>L. argentatus</i> (508)	57.1 ²	20.1 ²	22.8 ²	-
<i>L. marinus</i> (101)	84.2 ¹	6.9	8.9 ²	-
Muddy shores:				
<i>L. f. fuscus</i> (39)	92.4	7.7	0	0
<i>L. argentatus</i> (212)	67.0 ²	16.5 ²	14.1 ²	2.4 ¹
<i>L. marinus</i> (70)	81.4 ²	8.6	7.1 ¹	2.9 ¹

^{1,2}difference between species and nominate *fuscus* significant at 0.05 and 0.01 level, respectively (goodness of fit χ^2 -test, $df = 1$).

Table 4. Proportion (in %) of nominate Lesser Black-backed, Herring and Great Black-backed Gulls showing plunge-diving during feeding over water in northern Norway. Number of birds observed given in parentheses.

Species	Shallow water	Deep water
<i>L. f. fuscus</i>	20.0 (30)	27.4 (387)
<i>L. argentatus</i>	8.1 (1470) ¹	9.1 (1325) ¹
<i>L. marinus</i>	4.9 (673) ¹	4.2 (840) ¹

¹difference between species and nominate *fuscus* significant at 0.01 level (goodness of fit χ^2 -test, $df = 1$).

Table 5. Proportion (in %) of Lesser Black-backed, Herring and Great Black-backed Gulls (67 flocks) feeding upon shoaling fish off Ørnes, compared to the breeding bird composition in the area.

Species	Feeding on fish (%)	Breeding (%)
<i>L. f. fuscus</i>	46.1	14.5
<i>L. argentatus</i> ¹	39.8	58.2
<i>L. marinus</i> ¹	14.1	27.3
Total	6200	5500

¹difference between species and nominate *fuscus* significant at 0.01 level (goodness of fit χ^2 -test, $df = 1$).

ious pattern that was shared with Common Gulls and Arctic Terns *Sterna paradisaea*. *Fuscus* was never seen making attempts at robbing either Great Black-backed or Herring Gulls, but made a series of attempts at robbing Common Gulls (small-sized pieces of offal 12%, medium-sized pieces 9%, large-sized pieces 6%). *Fuscus* was also seen robbing conspecifics relatively frequently (Table 7).

Table 6. Ability of three species of gulls feeding in multispecies flocks (% of birds of each species successfully taking offal of that size), in catching fish offal of different sizes (see text) thrown out from a stationary or slow-moving fishing boat off northern Norway. Number of birds feeding given in parentheses.

Species	Size group of offal		
	Small	Medium	Large
<i>L. f. fuscus</i> (134)	36.6	33.5	29.9
<i>L. argentatus</i> (892)	16.9 ²	36.2	46.9 ²
<i>L. marinus</i> (450)	14.0 ²	40.2 ¹	45.6 ²

^{1,2}difference between species and nominate *fuscus* significant at 0.05 and 0.01 level, respectively (goodness of fit χ^2 -test, $df = 1$).

Table 7. Proportion (in %) of gulls attempting to rob *L. f. fuscus* (including intraspecific robbing) when feeding in multispecies flocks upon fish offal of a certain size class (see text) thrown out from a stationary or slow-moving fishing boat off northern Norway. Number of gulls feeding given in parentheses.

Species	Size group of offal		
	Small	Medium	Large
<i>L. f. fuscus</i>	6.7 (104)	28.2 ¹ (209)	36.1 ¹ (194)
<i>L. canus</i>	0 (40)	0 (40)	0 (52)
<i>L. argentatus</i>	2.6 (466)	1.9 (890)	1.4 (738)
<i>L. marinus</i>	0 (230)	4.3 (465)	2.0 (634)

¹difference between species and nominate *fuscus* significant at 0.01 level (goodness of fit χ^2 -test, $df = 1$).

Nominate *fuscus* appeared to be far more efficient in obtaining food thrown from a fast-moving boat than Great Black-backed or Herring Gulls (Table 8).

DISCUSSION

Feeding biology

Our results show clearly that nominate *fuscus* in northern Norway is a real 'sea-gull', while Herring, Great Black-backed and Common Gulls are typical 'shore-gulls'. Nominate Lesser Black-backs forage largely offshore, obtaining most of their food on the wing. So, in this respect they are ecologically closer to Kittiwakes *Rissa tridactyla* and terns *Sterna* spp. than to other Norwegian *Larus* gulls. At sea, they make effective use of their wing-loading: the birds plunge-dive more often than the other gulls we studied (cf. also Bergman 1960, Goethe 1975), they are more frequently found feeding over pelagic fish shoals and are more successful in snatching food items thrown from fast-moving vessels than the other species. In Scandinavia, nominate *fuscus* is therefore the typical 'ferryboat-gull' (Bergman 1960, Hunt & Hunt 1973, Strann 1985).

Nominate *fuscus* does not feed very often on the shore; the birds obtain virtually all their food through

Table 8. Success index (number of pieces of food taken divided by number of gulls of each species present) for three species of gulls feeding in multispecies flocks upon food thrown out from a boat travelling at a speed of 7.2 m·s⁻¹ off northern Norway. Number of feeding gulls given in parentheses.

Species	Food type	
	Bread	Offal
<i>L. f. fuscus</i>	1.82 (93)	1.91 (101)
<i>L. argentatus</i>	0.45 ¹ (285)	0.41 ¹ (416)
<i>L. marinus</i>	0.53 ¹ (38)	0.44 ¹ (80)

¹difference between species and nominate *fuscus* significant at 0.01 level (goodness of fit χ^2 -test, $df = 1$).

generalised surface-pecking. Specialised shore-feeding methods, such as moving stones and seaweed aside, digging in sand, shell-dropping, food-robbing, predation upon eggs and pulli, and predation on adult seabirds, are only rarely used, in contrast to the situation in the large 'shore-gulls' (Table 9).

A further characteristic trait of nominate *fuscus* is its 'timidity' (Goethe 1955). The birds are clearly inferior to Herring and Great Black-backed Gulls when in direct competition for stationary and concentrated food resources. In fact they largely appear to avoid such competition. Bergman (1982) surmised that the long wings of nominate *fuscus* give the birds of this taxon a severe handicap when feeding in dense flocks of flying gulls, but it is not immediately clear why this should be the case. Whether the virtual absence of feeding nominate *fuscus* from places such as refuse dumps, fish-factories and cities is a result of *fuscus*' specialised offshore feeding habits, avoidance of competition or a combination of the two, is unclear. In competition for food behind stationary or slow-moving fishing boats, nominate *fuscus* usually keep to the outside of the throng of birds, and the birds compete most successfully with other species for the smallest pieces only.

There are no earlier published studies on the feeding biology of nominate *fuscus* in Norway. Finnish investigations (e.g. Goethe 1975, Bergman

Table 9. Proportion (in %) of simultaneously feeding *L. f. fuscus*, *L. argentatus* and *L. marinus* showing robbing, shell-dropping and predation (summarised from Strann 1985). Number of birds feeding given in parentheses.

Species	Robbing	Shell-dropping	Predation	
			Eggs/chicks	Adults
<i>L. f. fuscus</i>	7.4 (617)	0.6 (350)	0 (610)	-
<i>L. argentatus</i>	13.0 ¹ (2004)	13.0 ² (21103)	7.1 ² (2210)	-
<i>L. marinus</i>	11.1 ¹ (1140)	5.1 ¹ (2911)	22.3 ² (810)	+

^{1,2}difference between species and nominate *fuscus* significant at 0.05 and 0.01 level, respectively (goodness of fit χ^2 -test, $df = 1$).

1982, and references therein) give the impression that during 1930-60 nominate *fuscus* in Finland had a feeding ecology very similar to that in northern Norway, albeit with a somewhat larger terrestrial food component (earthworms, beetles, berries). The main foods however, consisted of fish, self-caught or from fishing boats, and blue mussels (a sublittoral food in the Baltic!). In later years after fishery activities had declined and the number of Herring Gulls had shown a large increase, small numbers of nominate *fuscus* were found feeding on refuse dumps, and a few specialists started to take ducklings or to practice food-robbing habits, which previously were almost unknown for this taxon in the area (Bergman 1960, 1982). Even so, the numbers of gulls participating in these specialised feeding activities were small, and the general picture remains quite similar to that in northern Norway.

Some published reviews of the diet and feeding biology of the Lesser Black-backed Gull (e.g. Cramp & Simmons 1983, Götmark 1984, Thingstad 1986) do not differentiate between nominate *fuscus*, on the one hand, and *graellsii* and *intermedius*, on the other, and this has masked the considerable differences between the three taxa. There are a number of studies on *graellsii* (e.g. Harris 1965, Verbeek 1977a, 1977b, Noordhuis & Spaans 1992), and a few on *intermedius*, none from Norway (Goethe 1957, Götmark 1984). The results for the three taxa are reviewed by Cramp & Simmons (1983, p. 806) as follows: 'Omnivorous... Often feeds in flocks of hundreds on rubbish dumps or over shoals of fish at sea.... Much food obtained by scavenging, and by

food-piracy, both intra- and interspecific'. The data in the literature give the impression of a feeding biology intermediate between that of nominate *fuscus* and the Herring Gull, with *graellsii* and *intermedius* feeding coastally and by scavenging to a far greater extent, and far better able to compete with Herring Gulls, than nominate *fuscus*. In the southern North Sea, where the very dominant Fulmars *Fulmarus glacialis*, Gannets *Sula bassana* and Great Skuas *Stercorarius skua* (cf. Hudson & Furness 1989) are scarce, an increasing population of *graellsii* has even been able to force the local Herring Gulls to change their diet resulting from interspecific competition around fishing boats (Noordhuis & Spaans 1992).

Population decrease of nominate *fuscus*

Nominate *fuscus* has declined dramatically in number in northern Norway, and it is now generally considered to be threatened. In Finland nominate *fuscus* is decreasing in number, following a numerical increase between 1930 and 1960, but the situation is most dramatic in northern Norway (Kilpi *et al.* 1980, Bergman 1982, Kilpi 1983). On Bornholm nominate *fuscus* is also decreasing in number (Møller 1978). In Finland the numerical decrease of nominate *fuscus* is thought to have been caused by decreased food resources resulting from decreasing fishing activities, an increased competition for food from a much grown Herring Gull population, and an increased disturbance by recreational boating to which the late breeding nominate *fuscus* is particularly vulnerable (Bergman 1982, Kilpi & Saurola 1984).

In clear contrast to the situation in nominate *fuscus*, *graellsii* and *intermedius* have generally increased in number over most of their area of distribution, and *graellsii* has colonised Iceland (cf. Cramp & Simmons 1983, Evans 1984, Røv 1986). These increases, which occurred in spite of a large concomitant increase in the number of Herring Gulls, have generally been attributed to increased food supplies in the form of fishery waste and refuse. The same factors have probably caused the increasing number of wintering *graellsii* in western Europe (e.g. Baker 1980).

Thingstad (1986) has discussed several possible explanations for the steady decrease of nominate *fuscus* in northern Norway during this century. However, neither changes in the African wintering area that could have resulted in an increased winter mortality, nor environmental contaminants in Norway seem to be prime factors. Competition with Herring Gulls and disturbance from recreational boating are suspected to be important factors for the decrease in the size of the Finnish *fuscus* population. However, in northern Norway recreational boating is not a problem, and Herring Gull numbers have not increased much in the area (Strann & Vader 1986).

The probable explanation for the numerical decrease of nominate *fuscus* in northern Norway is therefore a change in the food resources during the breeding season, as first suggested by Myrberget (1985) for a local population in southern Troms. This would explain the low weights and small eggs of nominate *fuscus* caught at the southernmost colony in Norway in 1984 (Thingstad 1986), as well as the very low breeding success in recent years (Røv 1986, Thingstad 1986, this paper), as a result of starvation of the chicks shortly after hatching.

We have no information as to what may have caused the numerical decrease of nominate *fuscus* in Troms and Finnmark early this century, although there are historical indications of a seabird crisis around 1905, with thousands of dead alcids washed ashore. For Trøndelag and Nordland it is tempting to associate the present decrease with the crash of the very large Atlanto-Scandic stock of the herring *Clupea harengus* in the late 1960s. The postlarvae of this fish species probably constituted an impor-

tant food source for many fish-eating birds in the area. The adverse consequences of this crash have been well demonstrated for the Puffin *Fratercula arctica* and the Common Guillemot *Uria aalge* (cf. Vader *et al.* 1990), but more casual observations have also shown widespread breeding failures in the Arctic Tern and Arctic Skua *Stercorarius parasiticus* in several years.

In 1989 the herring had quite a good spawning season, with a high breeding success of Puffins and Common Guillemots in the Lofoten Islands and of nominate *fuscus* in the central portion of the Norwegian coast (T. Anker-Nilssen, O. Vie). This strengthens the hypothesis that the herring stock is of major importance for nominate *fuscus* in this area in the breeding season.

Taxonomic speculations

The systematics of the large *Larus* gulls is still in a state of flux. The Yellow-footed Gull *L. livens* of the Gulf of California has only recently been recognized as a different species to the parapatric Western Gull *L. occidentalis* of the Pacific coast (McCaskie 1983). Until recently the Yellow-legged Gull *L. cachinnans michahellis*, occurring parapatrically with nominate *argentatus*, was considered to be a race of the Herring Gull. Recently *michahellis* has spread from the Mediterranean to Atlantic France, where it now occurs sympatrically with *argentatus* without hybridisation (Nicolau-Guillemet 1977, Marion *et al.* 1985), and it is now considered to be specifically different.

In several respects nominate *fuscus* is quite different from *graellsii* (and the very similar *intermedius*). It is, in spite of its more northern distribution, smaller and daintier, with extremely long wings (Barth 1968, 1975a), and a completely different migration route (Baker 1980, Kilpi & Saurola 1984), it moults in the wintering area (Barth 1975b), it has a different feeding ecology (this paper), and its population development in Europe is completely different.

Nominate *fuscus* and *intermedius* in Scandinavia apparently have a parapatric distribution at present, but more detailed studies in the bordering zone are needed at this point. In this respect it may be significant that only since the recent crash in the

number of nominate *fuscus* in northern Norway have light-mantled Lesser Black-backs been observed in the nominate *fuscus* area (K.-B. Strann). In 1991, light-mantled birds have been found nesting in the Lofoten islands for the first time.

Many of the listed differences between nominate *fuscus* on the one hand and *graellsii* and *intermedius* on the other, are interconnected, setting nominate *fuscus* apart as a long-winged 'sea-gull' with a long-distance migration and a smaller ability to compete with Herring Gulls for concentrated stationary food resources. The differences are considerable, and further comparative studies in the Scandinavian bordering zone of nominate *fuscus* and *intermedius* will be very worth while.

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SAMENVATTING

De nominaatvorm van de Kleine Mantelmeeuw *Larus f. fuscus* vertoont over zijn gehele verspreidingsgebied een onrustbarende achteruitgang. Met name in het noorden van Noorwegen is deze achteruitgang zeer manifest. In Finnmark is de soort als broedvogel zelfs vrijwel verdwenen. Deze ontwikkeling staat in schril contrast tot de toestand in west Europa (inclusief zuid Noorwegen), waar de broed-

vogelstand van de ondersoorten *graellsii* and *intermedius* haast overal vooruitgaat of op zijn minst stabiel is. De meest waarschijnlijke verklaring voor de afname van *fuscus* in noord Noorwegen is voedselgebrek in de broedtijd, met grote sterfte onder de kuikens daarvan als gevolg.

Dit artikel geeft de resultaten van een vergelijkend onderzoek naar de voedselzoekmethoden van de Kleine Mantelmeeuw, Grote Mantelmeeuw *L. marinus*, Zilvermeeuw *L. argentatus* en de Stormmeeuw *L. canus* in het kustgebied van noord Noorwegen. Uit dit onderzoek blijkt dat de nominaatvorm van de Kleine Mantelmeeuw, in tegenstelling tot de drie andere soorten, echte 'zeemeeuwen' zijn. In getijdegebieden is het voedselzoekrepertoire van de Kleine Mantelmeeuw opvallend eenvoudig. Gespecialiseerde methoden, zoals het verplaatsen van steentjes, met de snavel in de bodem peuteren, poottrappelen, laten stukvallen van schelpen, roven van eieren, kleptoparasitisme en predatie van jonge en oude vogels, ontbreken of zijn van zeer ondergeschikt belang.

Op zee stootduikt *fuscus* veel vaker dan de andere meeuwen. Door de betere vliegkunst en de grote wendbaarheid is *fuscus* duidelijk in het voordeel als het erom gaat kleine stukjes afval achter stilliggende of langzaam varende boten te bemachtigen. Het verschil met de grotere en tragere meeuwssoorten bleek ook in veldexperimenten waarbij verschillende soorten afval uit een relatief snel varende boot werden gegooid.

Fuscus is echter geen partij voor Zilver- en Grote Mantelmeeuwen in directe concurrentie om grote voedselbrokken of bij grote voedselconcentraties. Het ziet er zelfs naar uit dat zij zulke confrontaties schuwen. Kleine Mantelmeeuwen zoeken in noord Noorwegen haast nooit voedsel op vuilstortplaatsen of rond visfabrieken, in tegenstelling tot de situatie in west Europa.

In het algemeen kan worden gesteld dat *fuscus* een gespecialiseerde zeemeeuw is, met een haast sternachtige voedselzoekstrategie. De nominaatvorm wijkt in dit opzicht duidelijk af van de minder gespecialiseerde *graellsii* and *intermedius*. *Fuscus* is daardoor ook veel gevoeliger voor schommelingen in het aanbod van pelagische vissoorten (zoals haring *Clupea harengus* in noord Noorwegen) dan de andere ondersoorten.

De drie ondersoorten van de Kleine Mantelmeeuw verschillen duidelijk in morfologie, rui, trekbiologie, voedselzoekecologie en populatieontwikkeling. De verschillen zijn veel groter dan gewoonlijk tussen parapatrische ondersoorten het geval is, en het lijkt daarom de moeite waard eventuele isoleringsmechanismen nader te onderzoeken in het grensgebied tussen *intermedius* en *fuscus*.