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Movements and survival areas of Finnish common gulls *Larus canus*

Mikael Kilpi & Pertti Saurola

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Movements of common gulls ringed in Finland were analysed on the basis of 3292 recoveries. The species uses two distinct spatial units during the year, the Breeding Area and the Main Survival Area. The Survival Area is west of 14°E, from Denmark to Britain and France. Adults leave the Breeding Area as soon as breeding is over, the first year birds following shortly after. Transitory areas are exploited only briefly. The Main Survival Area appears the same for all studied age-classes (1-yr, 2-yr, 3-/4-yr and 4-yr+), but there is some indication of spatial segregation between northern and southern populations. Juveniles seldom return to the Breeding Area in summer, although there is movement out of the Main Survival Area. Older immatures (3-4-yr) resemble adults in their movements. There is some indication that adults may recruite into breeding populations distant from the natal colony.

The movements of Finnish common gulls are compared with other populations. It is argued that there is evidence for a latitudinal displacement migration pattern for the species in NW Europe.

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1. Introduction

The avian migratory life-style is based on the exploitation of several areas in the course of a year. The area used for breeding and the area used for survival during the main part of the year may be far apart, giving rise to seasonal migrations between these areas. All areas are important. Lack (1968) stated that "the size of the world population of a migrant species is probably determined by winter supplies of food", thus emphasizing the importance of integrating studies made in the non-breeding area with studies made in the breeding area in order to fully understand the population dynamics of a particular species. One fundamental step is finding the areas inhabited by the species in the non-breeding season. This is at least partly possible by using ring recoveries.

In this paper the areas used at different times of the year, and by different age classes of common gulls *Larus canus* ringed in Finland are described. Those populations of the common gull that appear to have a sympatric distribution with the Finnish gulls during the non-breeding season are also discussed. The main question is a simple one: where are the birds located at different times of the year? The second, underlying, question is "Why"? (see Gauthreaux 1982), and on the answer to this we can only speculate.

2. Material and methods

2.1. The recoveries

The ring recoveries used in this study accumulated in the files of the Ringing Office, University of Helsinki, between the years 1950-82. All the gulls considered have been ringed as chicks.

In all, 3292 recoveries were used. The number per age-class and month is given in Fig. 1.

The recoveries comprise two major categories: (1) birds reported as "found", and (2) birds reported as "found in fresh condition". The first set comprises birds accidentally found by the public, while the second set largely consists of birds that were shot or trapped by the finder. Both categories are included in the analysis. We have omitted a number of recoveries. These include all birds found decomposed, sick birds, and also recoveries reported under hazy circumstances (inaccurate dates or localities not given; no specification on the state of the bird when found). We have also omitted from this analysis a few recoveries from the Black Sea and the Mediterranean. These will be dealt with in a later publication.

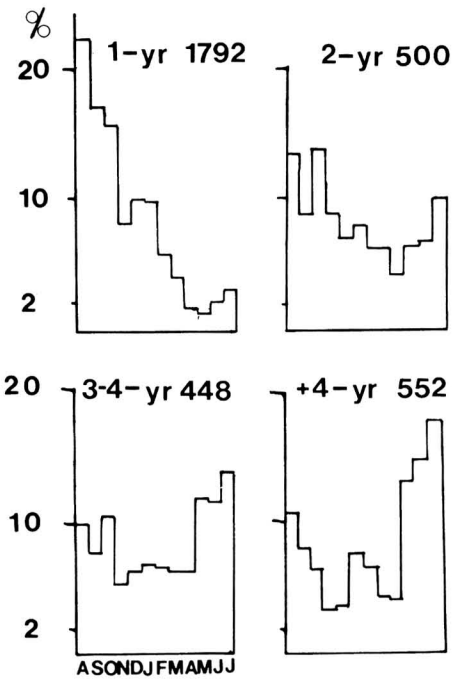

Fig. 1. The number of recoveries, and monthly percentages of the total material for the age classes studied.

2.2. Shortcomings and pitfalls of the material

There are several biases involved in ringing recovery studies (Perdeck 1977). All recoveries depend on the presence of a finder. The density of finders, hunting legislation, ornithological activity, and frequency of reporting differ from one area to another. Thus, the chances of recovery vary both spatially and temporally, and it is almost impossible to quantify this variation. One of the most obvious drawbacks is that we can establish the presence, but not the absence, of an individual. The recoveries of birds from categories (1) and (2) differ. When birds are accidentally found there is a certain time bias, since the bird may have been dead for some time before recovery. Decomposed birds are excluded, but whether a bird is considered dead or decomposed depends on the finder's subjective judgement. This bias is most critical when discussing the timing of events, and also, for instance, when analysing the site-fidelity of breeding adults. The biases involved in each case are discussed in the text.

Fig. 1 indicates that most of our recoveries concern first-year birds. This is the general pattern observed for a variety of gull species analysed, and is a consequence of heavy first-year mortality (Van Tets 1968, Parsons & Duncan 1978). The most detailed analysis is carried out on this inexperienced age-class, the movements of which may differ drastically from those of older birds (see Moore 1976).

Although beset with biases, ring recoveries provide the only means so far available of tracing spatially fluid birds over the entire yearly range.

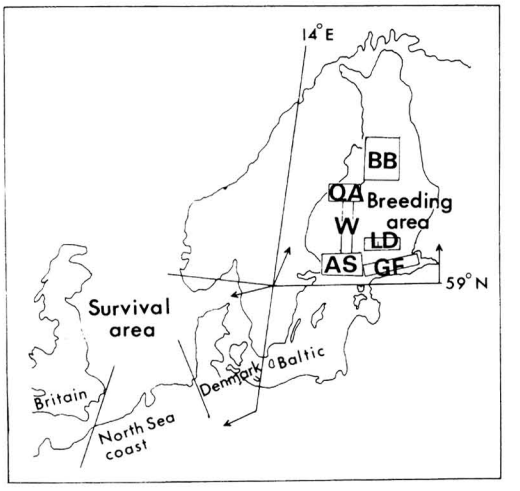

Fig. 2. The geographical areas used in the study (for further details see text).

2.3. Age classes and geographical regions

The birds were divided into four major age-classes. Juveniles in their first year of life are referred to as 1-yr birds. They are considered to be independent by August 1. In Finland most common gull chicks will be fully fledged and have left the colonies by mid-July. Juvenile 1-yr gulls become 2-yr gulls on August 1 in the second summer, and so on. Birds of the 3-yr and 4-yr age groups resemble adult birds in respect of their plumage (Grant 1982) but their breeding status is uncertain. We usually lumped these two age-classes together in our analyses. Birds of 4-yr+ age are considered to be breeding adults.

In addition, we have tentatively distinguished six study populations (Fig. 2) using longitudinal and latidutinal boundaries. Five of these are coastal, while one is an inland population. The following abbreviations are used: GF (Gulf of Finland), AS (the Archipelago Sea), W (West Coast), QA (the Quark) and BB (Bothnian Bay), LD (the lake district of Central Finland). Most of the ringing work within each area was carried out at only a few localities.

We treated all these populations separately when analysing the autumn and winter distributions of 1-yr birds, but the main analysis was done with pooled samples.

We divided the yearly range into major blocks (Fig. 2). We distinguished two main areas: the *Breeding Area* referred to below as BA which refers to an area north of 59°N where the absolute majority of the breeding adults are found during the breeding season; and the *Main Survival Area* referred to below as MSA where most birds are encountered during the non-breeding season. We have limited this area to a sector south of 59°N and west of 14°E. The Main Survival Area is then divided into three blocks (Fig. 2): Denmark, the North Sea Coast and Britain. Note that the boundaries do not accurately follow political boundaries, and that for practical reasons Britain also includes parts of France and even areas further south. The Baltic refers to an area east of 14°E and south of 59°N. We have abandoned terms like "wintering area" for the simple reason that the period of utilisation of the main

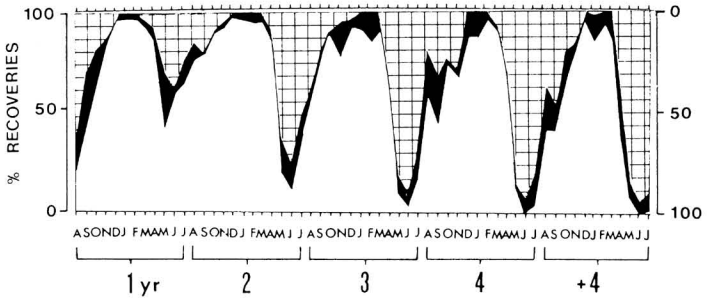

Fig. 3. Percentage of monthly total of recoveries of common gulls in the Main Survival Area (white, y-axis on the left), and in the Breeding Area (shaded, y-axis on the right). Black shading indicates the proportion recovered in other areas.

survival area is much longer than the thermal winter. Furthermore, pre-breeding age-classes may be "summering" in the "wintering" area, and use it for a considerable part of their pre-breeding lives. Again, we are discontent with the frequently used term "non-breeding area" (see Lack 1968). Since the birds outside the breeding season (or during their pre-breeding life) can be considered to maximize survival, we prefer to use a term emphasizing just this (see Greenberg 1980).

In this study the term migration is used to describe the act of moving from one spatial unit to another (Baker 1978). We have recognized two major spatial units (see above). Adults migrate between these two.

3. Results

3.1. General outline of the areas used and differences between age-classes

All age-classes of common gulls spend the year in two separated areas, with very little exploitation of areas between these two, as shown by the monthly proportions of recoveries (Fig. 3). Within the Main Survival Area (MSA), there are no drastic differences in the geographical distribution of recoveries of birds of different ages (Fig. 4). In January - February, however, the proportions of 3-4-yr gulls in the three blocks differ from both the adult proportions ($\chi^2 = 25.9$, $P < 0.001$), and the distribution of 1-yr gulls ($\chi^2 = 74.2$, $P < 0.001$). Other comparisons were not statistically significant. Thus, 3-4-yr common gulls seem to utilize the SW part (Britain) of the MSA to a higher degree than do other age-classes (Fig. 4). A high proportion of adults was found in the central part of the MSA, while 1-yr and 2-yr gulls were found in high proportions in the NE part (Denmark) of the MSA. The differences between adults and 1-yr and 2-yr gulls were not significant.

The main difference between the age-classes was in the length of the stay in the MSA. Very few 1-yr, and even 2-yr gulls, return to the Breeding Area (BA) in summer (Fig. 3). The proportion of 2-yr gulls recovered in the BA in May-July was significantly lower than the proportion of adult gulls ($\chi^2 = 46.4$, $P < 0.001$, N 2-yr = 117, N 4-yr+ = 254). An even lower proportion of 1-yr common gulls was found in the BA in summer, the difference in comparison with 2-yr gulls being highly significant ($\chi^2 = 58.3$, $P < 0.001$, N 1-yr = 115). Those 1-yr and 2-yr birds that return to the BA only stay there for a short while. Older immatures (3-yr and 4-yr) return like the adults, and some of them probably already breed. The timing of the autumn departure differs in newly fledged

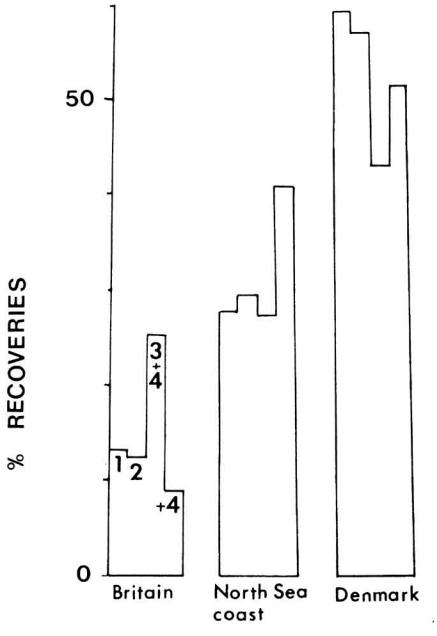

Fig. 4. Percentage of recoveries in January - February for common gulls of different ages in three sub-areas of the Main Survival Area (MSA). A few recoveries outside these three areas have not been included.

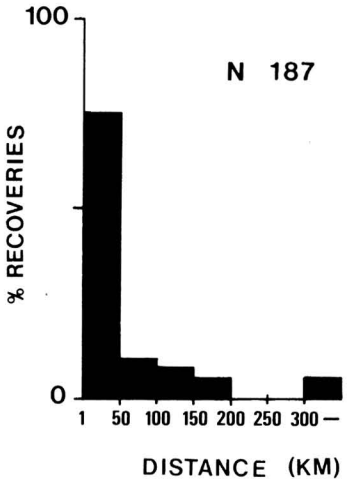

Fig. 5. Distribution of recovery distances for adults found in May - July.

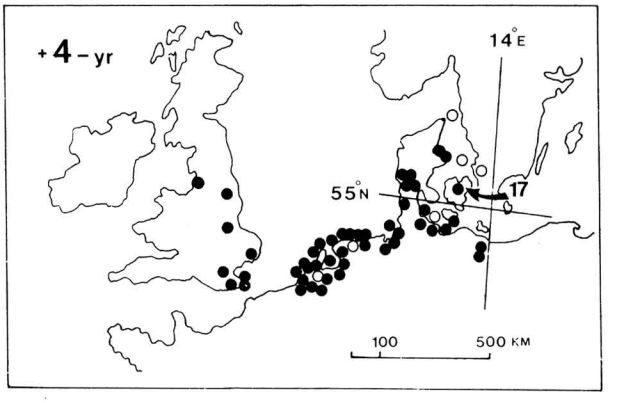

Fig. 7. Recoveries of adult common gulls in January - February. Southern birds (born in colonies south of 63°N, black dots) separated from northern birds (born north of 63°N, open circles). One recovery from the Bay of Biscay mentioned in the text not included here.

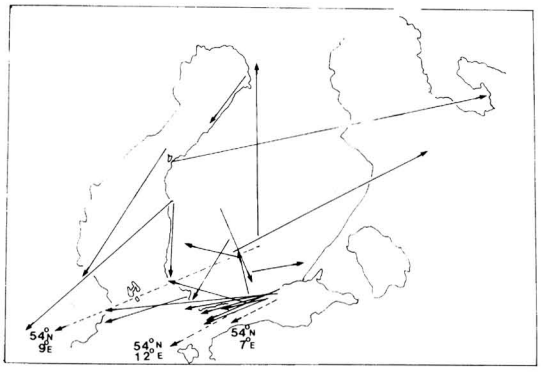

Fig. 6. Recoveries of adult common gulls in May - July more than 100 km from the natal site (base of arrow).

1-yr birds and adults. A significantly lower proportion of adults than 1-yr birds was encountered in the BA in August ($\chi^2 = 11.8$, $P < 0.001$, N 1-yr = 432, N 4-yr+ = 57). A very low proportion of 2-yr, 3-yr and 4-yr common gulls was found in the BA in August, suggesting a very early departure.

The return migration in spring seems to take place rapidly, covering only a short time period. Adult birds use the transitory areas between the MSA and the BA for longer periods in autumn than in spring.

The following sections are devoted to a more detailed description of the seasonal distribution of common gulls of different ages.

3.2. The yearly range of adult common gulls

Most adult common gulls are found close to the natal site in the breeding season (May - July). In June - July, 75% of all 4-yr+ gulls were recovered within 50 km of the natal site, and almost all (95.3%) within 200 km of the natal site (Fig. 5). Finds of adults in the breeding season at a distance exceeding 100 km from the natal site are given in Fig. 6. About half of these recoveries constitute birds found in a fresh condition (55.5%, $N = 27$). These recoveries suggest that adults may be recruited into more distant areas. Note that none of these individuals has been reported as actually breeding.

The distribution of January - February recoveries of 4-yr+ gulls (Fig. 7) illustrates the extent of the MSA. All recoveries in January - February, except one, occurred west of 14°E, and the majority of the recoveries between October and March were made west of this longitude. The distribution of recoveries can, however, change in time (Table 1). There is an increase in the proportion found on the North Sea coast as winter approaches. The two earliest recoveries from Britain were made in December, and only one March recovery is known from Britain. One adult was recovered at 44°N on the coast of the Bay of Biscay in December: this represented the most distant recovery.

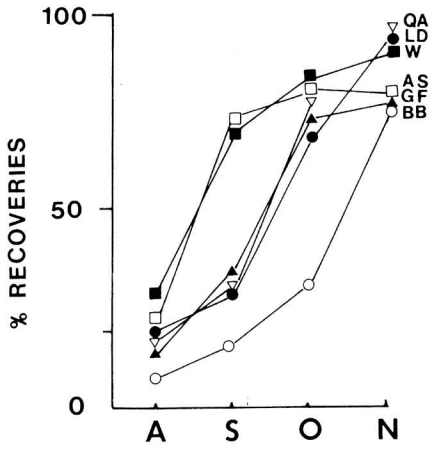

Fig. 8. Percentage of total recoveries of 1-yr common gulls per month in the Main Survival Area. All six populations separated over the period August - November.

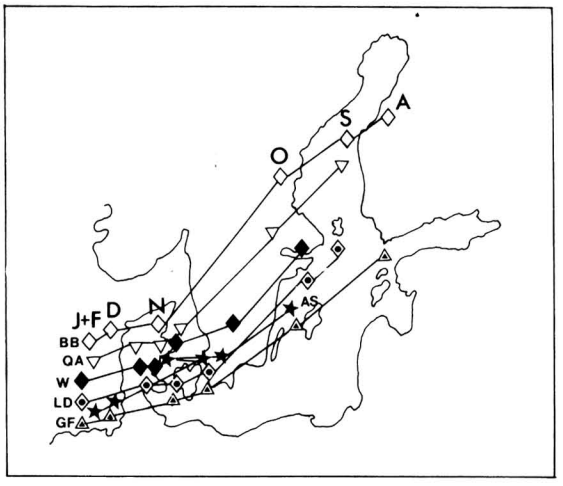

Fig. 9. Mean monthly positions of recoveries of 1-yr common gulls from six populations in August - February. Calculation of the positions after Perdeck (1977).

Table 1. Number (and percentage) of recoveries of Finnish common gull adults in different geographical regions in "winter". The area "others" refers to the Baltic east of 14°E.

	Nov - Dec	Jan - Feb	March
Denmark	21 (57)	37 (52)	11 (44)
North Sea coast	10 (27)	29 (40)	12 (48)
Britain	2 (5)	6 (8)	1 (4)
Others	4 (11)	- (-)	1 (4)
Total	37	74	25

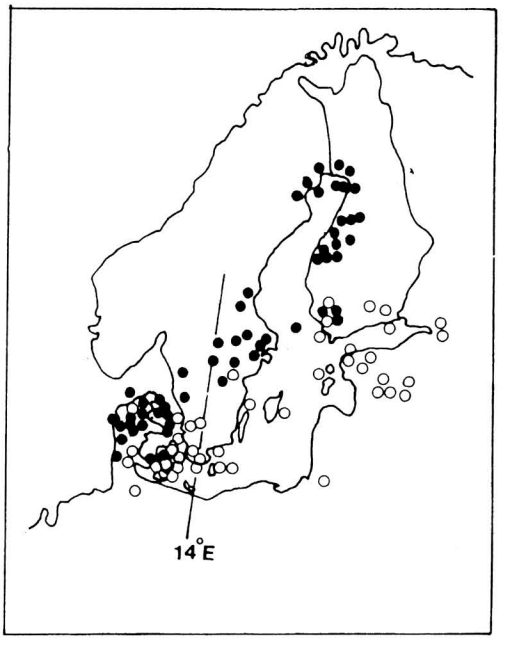

Fig. 10. Individual recoveries of 1-yr common gulls from BB+QA (black dots) and GF (open circles). Only recoveries made >100 km from natal site plotted. For GF, only August recoveries included, for BB+QA August - October.

3.3. Movements and survival areas of 1-yr common gulls

Most 1-yr common gulls were recovered west of 14°E as early as September, as shown by the total material (section 3.1.). The time of arrival in the MSA varies between the populations (Fig. 8). There was a very high frequency of recoveries of AS and W birds in the MSA in September. The other populations, except BB, reach similar proportions in October. It is not known whether these differences also hold true for adults, but this is probable.

The mean monthly positions of recovered 1-yr birds suggest that the populations are spatially segregated during migration (Fig. 9). When individual recoveries are plotted, it appears that the birds have a narrowly confined route to the target area in SW Europe (Fig. 10).

The MSA of 1-yr common gulls is roughly the same as that of adults (Fig. 13). The most extreme recoveries come from the Bay of Biscay (three birds) and from the coast of Morocco (35°N, one bird).

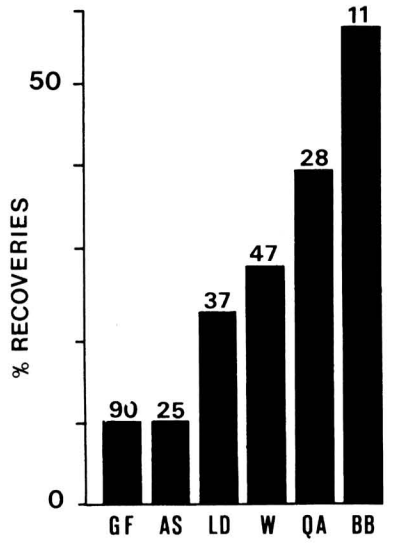

Fig. 11. Percentage recoveries made in January - February north of 55°N for 1-yr common gulls from the six study populations. Sample size is given.

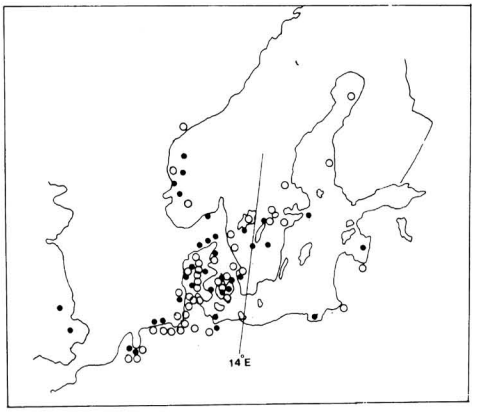

Fig. 12. Recoveries of 1-yr common gulls (pooled data, all populations) in May - June (black dots) and July (open circles). Only recoveries made >100 km from natal site accepted. Note that only a minor fraction is recovered close to the natal site in the Breeding Area, compare with text.

Birds of different populations are found to some extent in different areas. Common gulls of northern origin are found in the northern part of the MSA more often than birds of southern origin (Fig. 11). A significantly higher proportion of BB+QA gulls than of AS gulls ($\chi^2=9.2$, $P<0.01$) or of GF gulls ($\chi^2=37.0$, $P<0.001$) is found north of 55°N. The proportion of recoveries of juveniles from different populations in the three major blocks of Table 2, however, do not differ (χ^2-tests).

The data from the spring and summer months are not sufficient to allow an analysis of separate populations to be made. Very few 1-yr common gulls seem to utilize the BA in summer. Thus, most of them do not migrate back all the way. There were 115 recoveries available from May - July, and 27 (23.4%) were reported from within 100 km of the natal colony. Ten of these were reported in, or very near, the natal colony, and since they were not found in a fresh condition they probably did not leave the colony the previous summer. The proportion of 1-yr gulls encountered in the BA is higher in June than it is in July (Table 3, $\chi^2=10.8$, $P<0.001$). This implies that the returning birds only make a brief visit.

The proportion of recoveries of 1-yr common gulls west of 14°E is lower in the summer (Fig. 12). Of the May - July recoveries ($N=116$), 59.2% were recovered west of 14°E, as compared to 82.7% of the January - February recoveries ($N=238$). The difference is highly significant ($\chi^2=23.2$, $P<0.001$). The number of recoveries from Britain and the North Sea coast also declines (from the two areas combined, January - February, 13.0% in May - July), as does the proportion found in Denmark (59.6% in the winter, 35.6% in the summer). Both differences are significant ($\chi^2=11.4$, $P<0.001$, $\chi^2=6.6$, $P<0.01$). Thus, most birds leave the MSA in the summer. The recoveries plotted in Fig. 12 indicate that areas along the migration track towards the natal area are used. A number of recoveries along the Norwegian west coast indicate that in the summer 1-yr common gulls also exploit areas which are not used during either the autumn or the winter.

Table 2. Number (and percentage) of recoveries of 1-yr common gulls from Finnish populations in different geographical areas in January - February. Category "others" refers to the Baltic east of 14°E.

	Populations				
	BB+QA	W	LD	AS	GF
Denmark	29 (64)	29 (62)	17 (46)	16 (64)	39 (55)
North Sea coast	9 (20)	12 (25)	13 (35)	6 (24)	22 (31)
Britain	7 (16)	6 (13)	7 (19)	3 (12)	6 (9)
Others	- (-)	- (-)	- (-)	-(-)	4 (6)
Total	45	47	37	25	71

Table 3. Number (and percentage) of recoveries of immature age classes of common gulls within 100 km of natal site in summer.

	1-year		2-year		3-year		4-year	
	<100 km	Total	<100 km	Total	<100 km	Total	<100 km	Total
May	7 (29)	24	20 (63)	32	21 (70)	30	13 (59)	22
June	14 (40)	35	23 (68)	34	26 (81)	30	17 (85)	20
July	6 (11)	56	26 (51)	51	24 (68)	31	26 (81)	30

3.4. Yearly range of 2-yr and 3-4-yr common gulls

2-yr birds

As indicated in section 3.3., 1-yr common gulls mainly utilize southern areas outside the breeding area in the summer. Birds which become 2-yr individuals on August 1 return in the autumn to the MSA from the summer areas. The main survival area west of 14°E already begins to fill up in August, and the majority of the birds are found here in August - September, with very little change in proportions occurring later in the year. The MSA seems to be the same as that of adults and 1-yr gulls (Table 4, Fig. 13).

Of 2-yr gulls recovered in May - July ($N=117$), 73.5% were found in the BA. The summer recoveries show that the total area utilized is as large as that of 1-yr birds. The 2-yr birds only stay for a short time in the BA. There is a significant decrease in the proportion of these from June to July (88.2% versus 56.9%, $\chi^2=9.4$, $P<0.01$, $N=34$ and 51). The majority of finds in the BA were made near the natal colony (Table 3).

3-4-yr birds

Most 3-4-yr common gulls return to the BA for the breeding season. In May - July, 88.9%

Table 4. Number (and percentage) of recoveries of immature common gulls in January - February in different geographical areas. The area "others" refers to the Baltic east of 14°E.

	2-year	3-4-year
Denmark	47 (57)	24 (44)
North Sea coast	21 (29)	15 (27)
Britain	9 (13)	14 (25)
Others	- (-)	2 (4)
Total	72	55

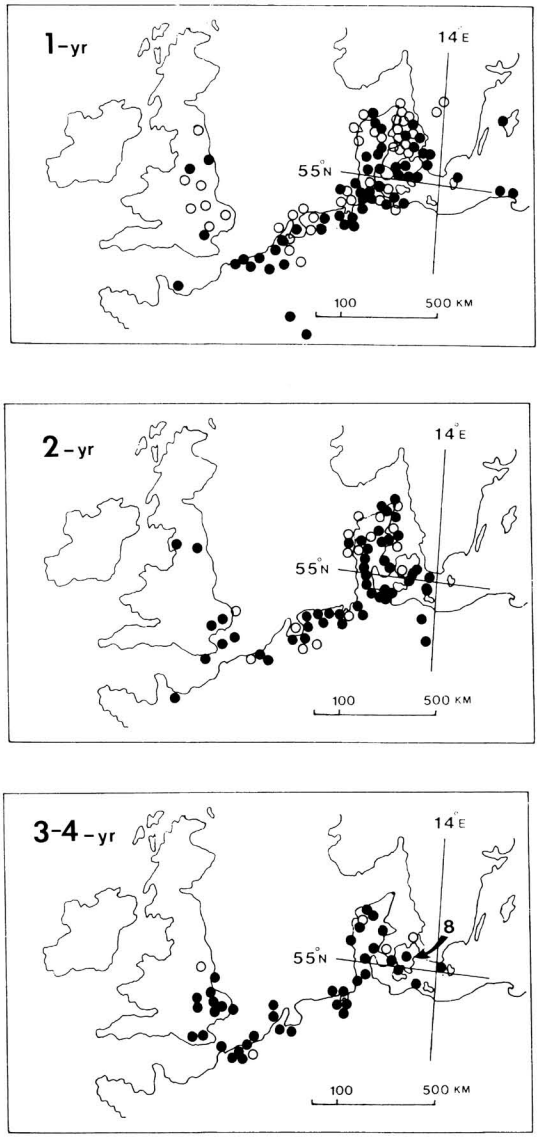

Fig. 13. Maps showing recoveries of 1-yr, 2-yr and 3-4-yr birds in January - February. Birds born north of 63°N (black dots) separated from southern birds (open circles).

of the 3-yr birds ($N=90$) and 93.1 % of the 4-yr birds ($N=72$) were found in the BA. The majority of these were found near the natal colony (Table 3).

These birds abandon the BA as early as August: only 31.9 % of the August recoveries were reported from the BA. Generally the MSA is the same as for other age-classes (Fig. 13).

4. Discussion

4.1. Interpreting the distribution

Movement is a fundamental response to adversity (Gauthreaux 1982). This should apply the movements on both a regional and a local scale. For instance, the trivial response to climatic adversity by birds in temperate regions is migration to a more favourable area. On a local scale within, for instance, the breeding area or the survival area, intra- and interspecific competition and social hierarchies may well lead to migration (Alerstam & Högstedt 1982, Gauthreaux 1982, Salomonssen 1955). The common gull satisfies Lack's criteria for true migrants — there is very little overlap between the area used for breeding and that used outside the breeding season. There is no doubt that the climatic conditions within the breeding area during the coldest part of the year do not permit the survival of a very large fraction of northern common gull populations, and migration is thus obligatory.

The data we have presented show that Finnish common gulls exploit the breeding area for a brief part of the year. Adults and first-year birds leave the breeding area as soon as the young are able to fly. Immature age-classes stay in the breeding area for even shorter periods, and some do not exploit it at all. The early departure remains unexplained. We have available no measurements of any environmental factor indicating a decline of the carrying capacity of the breeding area in late summer.

The migration to the MSA is rapid. Transient areas are exploited for short periods only. Finnish common gulls thus appear to be adapted to exploiting two very distinct areas during the year.

This strategy can be compared with that employed by Finnish herring gulls *Larus argentatus*. The herring gull exploits the BA extensively in autumn (Kilpi & Saurola 1983a, b), and migrates to the SW part of the MSA only for the coldest months, when the breeding area is uninhabitable due to ice and snow.

Within the MSA, all Finnish common gull populations mix extensively. We demonstrated, however, that northern populations tend to use more northern areas, i.e. that there is some segregation. No segregation between the age-classes could be detected. However, it is possible that segregation between age-classes does exist on a local scale. Juvenile gulls are often considered socially inferior to older birds (Ulfstrand 1979), and this may lead to spatial segregation (Gauthreaux 1982). Segregation may be advantageous because it reduces clumping and thus possibly lessens competition for food. We have previously presented some evidence (Kilpi & Saurola 1983a) for age-dependent differences in the distribution within the survival area of the related herring gull. In this species, adults tend to clump while juveniles rove over larger areas. However, all speculation on the role of competition and social dominance in governing spatial distribution during the non-breeding season is beset with the difficulty that very little is known about interactions between different age-classes.

Immature common gulls exploit the survival area for prolonged periods. We demonstrated a tendency to shift away from the SW part of the MSA in the spring and summer. In spite of this shift, most 1-yr and many 2-yr gulls do not return to the breeding area. Why this is so is not known. Possibly there is little point in allocating energy to a return migration when there is nothing to gain in terms of reproduction, as these birds are unable to breed. Instead, immatures should maximize survival (Alerstam & Högstedt 1982, Taylor & Taylor 1982). The importance of the BA increases with increasing age when prospecting for vacant territories and suitable breeding colonies is important. Many *Larus* gulls are considered site-tenacious (Southern 1977). Young, first-time breeders usually return to the natal area, or colony, and adults tend to use the same nest site each year. However, both natal and breeding dispersal (Greenwood 1980) are important and occur in some of the birds. We have found that the three related gull species in the Finnish Gulf disperse at similar relatively high rates (Kilpi & Saurola 1983b). Dispersal is probably advantageous even for species breeding in relatively stable habitats (Hamilton & May 1977, McNicholl 1975). The extensive use of the survival area by

the juveniles indicates that this area is able to support a large number of common gulls during the breeding season. Why do young birds not settle to breed in the survival area, but return to the area of origin? This is probably the key question in the evolution of a particular migratory strategy (Sinclair 1983), and also one of the aspects of bird movement that is least understood.

Table 5. Estimated population sizes (pairs) of common gulls in NW Europe. Primary sources for data Cramp & Simmons (1983) and Glutz v. Blotzheim & Bauer (1982). The size of the Murman population and that of western Siberia is not known, but probably comprises several thousand pairs. Other European countries have very small numbers of breeding birds. The Finnish estimate is based on Palmgren (1983).

Country	Pairs	Country	Pairs
USSR White Sea	2000	Denmark	40000
Finland	60000	DDR	8000
Sweden	250000	BDR	9000
Estonia	40000	Netherlands	7000
Norway	150000	Scotland, Britain	40000

4.2. Comparison with other common gull populations

The common gull breeds in both the Palearctic and the Nearctic regions (Cramp & Simmons 1983). Four subspecies are usually recognized, of which the nominate *L. c. canus* breeds in NW Europe. The slightly larger subspecies *L. c. heinei* of western Siberia is found in NW Europe in winter (Kuschert 1983).

The bulk of the NW European population occupies a range with reasonably pronounced seasonality. For a summary of population estimates see Table 5). The population estimate put forward by both Cramp & Simmons (1983), and Glutz v. Blotzheim & Bauer (1982) for Finland (5000 pairs, increased lately, sic!) is a gross underestimate (Palmgren 1983).

How is this total European population of roughly 600000 pairs distributed in the non-breeding season? In Table 6 we have broadly outlined the timing of the major events, such as colony occupancy and desertion after breeding is completed, and the data available on

Table 6. Phenology and assumed Main Survival Area (MSA) for several European populations of common gulls.

Population	Colonies	Main migration period	Main survival area	Source
Murman coast 69°N	mid-May - end July	end August - September, 1-yr later than adults	Britain (Scotland ?)	Belopolskii 1961 Dementiev & Gladkov 1969
White Sea 67°N	mid-May - end July	September, most gone by October	Denmark, North Sea, Baltic	Bianki 1977
N Finland 63-65°N	early May - end July	August	Denmark, North Sea, Britain & France	von Haartman et al. 1963-72, Rauhala 1980, this study
S Finland 60-63°N	early May - mid-July	end July, mid-August, 1-yr later than adults	Denmark, North Sea, Britain & France	this study, Kilpi unpubl.
Estonia c. 59°N	early July	August, September, 1-yr later than adults	Denmark, North Sea, Britain, Baltic	Jögi 1958 Rattiste 1983
Denmark 55-56°N	April - early July	August, September	Britain, France, North Sea, Denmark	Salomonssen 1967 Halling Sørensen 1977
SW-Sweden 55-57°N	?	July - August (?)	North Sea, Denmark, Britain & France	Österlöf 1964-71
N Norway 67-69°N	May - end July	?	Britain (Scotland?)	Haftorn 1971
W Norway 60-64°N	end April - mid-July	?	Britain, France, North Sea, Spain	Haftorn 1971
S Norway 58-60°N	mid-April - early July	?	Britain, Denmark, North Sea	Haftorn 1971
Britain, Scotland 56-57°N	March - July	none	Britain, Ireland	Cramp & Simmons 1983 Sharrock 1976

main survival areas and movements of different populations. Unfortunately, very few ringing recovery studies on this species have been published, and the details of the picture emerging are somewhat obscure. The general pattern is early migration from the breeding colonies to a separate survival area. The survival areas used by different breeding populations seem to overlap quite extensively.

4.3. Migration routes, timing of migration and spatial relationships in the non-breeding season

The survival areas outlined in Table 6 for different populations of common gulls from NW Europe imply the following routes. Murman and North Norwegian birds migrate along the Atlantic and cross the North Sea directly to Britain and Scotland. Observations in spring (Bourne & Patterson 1962, Vernon 1969) indicate the same pattern. West Norwegian birds possibly also cross the North Sea, while South Norwegian gulls may move through Denmark. All Baltic populations and the South Swedish population move through Denmark. Finnish common gulls seem to move within a narrow corridor along the shortest route to the goal area in the southwest. White Sea birds appear to conform to the same pattern when crossing Finland.

There are latitude-dependent differences in the timing of the migration. On the south coast of Finland there is a pronounced peak immediately after the breeding season in late July - early August (Fig. 14). A similar peak is observed at bird stations in South Sweden (Falsterbo, Ottenby). These birds are possibly from the Swedish breeding population (Edelstam 1972, Ulfstrand et al. 1974). The early migration observed in these populations seems to apply to Estonian birds as well (Rattiste 1983). The sparse data on Norwegian birds indicate that migration starts in August. However, some birds, especially 1-yr individuals, remain close to the breeding grounds until November. In September - October there is a drastic decline in Denmark in the proportion of ringed common gulls of Danish origin, which indicates that the birds have migrated (Halling Sørensen 1977). The disappearance of the Danish birds coincides with the time the bulk of the Finnish migrants arrive in Denmark.

In Finland, there is usually a second migration peak in late October - early November

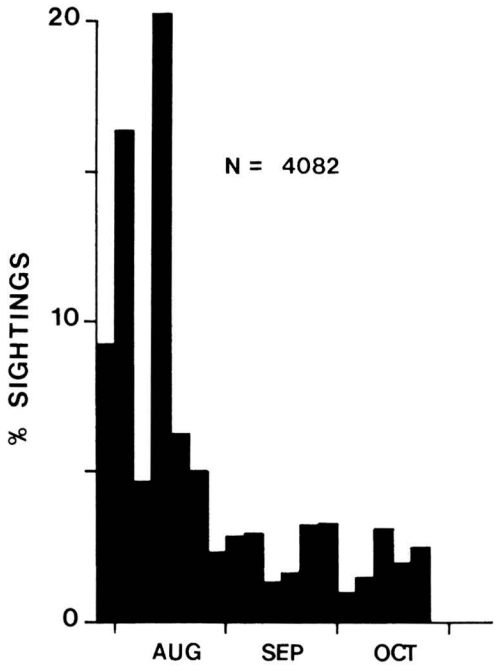

Fig. 14. Percentage distribution of sightings of common gulls in 5-day periods at Hanko Bird Station in 1979. The figures include both resting and migrating flocks. The counting effort has remained at about the same level in each 5-day period (J. Haapala and J. Saari, pers. comm.).

(Haapala & Saari pers. comm.). This peak probably represents White Sea birds en route through Finland. This view is confirmed by a number of recoveries of White Sea ringed birds made in Finland during this period of the year. Large numbers of migrating common gulls have been observed even much later. For instance, approx. 5000 birds were recorded migrating past the Lågskär bird station south of Åland on 20 December 1974 (J. Palmgren pers. comm.). A large number of gulls usually stay on the Finnish coast until the end of the year, and according to our recoveries these birds are not of domestic origin.

In Fig. 15 we have indicated the survival areas of a few populations for which at least some ring recoveries were available. It appears that the populations do not completely mix. There is some indication of a latitudinal displacement pattern (Ketterson & Nolan 1982), i.e. northern populations tend to winter north of more southern populations (compare the distribution of White Sea, Finnish and Danish birds in the winter). This trend was to be found even between different Finnish populations.

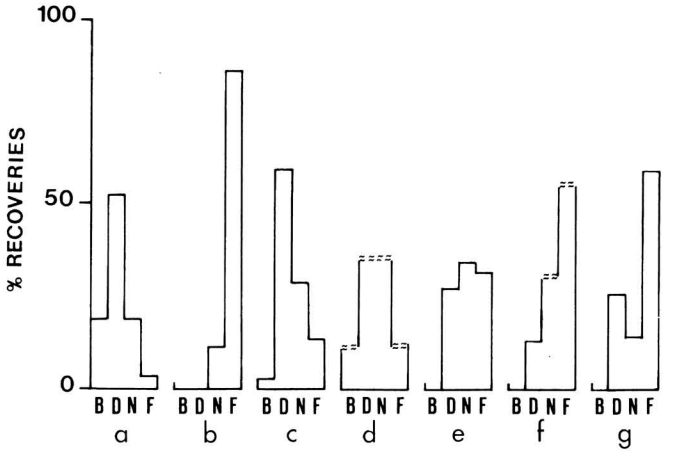

Fig. 15. Distribution of "winter recoveries" according to area (B = Baltic, D = Denmark, NS = North Sea coast and F = Britain and France) and population of origin. Kandalaksha Bay (a), 23 recoveries in December - February (Bianki 1977), (b) western Norway, 47 recoveries in December - February (Haftorn 1971), (c) Finland in January - February (this study), (d) Estonian SSR, 164 recoveries in December - February (Rattiste 1983), (e) SW Sweden, 47 recoveries in January - February (Österlöf 1964-71), (f) Denmark, c. 120 recoveries in January - February (Halling Sørensen 1977), and southern Norway (g), 41 recoveries in December - February (Haftorn 1971). Note that the material is heterogeneous, since a mixture of recoveries with respect to age has been used. Whenever the percentages have had to be approximated from graphs with absolute figures, or from plotted recoveries on maps, this is indicated by a wavy line on the bar.

4.4. Why do southern birds migrate?

In many birds occupying temperate areas, a tendency has been found for birds from northern areas to spend the winter south of more southern conspecific populations (leapfrog migration, Salomonsen 1955, see also Alerstam & Högstedt 1980). Competition is probably involved in such segregation between populations during the non-breeding season. We have here argued that northern Finnish common gull populations tend to winter north of more southern populations. This pattern seems to apply on a larger scale, too. One possible explanation of the pattern is that southern birds escape competition by moving out before there is a heavy influx of northern birds. The distances covered are short, and survival may be higher in an uncrowded area. This advantage may be greater than the advantage of staying near the breeding area. Northern birds may also be better adapted to a harsh environment and there would be no benefit in continuing further south, into an already occupied area. Barth (1967) has argued that there are no differences in body size between NW European common gulls. Thus, all common gulls in this area are presumably equal competitors. The dominance-based models for dispersal presented by both Fretwell (1980) and Gauthreaux (1978, 1980) seem to require, at least indirectly, a difference in body size (Burger et al. 1979). There is, however, a large race of the common gull, *L. c. heinei*, which breeds in western Siberia and winters in NW Europe (see Kuschert 1983). This subspecies is considerably larger than *L. c. canus*, and it could well be dominant and better adapted to harsh environments. This subspecies probably has the northernmost wintering area in the Baltic.

Morphometric and food availablity studies within the MSA of NW European common gulls could give significant insight into the evolution of the latitudinal displacement migration pattern outlined here (see also Ketterson & Nolan 1982). At present, the causes and consequences are obscure.

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