# **Migration and wintering strategies of juvenile and adult** Larus marinus, L. argentatus and L. fuscus from Finland

Mikael Kilpi & Pertti Saurola

Kilpi, M. & Saurola, P.: Migration and wintering strategies of juvenile and adult Larus marinus, L. argentatus and L. fuscus from Finland. — Ornis Fennica 61:1—8.

Finnish ringing data were used to examine the migratory patterns of adult (+5 yr) and juvenile (1 yr) Great Black-backed, Herring and Lesser Black-backed Gulls from the SW coast of Finland. The birds generally leave the breeding area in autumn, the Great Black-back making the shortest journey and the Lesser Black-back migrating up to 7500 km. The two larger species winter within the Baltic, while the Lesser Black-back has a large wintering area, which extends down to Equatorial Africa. In contrast to the other two species, the Lesser Black-back largely uses freshwater habitats in winter. There is some evidence that age-dependent differences exist in all species.

Juveniles were found to perform a return migration in spring, but considerably (2-3 months) later than the adults. In all three species, some individuals evidently stay in the wintering area during summer.

The comparatively late return of the Lesser Black-backed adults is suggested to be responsible for the present poor breeding success. Comparison is made with other European populations. It is argued that adults and short-range migrants are better able to adjust their migratory behaviour to the prevailing conditions than juveniles and long-range migrants. The settlement of adult breeders in marginal areas probably does not require a genetic change in migratory programming, but the pattern may be shaped by selection acting on the juveniles.

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#### Introduction

Earlier studies of the movements of several large Larus species (Coulter 1975, Drury & Nisbet 1975, Parsons & Duncan 1978) have revealed considerable heterogeneity in the tactics employed, both between and within species, populations and age-classes. The yearly ranges of bird species deserve study, since events outside the breeding season and the breeding area are of great importance in understanding the factors regulating the population dynamics. This study deals with the yearly movements of three large Larus species, the Great Black-backed Gull (L. marinus), the Herring Gull (L. argentatus) and the Lesser Black-backed Gull (L. fuscus), as deduced from ring recoveries collected under the Finnish Ringing Scheme. We have concentrated on winter survival strategies and return migration in spring, disregarding phenomena like post-nesting dispersal. Since migratory patterns are solutions to temporal and spatial changes in the environment (Gauthreaux 1979), we have tried to focus on the causes, function and evolution of the patterns observed. We will discuss the features of the migrational behaviour on a comparative basis, using three species and two age-classes.

#### Material and methods

The study populations. The three species considered here

breed sympatrically on the Finnish coast (v. Haartman et al. 1963-72, Kilpi et al. 1980). The Lesser Blackbacks belong to the nominate race *L*. *f. fuscus* (Barth 1975). The breeding range considered lies between  $60^{\circ}$  and  $62^{\circ}$ N and between  $20^{\circ}$  and  $27^{\circ}$ E, being restricted to the coast. The area thus includes the Gulf of Finland and the Archipelago Sea, and consequently covers a very large proportion of the coastal populations of the species in Finland.

The Great and Lesser Black-backed Gulls are treated as single populations, whose migratory behaviour is assumed to be the same throughout the study area. In the case of the Herring Gull, enough material exists for a division into two subpopulations, one inhabiting the Gulf of Finland (GF in tables and legends) and the other the Archipelago Sea (AS). In terms of interchange of breeding adults, the two populations seem to be fairly well separated (Kilpi & Saurola in prep.). The area covered is the main area for gull-ringing in Finland.

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For the juveniles, the starting-point of the autumn migration, the natal colony, is well known. The startingpoint of the adults, the breeding site, is assumed to be the place where they were once hatched and ringed. In Herring Gulls, however, a substantial part of the adult population has been found breeding up to several hundreds of kilometres away from the natatl colony (Drury & Nisbet 1975, Duncan & Monaghan 1979, Kilpi & Saurola in prep.), so this assumption is not entirely justified.

We have chosen to study juveniles, because they represent birds with no previous experience of migration. Furthermore, the juveniles are not expected to be fixed

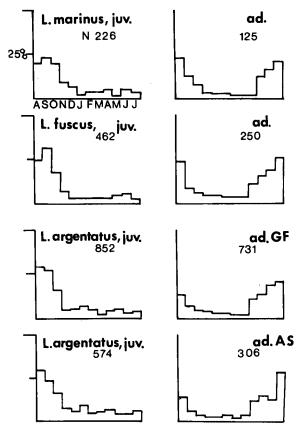


Fig. 1. Total number and monthly percentages (from August to July) of recoveries available for the cohorts studied. Total number of recoveries given.

to any definite locality in the following breeding season, since they will not breed. Adults represent the other extreme, experienced migrants that have to devote much of their activity to reproduction. We have treated only autumn movements in the directions indicated by the winter distribution, disregarding post-fledging dispersal in other directions, which, at least in the Herring Gull, is considerable (Kilpi & Saurola in prep.).

*Recovery material.* The basic material consists of recoveries of birds ringed as chicks. The total number of recoveries studied, and their monthly breakdown by species is given in Fig. 1. Two main categories of recoveries are used. Category (a) consists of birds reported as 'found dead', and obviously includes some time bias. since the birds may have been dead for some time before recovery.

Category (b) comprises birds 'found dead in fresh condition', usually birds shot. If not stated otherwise, the tables and maps contain information drawn from both categories. Additional information has been obtained from birds intentionally trapped or otherwise checked. We have excluded all birds that were decomposed or sick, and those for which no detailed information exists.

Reliability of the spatial distribution of recoveries. The spatial distribution of recoveries does not necessarily reflect the real distribution of the birds, because all recoveries depend upon human activity and presence. Category (a) is very much influenced by the density of potential finders, while category (b) is influenced by hunting legislation and practice. Trapped birds and observations depend on the amount of organized ornithological activity. Gulls have high mortality rates in the first year of life, especially in autumn (Burger 1981, Parson & Duncan 1978), and differential mortality is a problem when juveniles and adults are compared. Nevertheless, although admittedly biased, ringing data provide the only opportunity to study the populations of these species over their entire yearly range (Perdeck 1977, Saurola 1977, Southern 1980).

The environment. The environmental conditions prevailing on the south coast of Finland in winter are harsh. The coastal waters normally freeze (mean dates Helsinki 22 December, Turku 15 December) and the icc-cover lasts c. 100 days (mean Helsinki 103 days, Turku 111). The temperature in January is low (mean Helsinki —  $5.4^{\circ}$ C, Turku — $6.0^{\circ}$ C), and a lasting snow-cover normally develops (mean date of appearance: Helsinki 23 December, Turku 25 December).

The mean percentage of the total area of the Baltic annually covered by ice is 44 %. In a normal winter the ice cover will extend southward to about 59°N, but in exceptional years the Baltic will freeze completely, or not at all (data compiled mainly from Anon. 1981).

The concept of migration. Migration, in its most typical form, is regular, seasonal large-scale long-distance movement of a population twice a year between a fixed breeding area and a fixed non-breeding area (Lack 1968). In this study migration is any movement towards the area of winter occurrence, and return migration is any movement in spring towards the breeding area. Movements in other directions also occur (post-fiedging and post-nesting dispersal) but fall outside the scope of this study. We use the definition of Baker (1980): 'migration is the act of moving from one spatial unit to another'. The wintering strategy (and migration strategy) of the population considered, emerges from the combined migratory movements of the individuals in the population.

Table 1. Number of autumn recoveries south and north of 59°N (migrated and not migrated, respectively) and significance of difference in proportions of migrants between juveniles and adults in October.

Cohort	Number of Migrated recoveries		Not migrated	Difference between age-groups ( $\chi^2$ -test)	
L. marinus juv.	47	24	23		
L. marinus ad.	8	1	7	n.s.	
	46	25	21		
L. argentatus juv. (GF) L. argentatus ad. (GF)	25	5	20	P<0.01	
L. fuscus juv.	52	37	15		
L. fuscus ad.	12	3	9	P<0.01	
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### Results

Autumn migration. The withdrawal of gulls from the gross breeding area north of 59°N is shown in Fig. 2. The proportion of encounters south of this limit plotted against the month gives a crude image of the timing of migration in autumn. The histogram also shows the length of the period of migration. In juveniles the patterns for the species range from a pronounced peak early in the season in the Lesser Black-backed Gull to a very late peak in the Herring Gull. The Great Black-backed Gull has an intermediate pattern, with a steady increase in encounters outside the breeding area as autumn progresses. In all species the patterns differ between adults and juveniles. The histograms indicate that juveniles tend to migrate somewhat earlier than adults. This is partly corroborated by comparing the proportions of encounters south of 59°N for each species in the month with the highest difference (Table 1).

The Herring Gull material is large enough to allow comparison of the two neighbouring populations, GF and AS. The proportions encountered south of 59° do not differ significantly between the two populations in any month. The differences range between 1.4 and 14.4 % units (all samples exceed 20 recoveries).

The Great Black-backed and Herring Gulls mainly move in a SW direction during autumn. Plotting individual recoveries indicates that the birds use the coasts on either side of the Baltic to reach its southern part. The main direction taken by migrating Lesser Black-backs is S to SE across Europe, to the Black Sea and the eastern part of the Mediterranean. Some birds proceed along the Nile, eventually reaching Equatorial Africa. The Lesser Black-backed Gull is capable of rapid migration. Two juveniles have been recovered at distances of over 6000 km from the ringing colony in the last week of August. Since most Lesser Black-backs hatch in mid-June (v. Haartman et al. 1963-72, own data) these birds could hardly have been on the wing for more than a month.

Wintering. Both the Great Black-backed and the

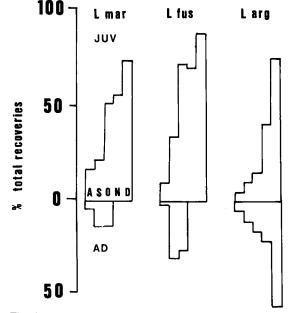


Fig. 2. Encounters in August-December south of  $59^{\circ}N$ , illustrating withdrawal from the breeding area. Herring Gulls from AS and GF combined. Upper histogram = juveniles, lower = adults. Controls have been excluded.

Herring Gull winter almost exclusively within the Baltic (Figs. 3—5), whereas the winter range of the Lesser Black-back is vast (Fig. 6b). The main features of the winter distribution of the cohorts studied are summarized in Table 2.

The maps showing the winter distribution of recoveries indicate that juveniles and adults use roughly the same areas. Exact comparisons are hard to make, because errors may be caused by differential mortality. The occurrence of Lesser Black-backs in the Baltic in winter is debatable. Of the juvenile recoveries of this species in winter, 35.7 % come from the Baltic Basin, the corresponding value for adults being 36.4 % (N=28 and 11, respectively). Some of these recoveries are probably actually Herring Gulls, misidentified as Lesser Black-backs by the ringer. Lesser Blackbacks have seldom been encountered in Danish

Table 2. Main features of winter distribution of the cohorts studied.

Cohort	Number of recoveries in January + February	% north of 59°N	x distance (km)	Range
L. marinus juv.	13	30.7	569	95— 862
L. marinus ad.	3			74—1180
L. argentatus juv. (GF)	69	15.9	737	24-1336
L. argentatus ad. (GF)	28	21.4	634	19-1019
L. fuscus juv. (AS)	48	12.5	688	78-1099
L. argentatus ad. (AS)	13	15.4	600	29-1110
L. fuscus juv.	17	0	3927	582-7777
L. fuscus ad.	9	Ō	3481	488-7566

L. marinus

Fig. 3. The spatial distribution of recoveries in January and February of adult and juvenile Great Black-backed Gulls. Includes controls.

waters during winter (N.O. Preuss, in litt.). How big a proportion of the winter recoveries of Lesser Black-backs in the Baltic relate to misidentified birds is unknown.

There is a peculiar scarcity of recoveries of adult Herring Gulls from the Stockholm area on the Swedish east coast. Ten juveniles from both populations have been found in this area, most of them being birds caught by ornithologists. Juveniles may be easier to catch than adults, so

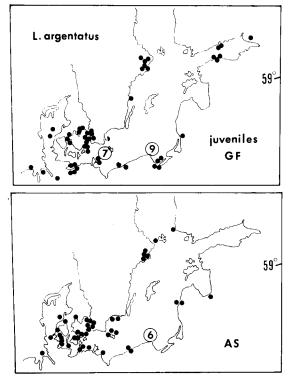


Fig. 4. The spatial distribution of January and February recoveries of juvenile Herring Gulls from the Archipelago Sea (AS) and the Gulf of Finland (GF). Includes controls.

it seems unlikely that adults do not use this area. On the other hand, these recoveries suggest that juveniles are more dependent on urban areas in winter. Adults may use more natural habitats, as indicated by the recoveries on the island of Gotland. No differences in the areas used during winter are apparent between populations GF and AS.

Juvenile Great Black-backed Gulls spend the winter in an area north of the main area of the Herring Gull. Recoveries from the interior of Sweden suggest use of inland habitats in winter, though the species uses coastal habitats almost exclusively in summer.

Return migration in spring. In April, adult recoveries of all three species were made almost exclusively within the breeding area, north of 59°N (Great Black-back 100 %, N=12, Herring Gull AS + GF 96 %, N=101 and Lesser Black-back 86 %, N=14). Field observations by one of us (MK) indicate breeding site occupancy by the Great Black-backed Gull as early as February in some years. The Herring Gulls normally start to appear in the area at the beginning of March. A series of observations on a rubbish dump on the south coast suggests that arrival of Lesser Black-backed adults reaches a peak in late April. At the time when most adults will have arrived in April, a comparatively small fraction of the juveniles in all three species is encountered north of 59°N (see Kilpi & Saurola 1983). Juveniles of both the Great Black-backed (Fig. 7) and the Herring Gull mostly return to the breeding area (or continue beyond it) during spring and early summer. The proportion of Herring Gulls encountered north of 59°N rises gradually from 25 % in April to c. 80 % in June-July (combined material, GF + AS). The timing of the return is about 2 months later than in adults. The recoveries plotted in Fig. 8 indicate that a fraction of the juvenile

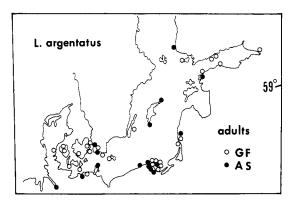


Fig. 5. The spatial distribution of January and February recoveries of adult Herring Gulls from AS and GF. Includes controls.

Lesser Black-backs returns to the breeding area of the adults during their second summer. According to the recoveries, the return is late, the birds mostly arriving in June-July. Again, there is a possibility that some of these birds are actually Herring Gulls. Second-summer Lesser Black-backs are virtually unknown in Finnish field ornithology. In all three species, a fraction of the juveniles spends the summer within the areas used for wintering, and does not return to the breeding area of the adults.

## Discussion

*Causes and consequences of the migration patterns.* The ultimate reason why so few individuals of the species studied here winter within the breeding area is no doubt the fact that food becomes scarce due to ice and snow. The only survival strategy

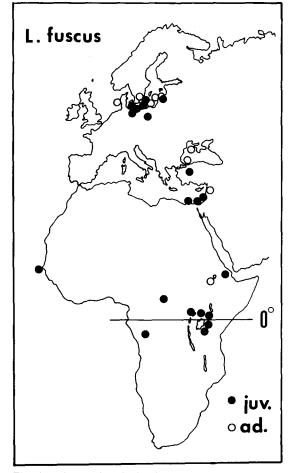


Fig. 6. The spatial distribution of December-February recoveries of juvenile and adult Lesser Black-backed Gulls. Includes controls.

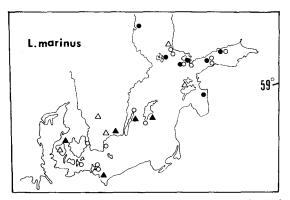


Fig. 7. Recoveries of juvenile Great Black-backed Gulls in April (triangles) and May-July (circles). Fresh birds indicated by filled symbols, those merely reported as "found" by open symbols.

available to the birds is to move to areas where foraging can continue undisturbed. The Great Black-backed Gull is the species evidently best adapted to a harsh environment. The data are still scanty, but the tactics used seems to depend on the age of the birds. Juveniles migrate further and use inland habitats. The adult strategy cannot yet be assessed, but adults probably winter out at sea close to the ice-border. The species seems to exploit refuse dumps very little, but frequently utilizes fish offal.

The Herring Gull is an omnivorous opportunistic.feeder, capable of using a wide variety of food items (Spaans 1971). On the Finnish coast Herring Gulls are encountered in high numbers on refuse dumps and in fishing harbours (Kilpi 1980, and unpubl.). This ability enables the adaptation of a flexible strategy. In exceptionally mild winters large numbers of Herring Gulls stay on the Finnish coast, and even in normal winters short warm spells always produce an influx of Herring Gulls, which disappear once a cold period starts (own obs.). Most birds employing this strategy seem to

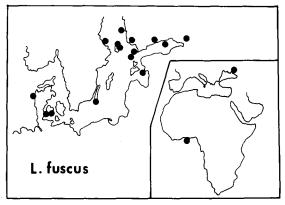


Fig. 8. Recoveries of Lesser Black-backed juveniles in April-July. Includes only fresh (shot or control) re-coveries.

be adults, but reliable field data are still needed to examine this further. It is probable that predictable resources such as dumps and fishing harbours promote the adoption of a more sedentary, flexible, strategy.

The Lesser Black-backed Gull differs from the two other species in its feeding ecology. It uses natural food extensively, especially fish (Goethe 1975, Lemmetyinen 1963), and is encountered only in low numbers on rubbish dumps (Kilpi unpublished). The early departure of the Lesser Black-backed Gull is probably prompted by autumn storms and an early ice-cover, which make foraging difficult. The late arrival in spring also suggests that the species is dependent upon icefree waters. A change in migratory tactics has possibly occurred; in the years 1920-1940 Lesser Black-backs were frequently encountered within the Baltic in winter. Of the 12 recoveries of juveniles in that period, 10 (83.3 %) came from the Baltic, as compared with a current proportion of 35.7 % of 28 recoveries ( $\chi^2 = 5.8 \text{ P} < 0.05$ ). The comparison may be impaired by a lower probability of recovery in Africa at the time, but older Finnish field observations also point to a possible change (v. Haartman et al. 1963-72).

The Great Black-backed and the Herring Gull, both breed comparatively early in the season and commence laying in the first half of April (v. Haartman et al. 1963—72), when the sea is normally still ice-covered. Early breeding is clearly advantageous, since it enables them to avoid human disturbance (Kilpi et al. 1980). The late arrival and consequent late nesting of the Lesser Black-backed Gull bring it into conflict with territorial Herring Gulls (Bergman 1965, Hario 1981, Kilpi, in prep.) and expose it to human interference. The reproductive output is at present very low (Hario 1981), and the observed decline can at least partly be attributed to the migratory habits of the species.

Comparison with other European populations. In most of its range in Europe, the Great Blackbacked Gull performs only short-range movements in the non-breeding season (Bruun 1963, Salomonssen 1972). Populations from North Norway and the Soviet Union, at latitudes of 69°— 70°N, may move longer distances. Birds marked with Finnish rings in the Petsamo area (c. 69°N) are known to have reached the North Sea.

European Herring Gull populations associated with tidal coasts at low latitudes are extremely sedentary (Parsons & Duncan 1978, Spaans 1971). At higher latitudes more birds seem to cover larger distances, and Herring Gulls from Arctic Norway and the Murman coast are encountered in Britain in winter (Stanley et al. 1981). In the southern part of the Baltic, Herring Gull populations are sedentary (Goethe 1956, Jørgensen 1973). Populations breeding on Christiansø and Gotland, the latter at c. 58°N, are said to move south for the coldest part of the winter (Jørgensen 1973, Olsson 1958). There is thus a very clear cline from south to north in the Baltic, the numbers of birds participating in long-range flights increasing with the latitude. Herring Gulls from the White Sea and Lake Onega likewise travel large distances (Bianki 1977, Dementiev et al. 1969). These birds inhabit an environment that becomes very hostile in winter. Herring Gulls from the White Sea and Lake Onega use a migration route that runs across Finland, and according to ring recoveries they winter mainly southwest of the area used by the birds studied here. This is an example of the classical leap-frog pattern (Salomonssen 1955), with northern populations travelling further than more southern populations.

The Lesser Black-backed Gull breeds only in NW Europe, including Iceland and the British Isles (Barth 1975). Britain and Iceland are inhabited by L. f. graellsii, L. f. intermedius breeds in southern Norway and on the Swedish west coast, while L. f. fuscus breeds in northern Norway, on the Swedish east coast and in Finland. The races graellsii and intermedius are associated mainly with tidal ocean coasts, while *fuscus* is associated mainly with brackish and freshwater habitats. L. intermedius and graellsii migrate long distances, and are confined to the eastern Atlantic shore (Baker 1980, Haftorn 1973, Harris 1970, Salomonsen 1972). L. fuscus remains true to freshwater and brackish habitats the whole year (Moreau 1972). It also uses a completely isolated migration route across Europe, and isolated wintering areas, apparently very seldom coming into contact with the two other races.

Age-dependent differences. Age-related differences in movement patterns have been noted in large Larus species by several authors (Coulter 1975, Moore 1976, Parsons & Duncan 1978, Smith 1959, Spaans 1971). First-year birds usually tends to move longer distances than adults. We suggest that in the populations examined both the timing of migration and the use of habitat in winter differs between 1-yr and adult birds. During winter juveniles possibly use a wider range of habitats and areas, and they also tend to migrate earlier than do adults. The use of extreme areas may be attributed to inexperience or to exclusion by adults. Drury & Nisbet (1975) have reported that juveniles tend to winter in areas with lower survival value than adults. Moore (1976) considered differential migration in juveniles and adults to be highly adaptive, since it reduces intraspecific competition for food. Factors relating to food competition between age-groups and the general fact that juveniles are far less efficient feeders (Verbeek 1977) may all contribute to the differences. Berthold (1977) reported that the first migration of inexperienced Garden Warblers Sylvia borin is (almost) exclusively based on endogenous factors. In the juveniles the movements will thus be more strictly programmed, whereas in adults, the yearly range will be adjusted by experience and/or heavy selection against extreme movements. We would expect adults of typically migrant species in the strict sense of Lack (1968) to be able to adjust the yearly range to a smaller extent than adults of less typically migrant species. In this study both the Great Black-backed and the Herring Gull seem to show more flexibility in adult migration tactics than the Lesser Blackback. The interesting change in migration pattern in L. f. graellsii in recent years (Baker 1980) also seems to emphasize the importance of the endogenous program for juveniles; increasing numbers of adults are wintering close to the breeding grounds, while the migration of the juveniles seems to be continuing much as before.

In the Herring Gull such changes in migratory behaviour have been documented several times for different populations (Drury & Nisbet 1975, Ingolfsson 1978). The changes have been brought about by shifts in breeding areas in adult Herring Gulls. The advantage of moving out to marginal areas to breed can be assumed to be higher reproductive output in less crowded areas (Lack 1968, Alerstam & Enckell 1979). The prerequisites for migration and the formation of a new migratory trait seem to be an inclination to travel long distances and a lack of site fidelity in adults (Drury & Nisbet 1975, Duncan 1978, Duncan & Monaghan 1979). The movement from the newly established breeding areas to the areas used for survival in winter may not require a change in the genetic program for migration behaviour in adults. The migrational behaviour is brought about by the experience of the areas used in winter (where the adults originate), coupled with the ability to react in a meaningful way to deterioration of the conditions in the breeding area as autumn progresses. The Finnish coastal Herring Gull population may have been founded by adults emigrating from Denmark or the North Sea area early in this century. Unfortunately there are no ringing data that confirm this. If juveniles have an innate predisposition to move in certain directions (Gwinner & Wiltshko 1978), then selection may rapidly eradicate birds moving in the 'wrong' directions from the point of view of current survival opportunities, thus shaping the existing patterns.

The strength of the genetically programmed migrational behaviour thus shaped, apparently varies. Generalist birds, such as the Herring Gull, with expansive tendencies may rapidly alter their migrational behaviour. On the other hand the tradition of the Lesser Black-backed Gull in Finland has evolved over a comparatively long period. The rigidness of this migrational tradition has been increased by the fact that the Lesser Black-back is apparently unable to utilize new ample food resources, such as dumps. It seems clear that the change in migrational behaviour in the British Lesser Black-backed Gull was made possible by the use of man-made food sources (Baker 1980). The change has resulted in a situation were juveniles and adults use highly different strategies for survival during the winter, which seems to underline the importance of the fixed program for juveniles.

The differences in migrational behaviour in spring are of course very predictable. Juveniles do not breed and have therefore several alternatives. They may migrate back to the natal area, or spend the summer in the winter area or somewhere else. In long-range migrants, there seems to be a limit beyond which spring migration is not advantageous for juveniles. Juveniles of several species have been shown to fail to return to the home area in their second summer, e.g. the terns Sterna paradisaea and S. sandvicensis (Møller 1982, Salomonsen 1972). The juveniles of the Great Black-backed and Herring Gull studied here returned to the home area more frequently than juveniles of the Lesser Black-backed Gull. The late return of juveniles observed here, would allow the birds to locate active breeding colonies, a factor probably important in the subsequent choice of colony and nestsites.

Acknowledgements. We are grateful to Prof. O. Järvinen for reading the first version of this paper.

# Selostus: Meri-, harmaa- ja selkälokin muutto- ja talvehtimisstrategioista

Artikkelissa analysoidaan aikuisten (yli 6 kv) ja nuorten (1 kv/2 kv) meri-, harmaa- ja selkälokkien muuttoa ja talvehtimista rengaslöytöjen avulla. Yleisesti ottaen sekä harmaa- että selkälokki ovat selväpiirteisiä muuttolintuja. Nuoret merilokit niinikään tuntuvat olevan muuttajia, mahdollisesti vanhat linnut suureksi osaksi ovat paikkalintuja. Meri-ja harmaalokit talvehtivat Itämeren piirissä, selkälokin talvehtimisalue ulottuu aina päiväntasaajan eteläpuolelle. Selkälokki näyttää talvisin käyttävän sisävesiä, poiketen näin molemmista sukulaislajeistaan. Syysmuuton ajoituksessa on eroja nuorten ja vanhojen lintujen välillä ainakin harmaa- ja selkälokilla. Nuoret linnut muuttavat pois kotimaasta aikaisemmin kuin vanhat.

Keväällä nuoret linnut osittain palaavat kotimaahan, mutta muutto tapahtuu huomattavan myöhään, 2—3 kuukautta aikuisia myöhemmin. Diskussiossa verrataan saatuja tuloksia julkaistuihin tietoihin muista eurooppalaisista populaatioista. Ehdotetaan että vanhat linnut, ja lyhyen matkan muuttajat, ovat joustavampia kuin pitkän matkan muuttajat, ts. pystyvät paremmin sopeuttamaanmuuttokäyttäytymisensä vallitseviin ulkoisiin olosuhteisiin. Muuttostrategian muovautuessa kohdistuu rankin valintapaine kokemattomiin nuoriin lintuihin.

#### References

- Alerstam, T. & Enckell, P. H. 1979: Unpredictable habitats and evolution of bird migration. Oikos 33:228-232.
- Anon. 1981: Environmental statistics 1980. Statistical Surveys N:o 67, Central Statistical Office of Finland. Baker, R. R. 1978: The evolution ecology of animal
- migration. Hodder & Stoughton, London. Baker, R. R. 1980: The significance of the Lesser Black-
- backed Gull to models of bird migration. - Bird Study 27:41-50. Barth, E. K. 1975: Taxonomy of Larus argentatus and
- Larus fuscus in northwestern Europe. Ornis Scand. 6:49-63.
- Bergman, G. 1965: Trutarnas konkurrensförhållanden, födobehov och relationer till andra skärgårdsfåglar (Zusammenfassung). - Zool. Revy 27:58--77.
- Berthold, P. 1977: Endogene Steuerung des Vogelzuges.
   Die Vogelwarte 29, Sonderheft: 4—15.
   Bianki, V. V. 1977: Gulls, shorebirds and alcids of Kandalaksha Bay. Israel Program for Scientific
- Translations, Jerusalem.
- Bruun, B. 1963: Svartbagen (Larus marinus L.). i Danmark. Dansk Orn. Foren. Tidsskrift 57:94—98.
   Burger, J. 1980: The transition to independence and
- postfledging parental care in seabirds. In Burger, J., Olla B.L. & Winn H. E. (eds.): Behaviour of marine animals, Volume 4: marine birds 367—448. Plenum Press, New York. Chabrzyk, G. & Coulson J. C. 1976: Survival and re-
- cruitment in the Herring Gull Larus argentatus. -J. Anim. Ecol. 45:187—203.
- Coulter, M. 1975: Post-breeding movements and mortality in the Western Gull, Larus occidentalis. - Condor 77:243-249.
- Dementiev, G. P., Gladkov, N. A. & Spangenberg, E P. 1969: Birds of the Soviet Union, Vol. III. - Israel
- Program for Scientific Translations, Jerusalem. Drury, W. H. & Nisbet, I. G. I. 1975: The importance of movements in the biology of Herring Gulls in New England. In Population ecology of migratory birds: a symposium. - Wildlife Research Report 2:173-212.
- Duncan, N. 1978: The effects of culling Herring Gulls (Larus argentatus) on recruitment and population dynamics. J. Appl. Ecol. 15:697-713. Duncan, W. N. M. & Monaghan, P. 1977: Infidelity
- to the natal colony by breeding Herring Gulls. Ringing and Migration 1:166-172.
- Gauthreaux, S. A. Jr. 1979: Priorities in bird migration
- studies. Auk 96:813—815.
  Goethe, F. 1956: Die Silbermöwe. Neue Brehm-Bücherei 182, Wittenberg, Lutherstadt.
  Goethe, F. 1975: Zur Biologie der Heringsmöwe Larus
- besonderer Berücksichtigung fuscus unter ethologisher Aspekte. II Nahrung und Nahrungser-
- werb. Ornis Fennica 52:5—12. Gwinner, E. G. & W. Wiltschko 1978: Endogeneously controlled changes in migratory direction of the Garden Warbler Sylvia borin. - J. Comp. Physiol. A. 125:267-274.
- v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963-72: Pohjolan Linnut värikuvin. — Otava, Helsinki.
- Haftorn, S. 1971: Norges fugler. Universitetsforlaget, Oslo.
- 1981: Harmaalokin vaikutus selkälokin Μ. Hario. poikastuottoon (Summary: Impact of the Herring Gull on the breeding of the Lesser Black-backed Gull). — Lintumies 16:25—29.

- Harris, M. P. 1970: Abnormal migration and hybridization of Larus argentatus and L. fuscus after interspecies fostering experiments. Ibis 112:488–498. Ingólfson, A. 1978: Population phenomena associated
- with the colonization of Iceland by Herring Gulls. - Ibis 120:126.
- Jørgensen, O. H. 1973: Some results of Herring Gull ringing in Denmark 1958-1969. - Dansk Ornithol. Foren. Tidsskrift 67:53-63.
- Kilpi, M. 1980: Harmaalokki-saariston lintuyhteisön musta lammas? (Summry: The Herring Gull: a pest in the archipelago). — Lintumies 15:102—107. Kilpi, M., Puntti, H. & Toivonen, T. 1980: Numbers
- of gulls nesting on the northern coast of the Gulf of Finland. — Ornis Fennica 57:153—160. Kilpi, M. & Saurola, P. 1983: Geographic distribution
- of breeding season recoveries of adult and immature Larus marinus, L. argentatus and L. fuscus ringed in Finland. — Ornis Fennica 60:117—125. Lack, D. 1968: Bird migration and natural selection.
- Oikos 19:1-9.
- Lemmetyinen, R. 1963: Lokkien esiintymisestä ja ravinnosta Gullkronan selän koillisosassa (Summary: Occurrence and feeding habits of gulls in the north-eastern part of the area of Gullkrona). — Suomen Riista 28:42-48.
- Moore, F. R. 1976: The dynamics of seasonal distribution of Great Lakes Herring Gulls. - Bird-Banding 47:141-159.
- Moreau, R. 1972: The Palaearctic-African bird migration system. — Academic Press, London. Møller, A. P. 1981: The migration of European
- Sandwich Terns Sterna sandvicensis. II. Die Vogelwarte 31:149-168. Olsson, V. 1958: Dispersal, migration, longevity and
- death causes of Strix aluco, Buteo buteo, Ardea cinerea and Larus argentatus. - Acta Vertebratica 1:1-128.
- Parsons, J. & Duncan, N. 1978: Recoveries and dispersal of Herring Gulls from the Isle Of May. -Anim. Ecol. 47:993-1005.
- Perdeck, A. C. 1977: The analysis of ringing data: pit-falls and prospects. Die Vogelwarte 29, Son-derheft: 33–44.
- Salomonsen, F. 1955: The evolutionary significance of birdmigration. Dan. Biol. Medd. 22:1—62.
- Salomonsen, F. 1972: Fugletraekket og dets gåder. -Munksgaard, København.
- Saurola, P. 1977: Suokukon muutosta rengaslöytöjemme valossa (Summary: On the migration of the Ruff in the light of Finnish recoveries). — Lintumies 12:14— 22.
- Smith, W. J. 1959: Movements of Michigan Herring Gulls. — Bird-Banding 30:69—103.
- Southern, W. 1980: Comparative distribution and orientation of North American gulls. — In Burger, J., Olla, B. L. & Winn, H. E. (eds.): Behaviour of marine animals, Vol. 4: Marine birds: 449–498. Plenum Press, New York.
- Spaans, A. L. 1971: On the feeding ecology of the Herring Gull Larus argentatus Pont. in the northern part of the Netherlands. — Ardea 59:75—188.
  Stanley, P. I., Brough, T., Fletcher, M. R., Horton, N. & Rochard, J. B. A. 1981: The origins of Herring Gulls wintering inlond in courth-cest Facland. — Bird
- Gulls wintering inland in south-east England. -– Bird Study 28:123-132
- Verbeek, N. A. M. 1977: Age differences in the digging frequency of Herring Gulls on a dump. — Condor 79:123—125.

Received September 1982