Ann. Zool. Fennici 19: 143–164. 1982

Population dynamics, colony formation and competition in Larus argentatus, fuscus and marinus in the archipelago of Finland

Göran Bergman

Bergman, G. 1982: Population dynamics, colony formation and competition in Larus argentatus, fuscus and marinus in the archipelago of Finland. — Ann. Zool. Fennici 19: 143–164.

The limited productivity of the brackish water and absence of tidal shores on the coasts of Finland originally allowed these gulls to breed only in sparse populations of single pairs. Refuse from fisheries permitted an early increase in *Larus f. fuscus*, since it winters in a partly tropical region, but the winter conditions in the North Sea prevented the increase of *L. argentatus* and *L. marinus* until the technical advances and urbanization improved their food supplies. In Finland, *L. argentatus* began to increase around 1930 and *L. marinus* around 1940.

Field records made in 1930—1982, mainly on the S coast of Finland, are used to examine: Population trends, changes in the proportion of single pairs and their causes, the tendency of single pairs to defend a feeding range around the breeding islet and the advantages of this feeding range, the change in feeding habits required for colony formation, and the breeding success of single pairs and colonial breeders. The location of single pairs and the formation, size and density of colonies are influenced by the location of food, inter- and intraspecific sociability and the topagraphy of the archipelago. Attention is paid to predation and other impacts on other shore birds, to the effect of food shortage on the occurrence of predatory single pairs in *L. argentatus* and the reasons why such are always adults, and to the causes of dispersal into non-marine landscapes in *L. marinus*.

Colony formation begins when the aggeression shown in defending of the feeding range no longer counterbalances sociability and the population pressure. In *L. fuscus* the long narrow wings prevent feeding in localities where flocks of gulls hover over the food. This disadvantage, together with the reduced fishery in the archipelago and the inability of *L. fuscus* to withstand *L. argentatus* on the small breeding islets, has led to a drop of its population.

G. Bergman, Zoological Museum of the University, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland.

1. Introduction

This study deals with the population development, the change from single-pair to colonial breeding, foraging habits and intra- and interspecific competition in the Herring Gull *Larus a. argentatus*, the Scandinavian Lesser Black-backed Gull *L. f. fuscus* and the Great Black-backed Gull *L. marinus*. The archipelago of Finland has provided excellent opportunities for field studies on these subjects. The question of territorial versus colonial breeding has been discussed by several ornithologists (eg. Fisher 1963, Horn 1968, Lack 1968, Krebs 1974), but only scanty information is available on the change from a population of single pairs to a population breeding colonially. As long as they depended mainly on natural food rescources in the Finnish archipelago the Herring Gull and the Great Black-backed Gull bred only in single pairs. When man provided new food supplies the population increased and colonial breeding developed rapidly in the Herring Gull, but much more slowly in the Great Black-backed Gull. For the Lesser Black-backed Gull full evidence of a single-pair stage is lackning, but in ancient times this species evidently also bred here exclusively in single pairs. Interesting questions are: Why did the Lesser Black-backed Gull increase and form colonies at a time when both the other large gulls were unable to do so? What has caused the recent decrease of the Lesser Blackback in areas with a dense population of Herring Gulls? In what way does the foraging behaviour of the Lesser Blackback differ from that of the Herring Gull and what is the reason for this difference? Why is the Lesser Blackback able to compete successfully with the Herring Gull on the British coast (cf. Harris 1970) but not in Finland?

The Baltic Sea was originally a poor habitat for large gulls. Food supplies are limited by the absence of tidal shores and the restricted productivity of the brackish water. Egg collecting and later

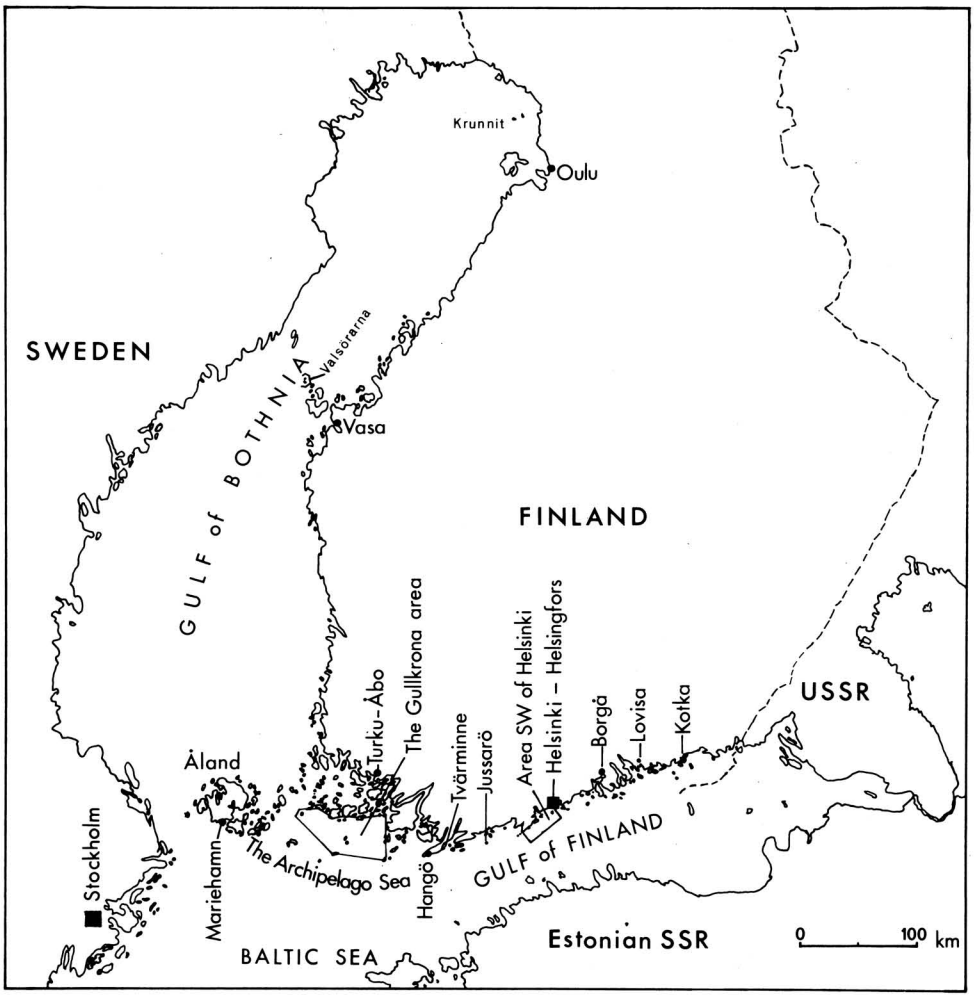

Fig. 1. The coasts of Finland with localities mentioned in the text. For localities in the area SW of Helsinki see Fig. 2.

shooting reduced the population of waterfowl, thus further decreasing the amount of food available for large gulls during the breeding season. Moreover, until the 1930s the size of the gull populations was also reduced by egg collecting and by persecution of the Great Black-backed Gull. However, technical advances and urbanization have had many repercussions on the living conditions of the gulls in the archipelago. The amount of refuse in urbanized areas has increased enormously and this source of food has been exploited by the Herring Gull in particular. Simultaneously, fishing methods have changed and the outer parts of the Finnish archipelago have become almost depopulated. The number of fishermen's cottages was highest there in the 1910s when the local fishery was intense; rapid depopulation began around 1955 and now there are only a few families still living in the old fishing villages. Earlier, herring was caught with nets in the outer archipelago and cleaned there, now it is fished with trawls on the open sea and with hoop nets in the innermost archipelago, and mostly brought uncleaned to the consumers and factories. Earlier, there was also many other kinds of fishery, especially in summer, when herring was not available. Now these are of secondary importance and the refuse from sport fishing at the many new summer cottages can feed only a small number of gulls.

This paper is based on field studies carried out over more than 50 years. My first records on gulls in the archipelago are from 1928, the most recent

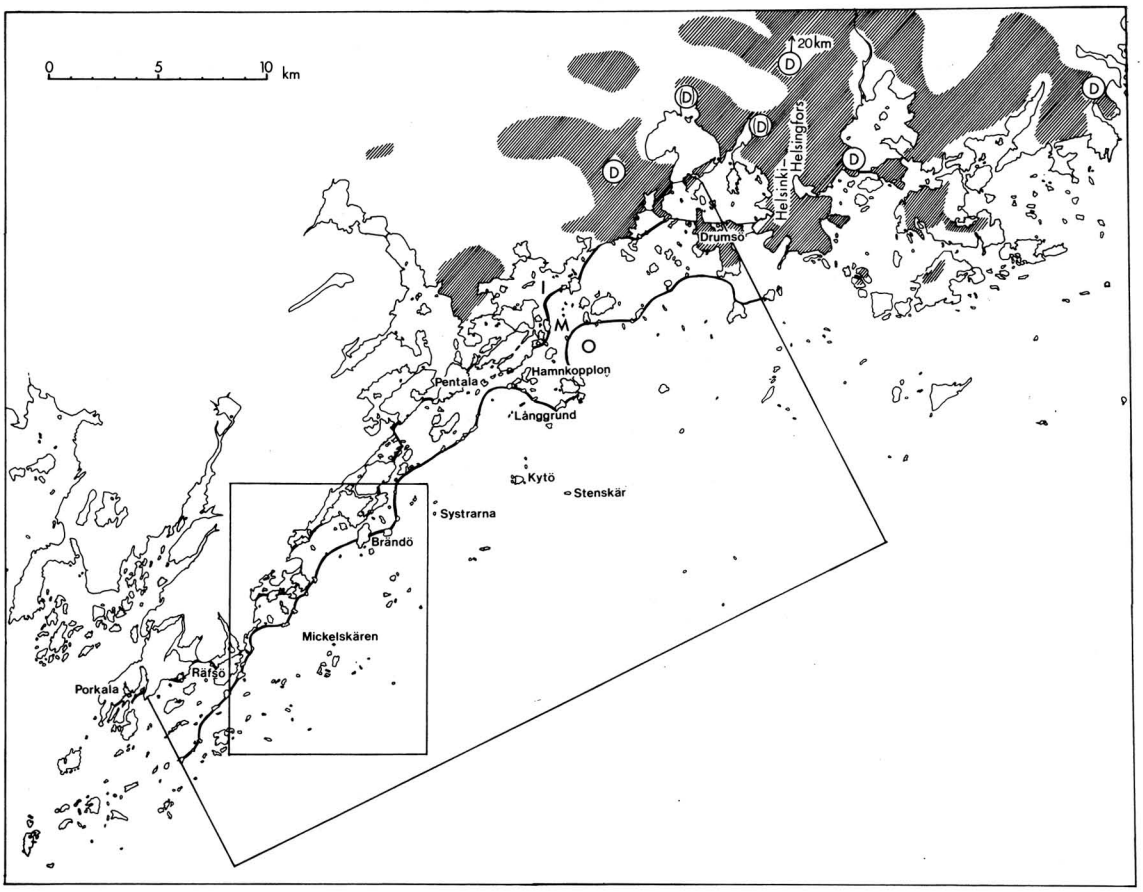

Fig. 2. The archipelago SW of Helsinki. For the area around the islet group of Mickelskären see Fig. 4. p. 158. I, M and O: Inner, middle and outer archipelago zone. D = garbage dumps, (D) dumps no longer used. Urbanized areas shaded.

from 1982. My main study area was the archipelago 15—40 km SW of Helsinki (for a description: see Bergman 1939, 1957, 1965), here called "the area SW of Helsinki", where all my summers have been spent. Since 1937 I have begun the field records in April or early May. Having lived in the area for at least 8 weeks every year between May and September, I have become very familiar with the avifauna of this archipelago. Material for comparison and additional information were provided by the numerous investigations on gull populations on the North Atlantic and North Sea coasts — beginning with Friedrich Goethe's and Nico Tinbergen's fundamental studies — and the quantitative surveys of the avifauna in the Finnish and Swedish archipelago.

For the location of the areas and islets mentioned in the text, see Figs. 1 and 2, and Fig. 4 (p. 158).

2. The Herring Gull Larus a. argentatus

2.1. Population dynamics

The Herring Gull population of the Finnish coast is controlled by the food supply in both the breeding area and the winter range. As long as man provided only scattered food supplies, the winter range was restricted to the southernmost Baltic and the North Sea region, especially the latter. In cold winters the death rate of the gulls was presumably high because the waters of these coasts may freeze over, preventing feeding, especially on tidal shores — the most frequented natural feeding localities of the species. The fish refuse earlier available to some extent in the Finnish archipelagoes was therefore not enough to cause any increase of the Finnish Herring Gull population. The increase began when the growing

garbage dumps and modern trawling for herring and cod began to provide plentiful food for the gulls even in the winter (references: see Spaans 1971, Kihlman & Larsson 1974, Hörnfelt 1981). As its population increased the Herring Gull was more or less forced to find new feeding sites in the breeding areas in the Finnish archipelago. It began to forage on new garbage dumps and increased still further, changing almost completely from breeding in single pairs to breeding in colonies. Now the strong increase of the Herring Gull has caused local food shortage in the breeding area and this has led to a slight increase in the proportion of single pairs. Recently the pricking of eggs in the colonies off Helsinki has caused many gulls to shift to islets earlier not inhabited by colonies and may also have contributed to the increase in the number of single pairs. In the early 1920s the Herring Gull population of the S coast of Finland still consisted of only some tens of pairs but no exact information is available. In the early 1930s there may have been 200 breeding pairs, but in 1980 the population comprised c. 11000 pairs (Kilpi et al. 1980). The Herring Gull is now also increasing in the Archipelago Sea of SW Finland (Bergman 1946, Grenquist 1965, Lemmetyinen 1980, Stjernberg 1982 b), along the W coast of Finland (Taxell 1934, Grenquist 1965, Väisänen & Järvinen 1977, Hildén et al. 1978, Hildén 1983) and in the lakes of S Finland (several pers. comm., especially P. Linkola; Kosonen & Mäkinen 1978). Similar trends are evident in the Baltic archipelagoes of Sweden and to some extent also in Estonia (Mathiasson 1964, A. Kumari 1967, Andersson 1968 a, 1970, Kastepöld 1972, E. Kumari 1976, Andersson & Staav 1980). At Karlsöarna off the island Gotland, where there has usually been some fishing during the winter as well, colonial breeding has evidently occured for as long as c. 120 years (Holmgren 1871).

In Finland the first Herring Gull colonies were established SW of Helsinki in the 1920s (on the islets Espskärskubb and Rönnbuskskubb). In June 1925 Hortling (1929—1931) saw about 50 Herring Gulls off Helsinki and in 1928 and 1929 I recorded Herring Gulls together with Lesser Black-backed Gulls (once c. 20 simultaneously) at hoop nets SW of Helsinki. The fishery, the dumps, and the ships and harbours in this area provided more food than elsewhere, and protected colonies of Lesser Black-backed Gulls in the outermost archipelago were attractive breeding localities. In the Åland area the first colony was recorded in 1931 (33 pairs, Valovirta 1931).

Table 1 illustrates the change from a population breeding exclusively in single pairs to a population breeding mainly in colonies in the area SW of Helsinki.

Table 1. The development of the Herring Gull population in the area SW of Helsinki during the period 1910—1982.

	Pairs		Proportion of single pairs (%)	Number of breeding localities
	in colonies	singly		
Early 1910s (R. Palmgren 1913)	a few	all	100	a few
1935 (Bergman 1939)	123	5	4	11
1943 (Bergman)	c. 300	2	0.6	c. 15
1965 (Bergman 1965)	c. 1200	7	0.6	
1980 (Kilpi et al. 1980)	c. 6500	c. 10	c. 0.2	c. 70 (Bergman)
1981 (Kilpi pers. comm.)	c. 6500	c. 25	c. 0.4 (Bergman)	c. 95
1982 (Kilpi pers. comm., Bergman)	c. 5000	c. 40	c. 0.8	c. 110

2.2 Colony size and colony formation

Effects of size and number of suitable islets

On coasts with a restricted number of suitable breeding localities, an increase in the population will more or less force the Herring Gulls to form large colonies. They may form several epicentra on the same island (Burger & Shisler 1980), which later may unite, so that thousands of pairs may occupy the same land unit or a few adjecent islands. The Baltic archipelagoes of Finland and Sweden contain numerous small and mostly low islets and islet groups fairly evenly distributed off the coast. The larger islands and less favourable for gulls, being mostly wooded and inhabited by man or mammal predators. However, most of the barren or almost barren islets are too small to accomodate large colonies. On an open coast, the Herring Gull population breeding in the 60—70 colonies SW of Helsinki could well gather in one large colony, and the same is true of the Herring Gull population of the Archipelago Sea of SW Finland (estimated size order: 5 000, of which about 3000 pairs breed in the Gullkrona area, roughly 70 x 40 km, a proposed national park, Stjernberg 1982 b), and of the population in the wide archipelago off Stockholm (in 1974—1975 c. 5250 pairs, Andersson & Staav 1980).

The largest Herring Gull colonies in Finland are situated in the area SW of Helsinki (in 1980 one of about 450 pairs, 4 of 300—400 paris). The commonest size of the Finnish colonies is 20—100 pairs. In England Parsons (1976) found that when the colony size exceeds 250 pairs the breeding success decreases, and Chabrzyk & Coulson (1976) distinguish between low- and high-density colonies (less or more than one pair per 4 m^2). In Finland hardly any colony can be considered dense. This difference between Finnish and British colonies is evidently due to the fact that almost

all the islets colonized in Finland are surrounded by numerous other islets, on which pairs begin to settle when the density of the old colony still is rather low. Thus, the rather small number of Herring Gulls in relation to the great number of attractive islets results in small colonies. More social stimulus in needed for colonization of new large land units than for colony formation on small attractive easily defended islands. The small size of the Finnish colonies and the low nest density in them allow high breeding success and a rapid increase of the population as long as enough food is available.

The islet Rönnbuskskubb (Fig. 4 p. 158) has shown the highest density occurring in Finnish colonies. Its area is c. 12 000 m, and in 1961 the gullery covered c. 9 000 m^2. Between 1961 and 1976 the number of pairs breeding on the preferred steep and rocky S slope rose from c. 60 to c. 150. Not only the small rugged cliffs but also the flat areas between them were occupied. On the S slope the mean area per pair was about 4 m^2, but the mean for the whole colony (c. 300 pairs) was c. 30 m^2. On the S slope dense settling is caused by numerous excellent nest sites situated close to each other. This part of the colony attracts new pairs more than the less dense parts of the colony (cf. Chabrzyk & Coulson 1976, Duncan 1978) and the rough terrain isolates the pairs and allow new pairs to settle on flat areas between the preferred sites. When gulls settle in March-April there is no fresh vegetation on the many soil strips on the flat upper parts of the islet. This lack of screening vegetation evidently contributes to the larger size of the territories on the upper parts of the islet than on the slope, where the terrain isolates the pairs from each other (e.g. Ewald et al. 1980).

Development from a single-pair locality to a colony

A single pair may settle on an islet, or, more commonly, it may join a colony of Lesser Blackbacks in April. If the pair feeds in the vicinity of the breeding locality and consequently behaves aggressively to conspecifics (see later p. 150), the islet generally remains a single-pair locality for many years. However, the pair may begin to use the same foraging sites as the Lesser Blackbacks (fisherman's cottage, harbours, hoop nets) or some more distant feeding site. In these cases they cease to be aggressive to conspecifics and both interspecific and intraspecific sociability may cause other pairs to settle near the first one. Herring Gulls that have become familiar with the islet in the previous season settle there 2—4 weeks before the other larids (except for some Great Black-backed Gulls), sometimes as early as February. Late-arriving Herring Gulls (mainly first-breeders, Bergman 1965) are attracted by pairs that have already settled and the colony grows rapidly. The early settling and large size of the Herring Gull makes it impossible for the other larids (except Great Black-backed Gulls) to drive them away. If the islet is small (less than c. 2 ha) it may be covered by territories of the Herring Gull within a few years.

As the most attractive islets are generally colonized first (the steepest — cf. Lönnberg 1929, Bergman 1939, Goethe 1960 — most barren, best protected) and high density increases the stimulus to settling (Burger & Lesser 1980), and as increasing population pressure tends to reduce the territory size (Chabrzyk & Coulson 1976, Burger & Lesser 1980), the number of pairs on the first islet may continue to grow for decades, even after the gulls have occupied nearby islets and perhaps spread elsewhere.

Overpopulation causes settling on nearby islets

If the distance from the old colony is only some ten metres it can hardly be called a new colony, only a new epicentre (Burger & Shisler 1980). But if the distance is some hundred metres or more, it may well be considered a new breeding locality. When the shift is caused by overpopulation the generally great fidelity of the gulls to the vicinity of their natal islet (cf. especially Spaans 1971, McNicholl 1975) and the inability of young individuals to settle in the centre of colonies (Coulson 1968) may lead to acceptance of localities not corresponding to the the normal requirements of the species. Such atypical localities are very flat small islets, bare shores of larger islands, and islets with sparse (pine) forest. Colonization of atypical localities has mainly occurred in the area SW of Helsinki, where the colonies are largest. Repeated egg pricking in the main colonies contributed in 1981 and 1982 to settling in atypical localities.

Settling near feeding localities

In an increasing population living on artificial food sources, a group of pairs may settle much nearer a foraging locality than the old colonies. After 1940, for instance, Herring Gulls occupied the outer archipelago between the islet groups of Espskären and Systrarna c. 25 km SW of Helsinki and the town. When this area became saturated they spread to more distant localities.

First they settle on islets fulfilling the normal requirements of the species, but in areas with a dense population they may also accept atypical localities. Both near Helsinki and off Stockholm (Andersson & Staav 1980) colonies have been established on wooded islands with summer cottages. On the wooded island Räfsö (c. 80 ha) 33 km SW of Helsinki some Herring Gulls settled in the 1970s on a lightly wooded rocky hill with open view in the middle of the island, but predatory mammals caused them to desert the locality. Sometimes single pairs settle near artificial food sources, but in most cases they are joined by other pairs in the same or the next season. Burger & Lesser (1980) describe the same mode of colony formation. The settling on rooftops in Helsinki (see below!) belongs to this type of colony formation.

Roosts change to colonies

Social feeding leads to flocking, especially in young individuals still not attached to breeding localities. These flocks roost on islets not too far from their main feeding localities: garbage dumps, harbours, mink farms, ship routes in the archipelago (as long as waste was dumped from ships). The flock becomes accustomed to the roost and the birds to each other, and when the gulls reach sexaul maturity they may begin to breed on the former roost. In the 1970s three roosts 1—13 km off Helsinki changed into breeding localities, and at least three colonies were established in this way on the ship routes in the Archipelago Sea.

Even when they cannot see the feeding locality gulls react to the rapid purposeful flight of other gulls moving towards food. Thus information of food sources is obtained at all localities, including roost, cf. Fisher 1963, Ward & Zahavi 1973, Loman & Tamm 1980, M. Andersson et al. 1981). This influences the choise of roosts, breeding localities and feeding localities.

Conditioning to man in juveniles enables rooftop breeding

First-year Herring Gulls become more easily accustomed to man the older birds. This is evident in harbours and especially in places where Mallards are fed by man. Some first-year Herring Gulls become just as tame as Mallards taking food from hand. These individuals will be extremely accustomed to man and traffic in the following seasons as well (cf. also Hildén 1965). It seems possible that rooftop breeding in Finland was initiated by such almost tame individuals. This is suggested by the fact that it first occurred in a small inland population in the town Tampere (central SW Finland) where a stream

allows winter feeding of Mallards (Kosonen & Mäkinen 1978), and not as a consequence of destruction of breeding localities in harbour areas, as in the coastal towns around the North Sea (cf. Took 1955, Goethe 1960, Monaghan & Coulson 1977, Monaghan 1979). Since 1980 roof breeding has also occurred in Helsinki (1980: 1 pair, 1981 and 1982: some single pairs and at least two groups of some pairs, all localities less than 600 m from the nearest harbour area but no pair on roofs at the harbours). These gulls live on the food given to the Mallards and on refuse in the town.

2.3 When, where and why do single pairs occur?

Where do single pairs settle?

Oceanic coasts have few or no small islets providing enough shelter against rough seas and tidal flooding, and most larids avoid breeding in single pairs on large islands where the territory is not easy to defend against predators (cf. p. 147). This and their strong sociability greatly reduces the number of single Herring Gull pairs in most parts of the breeding range. The Finnish coast has numerous islets corresponding to the requirements of the Herring Gull, but the natural food resources are not sufficient for a dense population.

The Herring Gulls breeding in the Baltic archipelagoes before man had considerably increased their food supply preferred rather marine areas, where food was most plentiful and where evidently attracted to colonies of other larids (cf. p. 147). During the breeding time these single pairs lived at least partly on eggs and especially on ducklings and chicks of other archipelago birds: Eiders and other diving ducks, larids (cf. Bergman et al. 1940). Pairs breeding in areas providing such food were not forced to undertake long time- and energyconsuming foraging tours. In any case the success of such tours would have been uncertain, except in areas where some food (fish refuse) was provided by man and the already rather numerous Lesser Blackbacks did not compete too strongly with the Herring Gulls for this food. Pairs that stay in the vicinity of the breeding locality most of the season learn to utilize all the food available and begin to defend a feeding range around the breeding locality.

Feeding range defence and persistence of the single breeding system

The feeding range tends to consist of the whole breeding islet, the nearby bare islets and shores and the surrounding waters within a radius of roughly 300—500 m from the nest. From the watching sites in the territory the pair constantly observes the behaviour of other, mainly smaller larids and other birds and thus obtains information, especially on food. Within the feeding range it is generally able to secure larger food objects before conspecifics or other large gulls find them. It utilizes eggs and chicks of other birds on and in the vicinity of the breeding islet. Within the feeding range the pair behaves more or less aggressively towards conspecifics and can usually prevent them from eating or catching chicks and ducklings. This increases the amount of food available for the single pair. The pair also learns where and when to catch ducklings successfully, and where and how to steal food from other birds.

Nowadays it also becomes accustomed to boating and tourists occurring in the feeding range, thus being able to ignore this disturbance and to utilize edible waste left by campers as soon as they depart. Single pairs defending a feeding range around their breeding locality are thus able to utilize the area much more efficiently than pairs visiting a locality only occasionally. The interest of other Herring Gulls in the feeding range of a single pair is decreased by the aggressiveness of the local pair, which commonly prevents successful feeding, and by the fact that the local pair mostly finds any available food before the other gulls can approach it.

Breeding in single pairs predominated as long as every pair found enough food during the breeding season within his own range and as long as aggressiveness counterbalanced sociability and population pressure. The pressure on the preferred localities increased as the numbers of Herring Gulls rose. When aggressive behaviour of the single pairs could no longer prevent new pairs from settling on the same islet, the Herring Gulls began to from colonies.

My records of the behaviour of single pairs at Mickelskären (see p. 150) show that conspecifics that do not seek for food within the feeding range of a single pair do not release so much aggresiveness as conspecifics trying to forage there, and may therefore settle more easily on islets inhabited by single pairs. Moreover, when a single pair of Herring Gulls detects a rich source of food rather far from the breeding locality (this may happen early in the spring before the feeding range provides food), the pair may begin to forage there more of less regularly. This will reduce their tendency to defend their own feeding range because so much time is spent on foraging tours out of sight of the breeding locality, and perhaps a diminishing need for food seeking around the breeding islet also has such an effect. Other pairs may then settle on the islet, and the old and new pairs become accustomed to each other. A regular source of food sufficient for several pairs but situated rather far from an optimally attractive islet may therefore lead to formation of a small colony. If enough food

is available the colony may continue to increase.

In the Lesser Black-Backed Gull the colony formation does not differ much from that in the Herring Gull. In the Great Black-backed Gull the tendency to maintain single pairs is much stronger, but the general principles of colony formation are the same. The differences are discussed in the sections dealing with the respective species. The Common Gull *Larus canus* may also shift to colonial breeding and to using a common feeding locality if it finds a constant source of food. This happened with three pairs on Mickelskären, which formed a small colony with the nests less than 4 m apart. As long as the pairs had separate feeding ranges the distance between the nests varied between 50 and 150 m.

When the Herring Gulls gradually began to increase SW of Helsinki in the 1920s an early 1930s, they first foraged mainly in the same localities as the Lesser Blackbacks: at hoop nets, in fishing harbours and in other localities providing fish refuse. They also followed ships. Later in the 1930s, when the number of colonial breeders was already about 150 pairs, the Herring Gulls began to feed mainly on the refuse dumps coming into use at that time. Colony formation coincided well in time with long foraging trips to constant sources of food.

Drury & Smith (1968) describe defence of a feeding area after the breeding season. Herring Gulls trying to obtain bread at feeding places for Mallards in Helsinki also display feeding-place aggressiveness towards conspecifies in spring and summer. At localities with plenty of food e.g. refuse dumps, herring trawls, every gull gets more food when it does not react agressively.

As described in Sect. 2.4, the strong increase of the Herring Gull in the area around Helsinki has lead to at least some shortage of food for these gulls. In such a situation some pairs may desert their old breeding locality and settle near a small local source of food. Using this source as feeding range may be more advantageous for the pair than social feeding, for instance on dumps. This is the main reason for the increase in the number of single pairs from c. 10 to c. 25 in 1980—1981. However, the disturbances caused by egg pricking in the colonies may have contributed to the shifts to new localities, especially in 1982. For instance at Mickelskären 3 groups of 2—6 pairs occupied islets, on which earlier no or only one pair had bred.

2.4. Breeding success, food supply and effect on other species

Breeding success in colonies and among single pairs

In 1980 and 1981 the number of Herring Gulls in the area around Helsinki was at least five times as large as in 1965. Simultaneously with the increase of the population there has been a very clear drop in the breeding success. In 1963—1965 the breeding success in the main colonies SW of Helsinki was around 1.8 fledged young per pair, in 1980 it was only about 0.9 (islets where no egg pricking was done: Hario 1981, data from the sanctuary Söderskär SE of Helsinki, and my own counts on Systrarna in 1975 and Salgrund in 1979 and 1980). In single pairs breeding in undisturbed localities and defending a feeding range, the breeding success was still high (1—2 pairs on Mickelskären in 1973—1981 mean 2.2, n = 9). Single pairs laid always clutches of 3 eggs, they mostly escape predation by Great Black-backed Gulls, and do not suffer from the cannibalism that nowadays reduces the breeding success in the colonies.

In 1963—1965 the breeding result in the westernmost colonies SW of Helsinki was already clearly lower than in the other colonies (c. 1.1 vs. 1.8—2), evidently because they were situated too far from the main feeding localities around the town and because these growing colonies had a high proportion of firstbreeders. In these colonies 8—40 % of the individuals had brownish feathers, whereas in old colonies this proportion was 4—8 % (Bergman 1965, cf. also Hunt 1972). On the main dumps around Helsinki in the 1960s attempts were made to burn the waste or cover it with soil. These measures did not completely prevent the gulls from obtaining food at the dumps, but the breeding result obviousiy dropped slightly — from c. 2 to c. 1.8 (Bergman 1965). Throughout the 1970s three large dumps (see fig. 2 p. 145) again provided much food for the gulls, but since the gull population increased vigorously, the food situation became more difficult. In 1981 the northernmost dump (located 3 km from the Helsinki-Vantaa airport) could be kept free from gulls by rapidly covering the waste with soil and by shooting of gulls (altogether c. 2000 Herring Gulls were shot in the Helsinki region in 1981; cf. also Vickholm 1982).

Shortage of food during the breeding season was shown by a drop of the breeding success in undisturbed colonies to 0.9. This must be considered a low young production in an area where the colonies are small and the pair density in them is low (cf. p. 146). However, in most colonies SW of Helsinki almost all the eggs had been pricked and only about 5 % of the total eggs had hatched. Despite of this the undisturbed colonies suffered from food shortage.

The shortage of food has clearly changed the feeding behaviour the Herring Gulls. They still forage in flocks at dumps, but single individuals and pairs are seen almost everywhere, and waiting for food occurs commonly (cf. Bergman 1960) in both the town with its suburbs, and the archipelago. Gulls also travel inland as far as 50 km and have there found smaller dumps, to which they have begun to return. The number of pairs trying to live on eggs and young of smaller larids and ducks is increasing. In the 1970s cannibalism became common at least in the main colonies (cf. Parsons 1971). Thomas (1972) describes an even more complete change of behaviour in an area where burning of refuse was started. In the area SW of Helsinki there are not many localities for

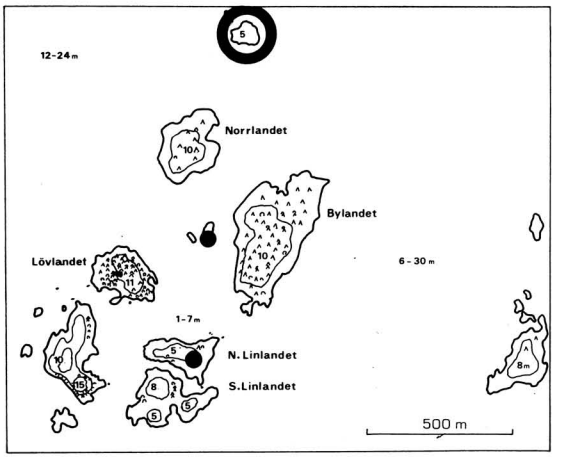

Fig. 3. The breeding localities of the Herring Gull *Larus argentatus* on the islets of Mickelskären in 1980—1981. Dots: single pairs; ring: a colony of c. 50 pairs. The heights of the islets and the depth of the sea well off the shores are given in metres.

single pairs offering food near the breeding site, but many individuals are trying to find new sources of food and may develop at least some feeding area defence. Most of the gulls, however, are still breeding at the colony localities.

Field records on feeding range and impact on other species

Comparisons between the feeding habits of sigle pairs and colony breeders were made on the island group of Mickelskären in 1973—1982. I was able to follow the activities of the gulls daily during at least two months in every summer. Occasional records on the feeding behaviour of single pairs were made at other localities SW of Helsinki, the first in 1930. The location of the Mickelskären colony, 30—50 pairs, and the nest sites of the single pairs are shown on Fig. 3. The colony breeders did not chase conspecifics elsewhere than just around the breeding territories, never as far as to the nearby islets Norrlandet and Bylandet 300—600 m from the colony. Some of them occasionally competed for small quantities of fish refuse or other food offered irregularly on the N shore of Bylandet and Norrlandet, but never for small amounts of food provided daily for gulls on the other shores of the islet group. The single pairs pursued conspecifics as far as 500 m, commonly flying over other islands than their breeding localities, and they caught ducklings and Common Gull and tern chicks within the islet group. The strongest attacks against conspecifics occured when these tried to catch Common Gull chicks in the colony on Norra Linlandet. The alarm behaviour of the Common Gulls evidently strengthened the attacks. In all the observed cases (21 recorded in detail) the Herring Gulls were able to prevent the foreign Herring Gull from catching chicks, but the Herring Gulls did not always succeed in preventing Great Blackbacks from catching Common Gull chicks. Between about 15 May and 10 July the single pairs at Mickelskären lived almost exclusively on eggs, chicks and ducklings taken within their feeding range. They did not leave the island group before 20—25 July. The colony breeders never cought or tried to catch any chicks within the island group, (but some cases of cannibalism on young occurred and some gulls from colonies situated SW of Mickelskären tried to catch young there). Thus the food strategy differed clearly between the colony breeders and the single pairs. The gulls from other colonies that tried to catch ducklings within Mickelskären were probably on their way to their normal feeding localites. The defence of the areas of the single pairs, the small amount of food available there, and the strong competition for this food from local conspecifics and Great Blackbacks was enough to prevent the colony breeders from developing any regular interest in the islet group of Mickelskären as a feeding locality.

In July 1980 the single Herring Gull pair on Norra Linlandet was shot, but in April 1981 it had been replaced by another single pair, using the same nest site as the first pair, and defending the same feeding range. In April 1981 the single pair on the small islet in the middle of the islet group was shot, but a few days later another single pair had replaced it. This pair also defendel a feeding range.

The (1—2) single Herring Gull pairs and two to three pairs of Great Blackbacks breeding yearly within the islet group of Mickelskären (see p. 159) depressed the breeding success of the other shore and water birds on the islet group severely in 1973—1981. The Herring Gulls consumed almost the whole production of eggs and chicks of the Common Gulls (c. 50 pairs on N. Linlandet: only 5—12 young fledged yearly), and many chicks of Common and Arctic Terns *Sterna hirundo* & *paradisaea* (10—25 pairs, never more than 3 young fledged, but the weather contributed to the losses of the tern chicks in all years and in 1981 to the mortality of the Common Gull chicks). Three to seven pairs of *Aythya fuligula* bred on the islets, but of the 30—45 young that stayed within the islet group, the number that fledged never exceeded 5. The gulls took all the ducklings (yearly 1—4 broods) of *Melanitta fusca* and *Mergus serrator*. In all the summers about half of the losses in these anatid broods were caused by the local Herring Gulls and were with few exceptions recorded by direct observation. In *Mergus merganser* some of the c. 10 females breeding on Mickelskären have been able to prevent the gulls to catch young, but the majority of the broods becomes destroyed by gulls. Similar predation by single pairs of Herring Gulls was recorded in the small bird sanctuary Brändö Grönfladan 5 km NE of Mickelskären in the 1970s.

In 1982, the number of single pairs breeding within or very close to small colonies of smaller larids in the ares SW of Helsinki had increased from less than 10 to about 20. In many colonies these pairs took all the eggs or young. Other single pairs had settled on wooded islets with summer cottages. The islet Norra Linlandet which had been a single-pair locality since 1973, had been invaded by 6 pairs, which ate all the eggs and young of the Common Gulls and terns.

In the 1930s small colonies of Arctic and Common Terns and Common Gulls bred regularly on 27 islets in the outermost archipelago SW of Helsinki. By 1981 they had been replaced by colonies of Herring Gulls on 23 of these islets. *Charadrius hiaticula* had disappeared completely (earlier 3—6 pairs), *Arenaria interpres* had declined from 20 to 10 pairs (but in the inner archipelago it is now more abundant than earlier). The colonies of the Caspian Tern have been destroyed by the Herring Gulls (cf. Staav 1979). The few remaining Lesser Blackbacks were in several cases observed to shift repeatedly to new islets when the Herring Gulls had invaded their old localities. The species is now endangered in the Helsinki archipelago (see p. 153). The only species that have been able to increase after the rapid growth of the Herring Gull population are *Cepphus grylle*, *Anser anser*, and the Eider. Now the Herring Gulls have begun to invade the gulleries and terneries in the middle and inner archipelago as well. Althoug shooting and egg pricking now has begun to depress their population in the Helsinki region, the damage done by them still is increasing.

The tendency of the Herring Gull colonies to spread all over islets (cf. p. 147) makes a fairly small Herring Gull population such as that breeding SW of Helsinki, more detrimental to smaller shore birds than larger populations forming huge colonies on bigger land units, on dunes or marshes, e.g. on Hall-

lands Väderö in S Sweden (Andersson 1968 b), in the New Jersey area (Erwing et al. 1981) or in Holland (Tinbergen 1953, Spaans 1971) and W Germany (Goethe 1937, 1956). A group of 5—10 pairs of Herring Gulls settling on a small islet is generally sufficient to prevent several other species from breeding there. Herring Gulls now settle in or near a wide variety of localities providing food: rocky shores of wooded islands with summer cottages, rooftops in towns, the vicinity of colonies of Common and Arctic Terns, (cf. also Hatch 1970) and near Helsinki in the vicinity or on the islets inhabited by four large colonies (1000—3000 pairs) of Black-headed Gulls *Larus ridibundus*. The number of single Herring Gull pairs using larid colonies as their main food habitat SW of Helsinki was in 1982 c. 30, four of which bred in the Black-headed Gull colonies and three on nearby islets. Herring Gulls breeding in colonies in the outer archipelago fairly often specialize on chicks of Black-headed Gulls in the innermost archipelago: In the Herring Gull colony (c. 150 pairs) on Stenskär c. 12 km SW of Helsinki, remains of many Black-headed Gull chicks ringed in a colony 10 km away were found around some nests (M. Kilpi pers. comm.). Non-breeding Herring Gulls (or at least individuals without chicks) stay in flocks in the vicinity of Black-headed Gull colonies, waiting to steal eggs and chicks. Some Herring Gulls have specialized on chicks of single pairs of Common Gulls in the inner and middle archipelago and catch them by flying along the water behind the cover of stones and bushes.

Predation on duck broods by Herring Gulls had already increased in the 1960s, and is now even more pronounced. Despite this the numbers om all the breeding duck species in the area SW of Helsinki was higher around 1980 than in the 1930s (Kilpi 1980, own records in 1981). The main reason is probably the almost complete discontinuance of waterfowl shooting around Helsinki in spring. Waterfowl may also spread into the Helsinki archipelago from other parts of the S coast where the Herring Gull is not yet very numerous and the fowling is of minor importance.

Why are the single pairs always adults?

Burger & Lesser (1960) discuss this question on the basis of observations on the coast of Maine. I should like to add the following points of view based on the feeding behaviour of such pairs. The new pairs replacing the single pairs shot on the islets of Mickelskären (see p. 150) evidently knew of the advantages of these localities from foregoing seasons. They probably also had bad experiences of breeding elsewhere; almost all the Herring Gull eggs on adjacent islets had been pricked in the foregoing three seasons. Young individuals lack such experience. They have not bred yet, and mostly visit the best feeding localities together with other Herring Gulls. When sexually mature, they try to join their natal colonies, or colonies on nearby islets, or they begin to breed on their former roosts, or they may join colonies in other areas. They settle in their territories much later than adult pairs and thus are less likely to find suitable unoccupied islets. The breeding succes (see p. 149) is better than in (undisturbed) colonies, and the single pairs thus tend to breed their whole life in the same locality, defending the islet as feeding range. The following record also illustrates the role payed by earlier experience in the choice of breeding locality. In early April 1981 an adult pair settled in the middle of an islet (Hamnarn 0.3 ha, at Hamnkopplon 13 km SW of Helsinki), occupied in the foregoing seasons by a colony of Black-headed Gulls and some Common Terns. The islet was still almost completely covered with snow and ice, and no Black-headed Gulls or terns had yet arrived. In earlier seasons Herring Gulls visited the islet to catch chicks.

3. The Scandinavian Lesser Black-backed Gull Larus f. fuscus

3.1 Population dynamics

The population in the past, the present and the future

By the middle of the 19th century the Lesser Blackback was already fairly numerous in most parts of the coasts of Finland and Sweden. As nowadays, it seems to have bred in both colonies and single pairs (v. Wright & Palmén 1873). The Lesser Blackback must have increased and begun to breed in colonies long ago, as soon as the fishery provided food for the gulls during the breeding season. The dependence of the Lesser Blackback colonies on the local fishery is well documented in several archipelago areas in the 20th century: the largest colonies are situated in areas with an intense local fishery, and cessation of fishery causes a decrease in the population (see later). The reason why the Lesser Blackback increased when the local fishery provided food, though the Herring Gull did not, is evidently the following. The Scandinavian Lesser Blackback breeds in a restricted area in N Europe, but spends the winter in a large, partly tropical region, where even a large relative increase in the small Baltic population does not affect the living conditions for the species. Thus lack of food in the winter range did not limit increase of the Lesser Blackbacks as did in the Herring Gulls wintering mainly in the North Sea region.

In the 1950s the Lesser Blackback was still the most characteristic gull in all the outer and middle archipelagoes of Finland. Now in most of S and SW Finland it has lost this status to the Herring Gulls. During the 20th century the Lesser Blackback increased most markedly in the period 1935—1960. The main reasons were cessation of egg collecting and creation of bird sanctuaries. Now it has begun to decrease in some areas. A slight increase occurs still only in the easternmost part ot the Gulf of Finland and the northern half of the Gulf of Bothnia (Kilpi et al. 1980, Väisänen & Järvinen 1977, Grenmyr & Sundin 1981; off Oravais 50 km N of Vasa, C.G. Taxell pers.

comm. 1982), partly due to the fact that egg collecting depressed the population there longer than elsewhere.

In 1960 the number of Lesser Blackbacks breeding on the S coast of Finland was estimated at 1800 pairs and in 1980 at 1400 (Kilpi et al. 1980). The number of pairs breeding in the area SW of Helsinki were: 1935 250, 1960 c. 450, 1965 c. 380, 1980 80-100 and in 1982 c. 50 pairs.

Sociability and breeding range

Richter (1938) stresses that the Lesser Blackback is somewhat less social than the Herring Gull and the fact that several single pairs fairly often breed near each other in the Finnish archipelago also seems to indicate such a difference in sociability. However, in colonies of equal size the territories of the Lesser Blackback and the Herring Gull do not differ in size in Finland. In the rather small Herring Gull colonies studied by Burger & Lesser (1980) on the coast of New Jersey, the density of the nests was just as low as in Finnish Lesser Blackback colonies of the same size. Only the largest Herring Gull colonies in the Finnish archipelago have a higher nest density than the Lesser Blackback colonies.

The difference in sociability thus does not appear in territory size, but in some difference in the tendency to maintain a single-breeding system even in population mainly feeding outside the territory and feeding range. The Scandinavian Lesser Blackback shows less pronounced avoidance of grassy and bushy vegatation and of open pine woods and a somewhat greater tendency to breed in single pairs. The Scandinavian Lesser Blackback occurs mainly in a geographical region where lakes, shores and archipelagoes provide only scattered food, not allowing any large population breeding in considerable colonies, and where the open localities suitable as breeding sites are mostly covered with much more vegetation than the corresponding coastal localities preferred by the Herring Gull in the main part of its range. In the Baltic archipelagoes the feeding habits (see below) also contribute to the disperse the Lesser Blackbacks in single pairs and depress the colony size.

On Gaddarna (W islet) the shortest distance to the neighbouring nest in a colony of 25 pairs of the Lesser Blackback in 1935 was 6—12 m (mean 8.7 m), for a colony of 14 pairs (Aspskär 80 km E of Helsinki, Koskimies 1952) these figures were c. 6—40 m (mean c. 22 m) and for colonies off Mariehamn (SW Åland, Nordberg 1950) roughly 6—12 (mean c. 10 m, colony size 50 pairs) and c. 3—20 m (mean c. 13 m, 42 pairs). These and the records from the Herring Gull localities studied by Burger & Lesser, are from islets or localities where the vegetation mostly is sufficient to screen the mest sites from each other.

Reasons for recent population changes

As early as 1940s Paludan (1951) observed that the increase of the Herring Gulls on the islet Graesholm near Bornholm (S Baltic) depressed the number of Lesser Backbacks. In Finland the decrease of the Lesser Blackbacks on the S coast (roughly between Borgå and Hangö) is caused mainly by the dense Herring Gull population of this area (cf. p. 146). In the Archipelago Sea a radical decrease has been recorded off Mariehamn. In an area inhabited by at least 100 pairs in the 1940s (Nordberg 1950) bred evidently no Lesser Blacks in 1981 (J. Harberg pers. comm.). The Herring Gull began to increase there as early as in the 1930s. In the NE part of the archipelago Sea some decrease has also been recorded in the 1970s (L. v. Haartman pers. comm. 1981). In most other parts of the Archipelago Sea the Lesser Blackback is now more numerous than in the 1930s and 1940s (own records, Grenquist 1942, Lemmetyinen 1980, Stjernberg 1982 b), and about as numerous as in the 1950s. However, where no fishery occurs and little refuse is available the species has decreased or locally completely disappeared.

In the extensive archipelago off Stockholm the population seems more or less unchanged, except in its ourtermost parts where cessation of the intensive herring fishery after the World War II has caused a pronounced decrease (Andersson & Staav 1980). The decrease on Valsörarna had begun before the first Herring Gull colony settled there (Hildén et al. 1978), and was evidently also due to the reduction of the herring fishery. The strong depopulation of the outer archipelago and the subsequent drop in the fishery, especielly that of herring, has probably contributed to the decrease in Gulf of Finland as well.

In the mid-1970s the Gullkrona area of the Archipelago Sea contained c. 1000 pairs of Lesser Blackbacks and c. 3000 pairs of Herring Gulls (Stjernberg 1982 b), and in the archipelagoes where the Lesser Blackbacks are still fairly numerous their number is at least one third of that of the Herring Gulls. But in the Helsinki archipelago the Lesser Blackbacks began to decrease rapidly around 1970 and this proportion has changed from about 1:4 (around 1963) to 1:100 ! Naturally several other factors than the numerical proportion between the two species also determine when the Lesser Blackback can no longer resist the pressure from the Herring Gull, but the proportion gives a general idea of the situation.

The Helsinki area is saturated with Herring Gulls. However, in most parts of the Archipelago Sea, in the main part of the Stockholm archipelago, and on all the coasts of the Gulf of Bothnia there is evidently still much food and many islets that could be exploited by Herring Gulls, but are still at least partly utilized by Lesser Blackbacks. The slower increase of the Herring Gull in the Gulf of Bothnia is probably due to the long distance from its main range; in the wide archipelago between Turku (Åbo) and Stockholm the reason may be the long distance (50—100 km) from the preferred old breeding localities in the outermost archipelago to the feeding localities on the mainland and the largest islands. This has enabled the Lesser Blackback to resist the pressure of the Herring Gulls in these areas better than off Helsinki and Mariehamn, where the short distance between the outer archipelago and the nearest dumps (< 30 km) promoted rapid increase of the Herring Gulls.

When the Herring Gulls increase so much that they begin to move from the dumps to feeding localities used by the Lesser Blackbacks the situation becomes very difficult for the latter. The Lesser Blackbacks begin to specialize on various scattered sources of food: fish and other refuse at summer cottages, in villages and towns, and ducklings in the archipelago (for specialization on ducklings, see litterature in Hildén 1964). When Herring Gull increases still more and begins to use the same food sources the situation becomes impossible for the Lesser Blackback, which is weaker than the Herring Gull. This is now the case around Helsinki, and the situation is also serious off Mariehamn. An additional complicating factor is the competition for suitable breeding localities. This is stronger in narrow archipelagoes with a smaller number of islets than in, for example, the Archipelago Sea and the Stockholm archipelago.

In some lakes of S Finland also, Herring Gulls have taken over the feeding and colony localities of the Lesser Blackbacks (P. Linkola pers. comm.). If the increase of the Herring Gull is permitted to continue, the Lesser Blackbacks will be in danger of exinction in large areas within a few decades, first on the S coast, then in the Archipelago Sea, later probably also on the W coast and perhaps even in the lakes of Finland.

Size and stability of colonies

The following observations and conclusions on the size and location of colonies and on the proportion of single pairs are based mainly on my own records and the following published studies: Nordberg 1932, 1950, Taxell 1934, Ahlqvist & Fabricius 1938, Grenquist 1938, 1942, Bergman 1939, 1965, v. Haartman 1945, 1948, Paavolainen 1957, Risberg et al. 1976, Väisänen & Järvinen 1977, Kilpi et al. 1980, Lemmetyinen 1980, Andersson & Staav 1980, Grenmyr & Sundin 1981.

The colonies of the Lesser Blackback in the Baltic archipelagoes must be considered small. As far as I know no colony in any typical archipelago in the Baltic has ever consisted of more than 120 pairs. In the 1930s the largest colonies in most areas on the Finnish coast consisted of only 20—40 pairs, but around 1960 the largest ones in several areas on the S and W coast reached the size of 60 — c. 110 pairs. The reason for the small colony size is dealt with on p. 156.

During the marked increase of the Lesser Blackback in c. 1936—1960 the new colonies formed in the areas SW of Helsinki were located only in the outermost archipelago, and only on islets earlier inhabited by single pairs. All six single-pair localities in the outermost archipelago changed into colonies. In the inner and middle archipelago the single-pair localities remained unchanged until the population began to decrease and until almost all the remaining Lesser Blackbacks were driven from the outermost islets by the Herring Gulls in the 1970s. The location of the new colonies in the outermost archipelago was probably due to the fact that the single-pair islets in the outer archipelago are larger (mean 1.3 ha) than in the middle and inner parts. Is is not so easy for single pairs to prevent conspecifics from settling on larger islets.

Is there perhaps also a "psycholgical advantage" in breeding off the coast? In the outermost archipelago the gulls have a free view of the foraging localities used by the colony members within a sector of c. 180°. For man the impression of such a free view is striking: the islets along the coast seem less far away than they are, and more easily attainable. In such a locality the gulls are able to follow the departure and return of their conspecifics and other larids on various foraging tours, which is also an advantage.

The location of undisturbed colonies is very stable. In the area SW of Helsinki I was told by old fishermen and ship pilots that at least 6 of the 10 islets inhabited in 1935 by colonies of at least 5 pairs (Gaddarna, Espskärskubb, Rönnbuskskubb, Enbusken, Lergrund and Salgrund) had been occupied by colonies of Lesser Blackbacks as far back as in the 1870s. In most areas egg collecting influenced both the size and the location of the colonies. The records from several bird sanctuaries (eg. Aspskären, Söderskären, islets off Mariehamn, and Valsörarna) show that the Lesser Blackbacks gather on protected islets. No egg collecting occurred in the outer archipelago SW of Helsinki in the late 1920s, in the 1930s or after 1955 and in 1959 the colony on Enbusken reached the size of 110 pairs, being the largest colony in S Finland in those times.

Väisänen & Järvinen (1977) discuss the effect of protected areas on different categories of archipelago birds. Chiefly larids concentrated on the protected Krunnit islands in the northernmost Gulf of Bothnia, and this depressed the species diversity of the bird fauna. The Krunnit islands are mostly larger and contain a greater number of habitat types than the small islets off Helsinki, so that a great number of species may breed on the same islet. The archipelago around Helsinki could be called a "Herring Gull and Black-headed Gull archipelago" as these two species tend to prevent most other species from breeding on the islets. In such a region as the Helsinki archipelago the effect of protecting islands tends to be even more drastic than in the Krunnit area, causing very low species diversity values.

Breeding success

Before the increase of the Herring Gull the breeding success of the Lesser Blackback was obviously mostly between one and two fledged

young per pair in undisturbed localities. Now it has dropped to a very low level in large areas of the S coast on Finland. In the Helsinki region is after 1980 has been almost zero. The low young production in the Helsinki archipelago shows clearly that the Lesser Blackback population cannot survive in areas where there is strong pressure from the Herring Gull population in both breeding and foraging localities.

In 1936 and 1937 I counted the fledged or almost fledged young swimming around the colonies on Gaddarna (W islet, 31 and 40 pairs) and Enbusken (72 and 57 pairs) in the last week of July when most of the young have fledged. The number exceeded the number of pairs (nests counted in June) by c. 50 %. My records from other colonies and single pairs on the S coast in the 1930s, 1940s also indicate breeding success of almost that order. In 1964 and 1965 14 pairs on Långgrund produced as much as 2.2 and 2 fledglings per pair, respectively, but the number of Herring Gull pairs was still as low as two. Nowadays in the area around Helsinki, hardly any Lesser Blackback young fledge on the islets occupied mainly by Herring Gulls, and on the few islets occupied mainly by Lesser Blackbacks the breeding success is only 0—0.2 fedgling per pair (Hario 1981, own records SW of Helsinki). Herring Gulls, Great Blackbacks and minks prey on the chicks, and man's recreational activities also contribute to the low breeding success (effect of disturbances in gulleries: cf. especially Gillet et al. 1975, Robert 1975, Davis & Dunn 1976, Hand 1980).

3.2 The single pairs

Proportion and location

The proportion of Lesser Blackback islets inhabited by single pairs is generally much higher than the corresponding proportion in the Herring Gull. In most parts of the archipelago of S and SW Finland c. 50 % of the breeding islets of the Lesser Blackback are inhabited by single pairs and the proportion of the population breeding in single pairs is about 6 %. Records from both sides of the N half of the Gulf of Bothnia show, however, that the proportion of single pairs is lower in areas where the islets are few and rather large. In the 1930s and 1940s the proportion of single pairs was almost the same in the W half of the Gulf of Finland, where no egg collecting occurred, and in the Archipelago Sea, where egg collecting continued to the 1940s. It therefore seems unlikely that disturbance at the breeding localities greatly increases the proportion of single pairs. However, the eggs of single pairs are hardly ever collected, which may increase the fidelity of such pairs to the breeding islets. In archipelagoes with clear-cut outer, middle and inner zones most single pairs settle in the middle and inner archipelago. Some settle on the outermost islands, but few in the archipelago directly bordering the mainland (cf. v. Haartman 1945). This is due mainly to the frequency of suitable localities in the different zones. In the outermost archipelago small islets with sufficient vegetation occur sparsely and the larger islets are occupied by colonies. In the innermost archipelago there is too much vegetatioin on the smallest islands, and more disturbance by man and predatory mammals than in the outer zones. The occurrence of food also determines the distribution of single pairs (cf. below).

Feeding range defence

Some single pairs vigorously defend a feeding range around their breeding islet, others merely prevent other single pairs from settling there. In 1933—1939 there were 9—14 single pairs breeding in the area SW of Helsinki. A two-pair group on the smallst of the islets Gaddarna may be considered an epicentrum (Burger & Shisler 1980) to the colony (12 pairs) on the nearby islet.

The single pair on Långgrund vigorously defended its breeding islet (a double islet of c. 1 + 1.5 ha, records in May-June 1943) against conspecifics, but a pair breeding in 1939—1940 on a minute rock (c. 150 m^2 S of the large woodes island Pentala) ignored conspecifics as long as they did not try to alight on the islet. The pair foraged regularly at fishermen's houses 1—3 km from the breeding islet. Two single pairs on the islets N of Kytö in the 1930s, also mostly ignored conspecifics flying nearby. A single pair bred on Mickelskären in 1978—1981. Until the single Herring Gull pair on the same islet stole its eggs or chicks it defended, though not regularly, a feeding range within a radius of c. 200 m but was unable to prevent the Herring Gull to use the same feeding range. The observations on these single pairs indicate that pairs mainly feeding outside the breeding locality do nôt react strongly to conspecifics as long as they do not alight on the islet, but pairs feeding mainly on or around their breeding islets defend this feeding range. When most of the Lesser Blackbacks were forced to desert the colony islets in the outer archipelago by Herring Gulls in the 1960s, the number of Lesser Blackbacks on the islet by Pentala increased to 4 pairs, but in 1981 the islet was taken over by the Herring Gulls.

3.3 Feeding habits

Effect of the long and narrow wings

As especially Goethe (1975) points out, the Lesser Blackback has proportionally longer primaries (higher wing index) and narrower and more pointed wings than the Herring Gull, which makes it better adapted to catch fish and other food on or just below the water surface. However, I like to stress that this type of wings greatly restricts the ability of the Lesser Blackback to feed in flocks or togerher with other gulls flocking at food. The

Lesser Blackback almost totally avoids flapping and soaring in dense flocks that are taking food at ground or water level. For the Herring Gull, and partly also for the Great Blackback, the Common Gull and the Black-headed Gull, this kind of feeding is a condition of the population increase in Finland. The fact that the Lesser Blackback does not normally join such flocks shows that it is unable to compete with other gulls under such circumstances. The size of the different species does not influence this feeding in flocks, Herring Gulls gather at the same food. As long as there is plenty of food easy to swallow immediately every individual tries to eat as much as possible and they do not display much aggressiveness towards each other.

The refuse dumps in the Helsinki region were not visited at all by Lesser Blackbacks in the 1930s, 1940s or 1950s, although the population in the area SW of Helsinki increased during that time (cf. p. 152). After the enormous increase of the Herring Gulls after the 1960s, food became scarce for the Lesser Blackbacks as well, and this now causes Lesser Blackbacks to visit dumps in the Helsinki region. On the westernmost dump the highest number of Lesser Blackbacks seen during 10 counts in June 1981 was 4, while the highest number of Herring Gulls was c. 430, which means that the few Lesser Blackbacks of the Helsinki area now frequent this dump almost as regularly as the Herring Gulls do. However, the highest number of Herring Gulls seen at a dump near Helsinki during breeding time in 1981 was roughly 3000 and the maximum number of Lesser Blackbacks was only 9 (Vickholm 1982). On SW Åland many of the c. 100 pairs pf Lesser Blackbacks breeding in the 1930s off the small town Mariehamn foraged regularly at a small dump on the "mainland" shore and in and around the town (Nordberg 1950). Nowadays the Lesser Blackbacks on the Bothnian coast of Sweden still forage on dumps in towns and villages (Andersson & Staav 1980). Thus lack of fish refuse may force the Lesser Blackbacks to feed on dumps, especially in areas where there are few or no competing Herring Gulls and the dumps are situated by harbours and on or near shores.

Verbeek (1977) found that 95 % of the rather numerous Lesser Blackbacks *L. fuscus graellsii* frequenting a dump on Walsney Island were stealing food from the Herring Gulls, not taking it directly from the dump. No regular stealing occurs at the dumps around Helsinki, but in the harbours of Helsinki some individuals regularly stole food from Herring Gulls and Black-headed Gulls in summer 1981. In 1982 these Lesser Blackbacks had disappeared. In a Caspian Tern colony in Sweden Lesser Blackbacks regularly took fish from adult Caspian Terns (Forssgren 1981). The wing anatomy apparently fits the Lesser Blackback for kleptoparasitism.

Plunge-diving

The ability of the Lesser Blackback to catch food by diving in a tern-like manner — see my sketch from a film in the paper by Goethe (1975) — is important when the gulls are fishing by hoop nets and when they try to take fish refuse that is just sinking or lying on the bottom in shallow water (depth < c.80 cm). However, diving for living free-swimming fish occurs very seldom in the Lesser Blackbacks at least in the Finnish archipelago. I have noted less than 10 such cases during 50 years of observation and none after the filmed performance (10.6. 1954). The fact that bones of *Rutilus rutilus* and *Perca fluviatilis* predominated in the pellets of the Lesser Blackback in Tvärminne (Goethe 1975) is not proof that they dived for living fish. These species are the main catch of the numerous summer visitors who leave the fish refuse on the shores for the gulls.

Attitude to man

At least nowadays in Finland most Lesser Blackbacks take flight at greater distances from man than most Herring Gulls. This gives the latter species an advantage over the Lesser Blackback at the breeding islets and in localities where both species would be able to forage, but there is frequent disturbance by man. This is the case at all kinds of fishing localities and may also be a reason for the scarcity of Lesser Blackbacks at dumps. In the area SW of Helsinki many Herring Gulls may alight on their nests and even feed their young while boating tourists lie in the sun only 15—20 m away, but all Lesser Blackbacks stay swimming off the shore as long as there are people ashore on the breeding islet. Off Helsinki the Lesser Blackback starts egg laying in mid-May, the Herring Gulls around 20 April. In April and May there are only a few people boating in the archipelago, in June there are a lot of boats every weekend and in July the outermost islets are visited all the time (if not belong to bird sanctuaries). Therefore the Lesser Blackback suffers more from this disturbance than the Herring Gull.

The difference in the escape distance is probably a consequence of the difference in wing anatomy, but may also be partly due to the different winter ranges. Many Herring Gulls forage all winter in the vicinity of man and his equipment. In their large partly tropical winter range the Scandinavian Lesser Blackbacked Gulls are less dependent on man. Moreover, most Lesser Blackbacks leave the breeding range as early as August-September, whereas the Finnish Herring Gulls mostly remain till September-October. Thus, unlike many young Herring Gulls, no young Lesser Blackbacks have the opportunity to become accustomed to man at feeding places in autumn.

However, in the 1970s there have been some signs of increasing conditioning to man in the Lesser Blackback in the vicinity of Helsinki. C. 10 pairs bred on a small islet, formerly used exclusively as a roost, only c. 1 km from the "South Harbour" of the town, and groups of pairs have attempted to breed on two other islets near the town. But in the area SW of Helsinki four single pairs that had settled on shores with summer cottages in May 1981 disappeared without laying eggs when the people began to visit their cottages and the gulls did not return in 1982. Single individuals and pairs that have evidently lost their offspring have begun to stay for several hours within sight of localities where they obtain food. Though commonly observed in the Herring Gull already during World War II such waiting for food was not seen earlier in the Lesser Blackback, except near fishermen's houses and equipment. In

June-July 1981 a pair of Lesser Blackbacks daily spent much time at the bus station in Helsinki, waiting mainly for empty ice cream cornets; another pair sat at lamp posts on a bridge W of Drumsö waiting for small fish rejected by angling children. In May 1982 a pair lived on the refuse from a restaurant in a park in Helsinki. In June—July 1981 and 1982, highway No. 51 SW of the town was patrolled, mainly early in the morning, by some Lesser Blackbacks looking for birds and mammals killed by the traffic, which they mostly could take over from the Hooded Crows *(Corvus corone cornix)* (8 records). The Lesser Blackback is thus able to develop new feeding habits, but only a small proportion of the population at the S coast of Finland has done so. The new feeding behaviour can do little to improve the serious situation of the species in the area SW of Helsinki, where the Herring Gulls develop similar feeding habits, occupy all the suitable breeding localities, catch chicks of the Lesser Blackbacks and depress their breeding success to near zero, and where the Lesser Blackbacks also suffer greatly from competition from other gulls able to feed in dense flocks.

Feeding habits and colony size

As the Lesser Blackbacks avoid feeding together in large flocks, the number of pairs utilizing a locality with plenty of food mostly remains small. There are rather few such localities on the Finnish coast and at least nowadays most of them are frequented by other gulls as well, which further restricts the number of Lesser Blackbacks that can use them. However, localities providing small amounts of fish refuse were earlier numerous. Dispersal of the feeding localities and the inability of the Lesser Blackback to make efficient use of localities with plentiful food lead to breeding in small colonies and in single pairs.

The presence of a larger number — sometimes as many as c. 150 — Lesser Blackbacks on or around a feeding locality mostly indicates that colonies have been destroyed, in the Helsinki area by Herring Gulls, elsewhere by egg collecting, which drives the gulls from the breeding islets. In such situations Lesser Backbacks may gather in flocks for days of weeks near localities providing enough food. Thus in the 1920s and the 1930s egg collecting in the E half of the Gulf of Finland yearly caused more than 150 Lesser Blackback adults to gather in June and July around the fishing villages on the island of Hogland (Suursaari), situated 50 km S of Kotka and now belonging to the USSR (H. Ahlqvist pers. comm. 1982).

In the 1930s, 1940s and 1950s the greatest number of Lesser Blackbacks sen following ships between Helsinki or Turku and Stockholm was of the order of 150 individuals. A few followed the ship from harbour to harbour. Most gulls came from colonies along the route and left the ship as soon as waste was thrown overboard. They usually took the food by swimming among the floating waste. As long as waste was thrown overboard in the archipelago, the ships evidently affected the size and location of the Lesser Blackback colonies more strongly than the food supplies in the harbours of the coastal towns.

How can the Lesser Black-backed Gull and the Herring Gull increase side by side in England?

Although there is a huge population of Herring Gulls at the British coast, the Lesser Blackback (there *L. fuscus graellsii)* has begun to increase at many British localities after about 1960 (Harris 1970). The feeding habits of the two species do not overlap there as much as they do in Finland. On the British coast the Lesser Blackbacks are able to take much of their food at sea, while the Herring Gulls feed mainly on the tidal shores, on dumps and in other localities with man-made food sources. In Finland the production of the brackish sea is limited and obtained by the great gulls mainly through the agency of man, predation on other birds or kleptoparasitism. Only a sparse population of gulls can survive without man-produced food. In Finland every increase of the stronger Herring Gull — even when partly permitted by exploitation of sources not used by the Lesser Blackback — leads to increasing competition for the Finnish gull populations. More important still, the British gulleries are mostly situated on rather large islands, on which each species is able to enlarge its area without interfering much with the other species. In Finland, where the two breed on the same small islets, the stronger Herring Gull interferes seriously with the weaker species especially in areas where food is scarce. It forces the Lesser Blackback to settle on other mostly less suitable islets, where other factors depress the production of young.

Barth's (1966, 1975) analysis of the colour and size variation in Herring Gulls and Lesser Blackbacks seems to indicate a greater anatomical similarity in British Lesser Blackbacks and Herring Gulls than in Scandinavian Lesser Blackbacks and Herring Gulls. This should also be considered among the possible reasons why the Blackbacks are better able to hold their own against Herring Gulls in Britain.

4. The Great Black-backed Gull Larus marinus

4.1. Population dynamics

Increase and expansion into the inner archipelago

On the S coast of Finland the population has increased since the mid-1930s from c. 50 to about 400 pairs (Bergman 1965, Kilpi et al. 1980). In the area SW of Helsinki the corresponding figures are 5—8 and c. 80 pairs. There and between Tvärminne and Jussarö (Ahlqvist & Fabricius 1938), in the W part of Gulf of Finland, signs of increase were recorded as early as1934—1939. In the Archipelago Sea (incl. Åland) hardly any growth occurred before the mid-1950s. Now the increase is of the same proportion as on the S coast (own records, Stjernberg 1982 b, Grenquist 1965, Lemmetyinen 1980). In some places on the W coast the population, though still sparse, consists of at least five times as many pairs as 30—50 years ago (Valsörarna: Taxell 1934 and Hildén et al. 1978, the Krunnit area: v. Haartman 1948 and Väisänen & Järvinen 1977).

Until the end of the 1950s the Great Blackback bred almost exclusively in the outermost archipelago. As shown in many studies in N and W Europe, the Great Blackback has a greater tendency than other gulls to breed in single pairs on minute barren rocky or boulder islets. According to my experience most breeding islets in Finland measure 0.02—0.5 ha. Today on the S coast and in the Archipelago Sea it also accepts small barren peninsulas on larger (sometimes even wooded) islands in the outer and middle archipelago, and minute barren islets in the middle and inner archipelago, though still mostly breeding in solitary pairs. Among Herring Gulls, it may also breed on the central parts of much larger islets (1—4 ha; first case in 1933 on Espskärskubb). The few pairs breeding on inland bogs in W Finland also seem to occur mostly with Herring Gulls (records: see v. Haartman et al. 1963—1976).

At most places on the S coast the dispersal into the inner archipelago has proceeded in the follwing way. When the population has increased for 10—20 years all the suitable small islets and peninsulas in the outer archipelago become occupied by (mostly) single pairs, and new pairs begin to settle in corresponding localities in the middle and inner archipelago. Simultaneously the proportion of 2-pair localities increases (see p. 160). In the Archipelago Sea other factors also contribute to the move into the inner archipelago. The Eider also penetrated large areas of the inner archipelago, and its ducklings provide food for the Great Blackbacks in June—July. Less fish refuse is available in the outer archipelago today than 30 years ago and trawling for herring ceases in June and July, when the gulls need more food than at other times in the breeding season (cf. also Blomqvist & Tenovuo 1980). The Herring Gulls have increased, especially in the inner parts of the Archipelago Sea, and use food at the dumps and harbours. The Great Blackbacks may use the same food, or prey on young of Herring Gulls. The boating tourists and the summer cottages are numerous there and provide some waste even for large gulls. Thus, the Great Blackbacks find more favourable conditions closer to the coast in this area. On the S coast also the distance to the main feeding localities of pairs forced to feed elsewhere than around the breeding islets may, in areas with wide archipelagoes, contribute to movement into the inner archipelago.

The increase and the expansion of the Great Blackbacks was followed around Mickelskären SW of Helsinki. Fig. 4 shows the changes occurring since 1937. Although a part of the population now breeds in colonies and pairs also settle in colonies of Herring Gulls on larger skerries, the preference for breeding alone on minute islets is still evident.

As in the Herring Gull, the Lesser Black-backed Gull and the Common and Arctic Tern, the pairs that breed singly (on islets without other larids) tend to avoid the larger islets used by pars forming colonies or breeding as single pairs in colonies of other larids. The choice by solitary pairs of a territory separated from larger land units and easy to defend is a widespread phenomenon in mainly social larid species. Living together with a large number of conspecifics or other larids reduces the individual requirement on defence and location of the territory. In the Great Blackback the preference for small land units may earlier have been strengthened by experience as well. People collecting eggs visited colony islets more regularly than small marine islets with hardly any waterfowl and only one gull nest.

Reasons for increase

According to Kilpi et al. (1980), the increase of the Great Blackback may be due to the at least 3-fold increase of the Eider population in the Baltic archipelago after the World War II. However, the increase of the Great Blackback clearly began before the increase of the Eider. Moreover, in the 1950s it was most obvious in the area SW of Helsinki, where the Eider population in the former Russian marine base Porkala had dropped below the level in 1943 (Bergman 1957). I suggest the following reasons for the increase of the Great Blackback: as in the case of the Herring Gull, the

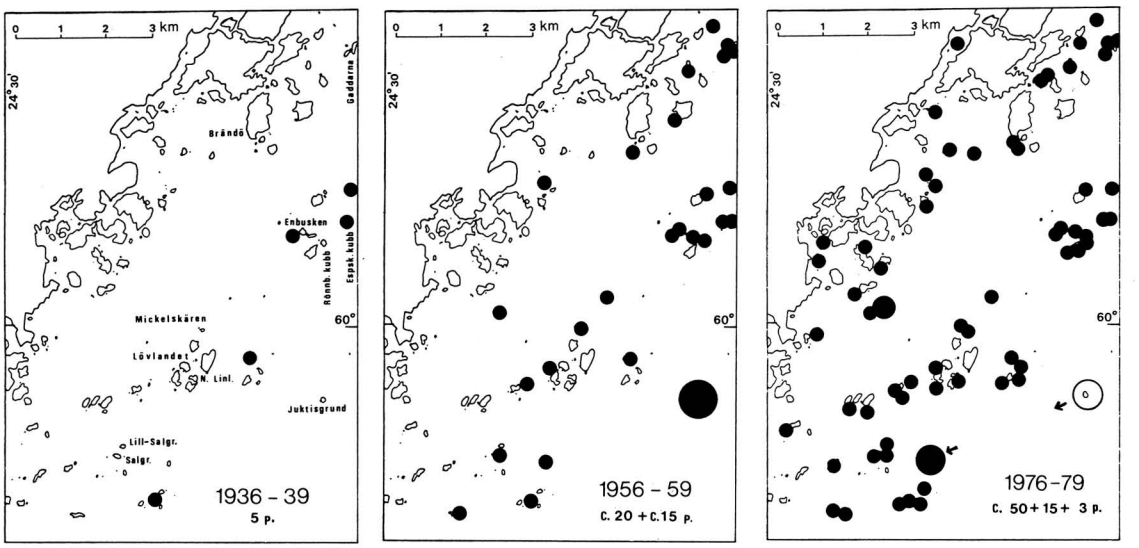

Fig. 4. The breeding localities of the Great Black-backed Gull *Larus marinus* in the late 1930s, late 1950s and late 1970s in an area c. 30 km SW of Helsinki. Small dots: a pair breeding during at least one of the seasons mentioned on the figure. The larger dots indicate colonies and the arrows shift of the colony to a new locality.

food supplies in the wintering area improved, during the 1940s and 1950s the shooting of adult Great Blackbacks ceased almost completely in the outer archipelago (earlier heavily persecuted because considered harmful to the broods of diving ducks); breeding success was good because of the ability of the Great Blackback to obtain enough food for its young even during the periods when Eider and other ducklings are not available. As at least 70 % of the Finnish Great Blackbacks still breed in single pairs, the species escapes the disadvantage of intraspecific competition on the breeding islet, which also improves the breeding result.

According to the official game statistics, the number of Great Blackbacks shot annually in its main breeding range along the S coast (extending eastward almost to Kotka) in the period 1975—1980 varied between 579 and 416 (mainly adult birds). In 1981 no new territory was established on the islets belonging to the groups of Espskären and Mickelskären SW of Helsinki; in 1982 the number of single pairs there had dropped from 16 to 11 and the number of pairs forming two small colonies near Mickelskären had dropped from c. 14 to 9. Thus there now is some evidence of ceasing of the increase on the S coast. The reason may well be the shooting of adults.

Breeding success

The breeding success was studied around Mickelskären in 1975—1981 in 8—15 pairs. Most of them bred singly, but in 1979—1981 there were two double pairs. The 269 first-clutch eggs produced 215 fledged young. The number of fledglings per pair in six seasons averaged 2.4, but in 1980 oil pollution decreased the figure to 2.2. The repeat clutches did not increase these figures significantly because disturbances mostly lead to low success of such late broods. As far as I could see, the losses in the clutches laid at the normal time in early May, were, directly or indirectly caused by man (some clutches pricked, a few chicks killed by man, in 1980 also by oil at the waterline). The Great Blackback chicks showed no signs of starvation.

Two small colonies of Great Blackbacks also bred near Mickelskären (7—15 and 3 pairs, see Fig. 4) but most of their eggs were destroyed by man. If the colony breeders are included, the mean breeding success in the area just around Mickelskären drops to about 1. These results agree with my records made on several hundred almost fledged broods during boat trips in S and SW Finland after the mid-1930s. Because the Finnish Great Blackback population breeds mainly in single pairs the mean breeding result of the Finnish Blackbacks may be estimated at about 2 young per pair.

The very varying number of Eider ducklings (total death rate of hatched young around 20 June 20—95 %) does not influence the breeding result of the Great Blackbacks, at least around Mickelskären. In 1978—1982 roughly 600—700 pairs of Eider bred within the area of the maps in Fig. 4.

4.2 Feeding range and colony formation

Difference in sociability between the Great Black-backed Gull and the Herring Gull

In accordance with its more predatory life, the Great Blackback is less social than the Herring

Gull; at least 70 % of the Great Blackbacks breed in single pairs, as opposed to less than 1 % of the Herring Gulls, at least in S Finland. Even in regions where large amounts of fish refuse have enabled the Great Blackback to increase heavily and it has formed colonies (cf. e.g. Belopolskii 1957, Karpovich & Tatarinkova 1968, Haftorn 1971, Salomonsen 1979 a & b) many single pairs breed near the colonies. The difference between the Great Blackback and the Herring Gull in this respect is also evident in the area SW of Helsinki. When the Great Blackbacks had increased from 6—8 to c. 80 pairs, 60 of the pairs still bred on islets without neighbouring conspecifics, whereas only 5 of the c. 130 pairs of Herring Gulls in the same area in 1935 bred singly.

In Finland the first colonies of Great Blackbacks (15—25 pairs) were established in the 1950s on two adjacent small flat very low rocky islets (Trutlandet and Slätlandet) in the open sea off Jussarö (W Gulf of Finland). After 1960 the species established or tried to establish colonies (3—30 pairs) on at least five more islets in the W half of the Gulf of Finland, and some colonies in the Archipelago Sea including Åland. In the late 1970s what was the largest colony in the Archipelago Sea consisted of more than 40 pairs (Blomqvist & Tenovuo 1980). Destruction of colonies by man has influenced their growth and location.

The size, geomorphology and number of islets influence the location of the pairs in different ways in different parts of the Baltic archipelagoes. For instance, in W Estonia most islands are rather large and low and there are only a few suitable islets below 1 ha. Therefore most Great Blackbacks, at least in the 1960s, bred on larger islets than in Finland, but in single pairs, mostly together with other larids and well separated from each other. Only 16 of 87 pairs bred on really small islets (Aumees 1967, M. Kumari 1967).

Changes in foraging behaviour

In several areas the increase in the Great Blackback population was accompanied by a partial change from feeding around the breeding localities to feeding farther away. This agrees with the theoretical conditions for colony breeding (e.g. Lack 1968, Horn 1968, Krebs 1974), but the majority of the single pairs, at least in Finland, still obtain most of their food around the breeding localities. There is commonly strong competition with other pairs breeding in the vicinity and this forces some of the single pairs to undertake long foraging tours. The colony breeders studied fed mainly far from the breeding locality.

In 1934—1939 I visited the 5—8 breeding localities in the archipelago SW of Helsinki at least four times every season in May-early July. On all these occasions both parents were present. All these single pairs evidently obtained the main part of their food just around their breeding islets. Although the breeding pairs seldom left the vicinity of their islets in the 1930s, adult individuals made foraging tours to the inner archipelago of the area studied. They stayed for many hours near nets and in the harbours of Helsinki, sometimes spending the night on stones well off the shore near a hoop net. This indicates that they were mostly individuals that hat lost their offspring. In my study of 1939 I erroneously concluded that not all adult pairs breed every season. The most probable reason for the occurrence of nonbreeding adults in the 1930s SW of Helsinki was persecution by man, and occurrence of pairs consisting of one adult and one subadult bird,which fairly often left their islet (cf. p. 160). The persecution was still strong at that time especially around Porkala a few km SW of my study area. Foraging in the inner archipelago also occurred elsewhere (v. Haartman 1945). However, Karpovich & Tatarinkova (1968) have found that food shortage prevents breeding in gulls on the Kola peninsula. In that area great variations occurs in the amount of fish refuse, on which the large gulls have to live.

In June 1980 the feeding habits of the Great Blackbacks were studied around Mickelskären in eight single pairs, a two-pair group and a c. 10-pair colony. I made several records on every pair from Mickelskären almost daily and boat trips among their breeding islets every week. Five single pairs and one pair in the two-pair group evidently never undertook foraging tours out of sight of their breeding localities. In most cases they returned to the islet or a nearby watching site within 15 minutes, staying longer only when the feeding itself (e.g. handling of a large fish, or a feathered duckling or chick) took more time, or when they had detected a larger amount of food (see p. 160). In most cases the food was obtained within a radius of less than 1 km from the breeding islet, or by flying straight to some nearby Herring Gull or Gommon Gull colony to catch chicks. Two pairs visited almost daily such colonies travelling distances of 0.5—3 km. Two single pairs, one pair in the two pair group and all the pairs in the colony daily undertook much longer feeding trips, evidently foraging in the inner archipelago or around Helsinki, since they returned almost without exception after 1—5 hours, from the N or NE. In 1963—1981 I made occasional observations on the foraging of the colony when it bred SE of Mickelskären (Fig. 4). They chiefly foraged elsewhere than in the nearby outer archipelago, and evidently never visited Mickelskären to catch Eider ducklings or gull chicks.

Nowadays, both adult and juvenile Great Blackbacks are seen regularly on the refuse dumps near Helsinki. During the breeding season the number of adults there is mostly 0.2—0.5 % of that of the adult Herring Gulls (M. Kilpi pers. comm. 1981). This agrees well with the number of pairs of these species off Helsinki and the proportion of Great Blackbacks that undertakes longer foraging tours.

Intraspecific competition, colony formation and feeding

In most cases the small islets preferred by the Great Blackbacks lie in little groups, rather close to each other, often in the vicinity of a somewhat larger at least partly wooded island. The distances to the nests of other single pairs may therefore be less than 200 m. This is mostly the case when more than one pair settles on a larger islet with a colony of Herring Gulls, although the pairs are well separated from each other (examples: Enbusken, Gaddarna, Salgrund, islets N of Kytö). Neighbouring pairs compete for food in the vicinity of the breeding locality, and Herring Gulls somewhat reduce the amount of food available, though most of these forage far from their colonies. Most single pairs defend a feeding range around the breeding islet. Weaker or new pairs of Great Blackbacks may be forced to forage at least partly elsewhere. My records around Mickelskären (see below) show that several of the single breeders feeded far from the breeding locality. When the population has increased so much, that all the most attractive single-pair localities are occupied,

pairs try to settle on islets already inhabited by another pair. When they succeed, this is the first stage of colony formation. Single pairs may more easily accept newcomers that do not compete with them for food. Back in 1918, Berg concluded that the formation of the first colony in the Baltic area, on Lilla Karlsö W of Gotland, was caused by the lack of suitable small islets in an area where the food supply allowed a considerable increase of the population. The reason for the first colonies in Finland, off Jussarö, was evidently the same. An additional factor there was the sociability released by a colony of about 20 pairs of Herring Gulls.

In the area around Mickelskären during the seasons 1963—1980, altogether 17 new territories (roughly one per season) were occupied, the size variation of the mostly disturbed colony SE and S of Mickelskären not considered. Eleven of these new territories belonged to single pairs. Two pairs settled on islets already occupied by another pair. On one of these two islets a third pair settled, the other harboured two pairs during four consecutive seasons. In five of the single pairs on the new territories, one of the birds still had much of its subadult plumage, but there were no pairs consisting of one clearly subadult non-breeding bird and a mature bird occupying a territory. Earlier in the area SW of Helsinki, new pairs rather regularly settled in territories 1—2 years before their first real breeding (for examples: see Bergman 1939, 1956). Nowadays the increased competition for breeding islets makes it impossible for immature birds to occupy and defend territories and the young and subadult Great Blackbacks stay around the common feeding grounds. This increases the attachment of the species to feeding localities far from the breeding localities and thus makes it easier for new individuals to settle on islets already occupied by single pairs.

In 1968 a pair settled on an islet (0.2 ha) in Mickelskären 500 m from an islet occupied by another pair since 1958. In 5 of 8 observed cases the older pair stole an Eider duckling caught by the newcomers and the newcomers were repeatedly attacked by the old birds in Mickelskären when they treid to catch Eider ducklings. — No really social attacks (Munro & Bédard 1977) of any gulls on Eider broods have been observed in this area.

On 10 July 1981 I provided the gulls with refuse from 15 small cod *Gadus morrhua* on an open shore at Mickeslkären. Eleven adult Great Blackbacks approached the food, but only four of them ate the refuse. The others, together with three Herring Gulls, were driven away or did not dare to come close to the food. The behaviour of these gulls diverged markedly from the rapid simultaneous feeding of mixed flocks of Herring Gulls and Great Blackbacks at refuse dumps, harbours and trawlers. The four Great Blackbacks taking the food behaved aggressively towards all the other gulls, because the food lay within their normal feeding range (two pairs from the Mickelskären islets).

At present there are about 60 times as many Herring Gulls as Great Blackbacks in the Helsinki archipelago and any food that becomes available is first detected by a Herring Gull. If the Herring Gull is unable to swallow the food immediately, a Great Blackback generally approaches and takes the food from the Herring Gull, on the ground or water or in flight. Larger fishes, older downy ducklings, and older chicks of gulls and terns are commonly taken from Herring Gulls in this way.

There is some competition between the Great Blackback and the Herring Gull for Eider ducklings until about 20—25 June, when the Eider ducklings generally become to heavy to be taken by Herring Gulls. During the first half of June 1981 the c. 25 pairs of Great Blackbacks breeding within a radius of c. 3 km from Mickelskären caught about five times as many Eider ducklings as the about 200 pairs of Herring Gulls breeding in the same area. Despite the predation by the gulls, some years the proportion of the Eider ducklings that fledged around Mickelskären was 40 % of the number hatched, but in some years less than 5 % fledge (examples: 1973 and 1978). In 1982 the rate was c. 25 %, which may be considered a good year for the Eider. Local brood flocks in the middle archipelago SW of Helsinki may succeed even better, especially where the Eider is accustomed with boats and man. In such brood flocks 80 % may fledge.

The fact that the Eider population now is greater than in any period before the increase of the large gulls in Finland (cf. especially Stjernberg 1982 a) shows that predation by the Great Blackbacks and Herring Gulls is not a serious threat to the Eider, since the hunting pressure decreased (no spring shooting of migrating Eiders in SE Sweden, less spring shooting in Finland). This agrees with the results of swedish studies (e.g. Andersson 1968a). Around 10 July most of the Eider ducklings become too big to be taken easily by the Great Blackbacks, but some are caught even in early August, when they are feathered but still unable to fly. However, around 1 August the Great Blackbacks and Herring Gulls in general become less interested in catching ducklings. The moult of the primaries clearly influences their maneuvering ability. This may be the reason why almost all broods of the Velvet Scooter that hatch in July are taken by the large gulls, but broods that hatch in early August may escape serious losses. My observations show, that the Herring Gulls increase the competition for food around the

breeding localities, but on the other hand some pairs of Great Blackbacks prey upon the small and half-grown Herring Gull chicks. This was done regularly by two single pairs on the islet of Enbusken in 1979 and two single pairs near Mickelskären in 1980.

Interspecific sociability and expansion

In the archipelago SW of Helsinki competition with conspecifics leads to utilization of food sources far from the breeding localities, mostly those used by Herring Gulls. This tendency is increased by the interspecific sociability developing among all gulls flocking at food, and especially between Great Blackbacks and Herring Gulls. The Great Blackbacks are alerted to the occurence of food by small flocks of other large gulls, the sight of gulls trying to eat something they cannot swallow immediately, or the purposeful flight of gulls making for a feeding locality (cf. Ward & Zahavi 1973). This and the tendency of the larger gulls (especially young and subadult ones) to form mixed flocks are probably factors also causing dispersal of Great Blackbacks to inland localities colonized by Herring Gulls (inland bogs in the W coast region, lakes in S Finland, cf. Linkola 1976, Nieminen & Tolvanen 1979, Karlin 1980; cf. aslo roosts as information centres, Loman & Tamm 1980).

5. Summary

In Finland the limited productivity of the brackish waters of the Baltic and the absence of tidal shores originally restricted the populations of *Larus a. argentatus*, *L. f. fuscus* and *L. marinus*, allowing them to breed only in single pairs. Later, refuse from the local fishery permitted *L. fuscus* to increase, since it winters in a partly tropical region, but the winter conditions in the North Sea continued to limit the populations of *L. argentatus* and *L. marinus* until the technical progress in the 1920s provided new sources of food.

When nesting in single pairs, these gulls mostly feed in the vicinity of the breeding locality and defend a feeding range around it. This feeding strategy is adventageous because the distance to food is short, competition from conspecifics is reduced and the pair is able to become familiar with its feeding range. As long as the aggressive defence of the combined territory and feeding range counterbalances the intraspecific sociability and the population pressure, the single-breeding system persists. Breeding in colonies and breeding in single pairs may occur side by side because colonial breeders and single paris have different feeding strategies. The colonial individuals do not normally seek for food near their breeding locality and they commonly ignore small amounts of food available in its vicinity. In both *L. argentatus* and *L. marinus* the presence of a local pair in its feeding range was enough to prevent individuals from nearby colonies from taking food there. Colony breeders forage where food is available in large amounts and feed more or less socially without displaying much aggressiveness.

Colonial breeding begins to develop when man-made food sources allow the population to increase, developing most readily in *L. argentatus*. In the 1920s and 1930s the population of *L. argentatus* SW of Helsinki increased from parhaps 10 to 130 pairs and the proportion of single pairs dropped from 100 % to 1 %. It was still below 1 % when the population had increased to 6500 pairs in 1979. In increasing populations of *L. fuscus* most new colonies are established on somewhat larger islets already inhabited by single pairs. Thus increase of the population reduces the number of single pairs, especially in the outer archipelago, but on small islets in the inner parts of the archipelago *L. fuscus* still occurs in single pairs, efficiently defending their islets against conspecifics. Around 1950 in S and SW Finland c. 50 % of the breeding islets of *L. fuscus* were inhabited by single pairs, which constituted 3—6 % of the population. In decreasing populations the number of single pairs decreases roughly in the same proportion as the population. In *L. marinus* all the pairs settle singly as long as suitable small marine islets are available within an acceptable radius from natural or man-made food sources. Lack of free islets and shortage of food in the outer archipelago results in *L. marinus* chiefly in dispersal into the inner archipelago, but to some extent also in colony formation in the outer archipelago. Single pairs constitute 70—75 % of its population and occupy 95 % of the breeding localities. On the S coast of Finland the population has increased since 1933 from c. 50 to c. 400 pairs, and the largest colony in Finland consits of less than 50 pairs. The W coast of Finland still has a sparse breeding population but its increase since the war has been about fivefold.

Intraspecific sociability causes single pairs of *L. argentatus* to settle in colonies of *L. fuscus* and single pairs of *L. marinus* in colonies of *L. argentatus*. Such single pairs increase the readiness of their conspecifics to settle in the locality and may thus lead to colony formation. Settling in a locality occupied by a single pair occurs mainly when the old pair or the new pair, or both, have begun to forage far from the breeding locality. Islets utilized as roosts by juvenile *L. argentatus* may later change into breeding localities, and extreme conditioning of juveniles to man at feeding localities may contribute to acceptance of roofs in towns as breeding localities.

The high number of small islets in the archipelago restricts the colony size of *L. argentatus* to 20—250, max. c. 450 pairs, and the nest density in the colonies is low. Increasing density causes colonization of nearby islets. In 1965—1979 *L. argentatus* in the area 15—40 km SW of Helsinki increased from 1200 to c. 6500 pairs, but their breeding success dropped from 1.8 to 0.9 fledged young per pair, indicating shortage of food, and cannibalism became frequent. The proportion of single pairs has now begun to increase. These pairs prefer to settle by or in colonies of other shore birds, where they feed on eggs and chicks and defend feeding ranges. Predation on other gulls, especially *L. ridibundus*, allows indirect utilization of man-made food sources not directly available to *L. argentatus*. The single pairs generally have very high breeding success. Occupying most islets, especially off Helsinki, and preying on chicks and ducklings, *L. argentatus* reduces the populations of other species, including *L. fuscus*. The long and narrow wings of *L. fuscus* prevent it from foraging in localities where flocks of gulls hover above the food. When disturbed and robbed by *L. argentatus* on the breeding islets, it tends to leave and settle elsewhere, but in the new localities disturbance caused by man mostly has been fatal for the offspring, or *L. argentatus* may invade also the new localities. *L. fuscus* is decreasing on the S coast, most rapidly around Helsinki, where almost no young nowadays are fledged. In areas with enough artificial food for large gulls it survives better, until *L. argentatus* increases so much that it begins to feed in flocks in the same localities. The simultaneous increase of the two species on the British coast is probably explained by feeding in different habitats, and large breeding localities with space for both gulls.

In *L. marinus* the mean breeding success for single pairs is 2.4 young fledged. Some of the gulls have begun to feed on garbage gumps, especially in the Helsinki area, where the ratio of *L. marinus* to *L. argentatus* is c. 1:70. Almost all *L. marinus* prey

on ducklings, especially those of *Somateria mollissima*. SW of Helsinki they take five times as many ducklings as *L. argentatus*, and change to chicks of larids when ducklings are not available. The predation is not a serious threat to *Somateria*, but for other archipelago ducks the predation can be locally diastrous. Broods hatching in August survive better because moulting of the wing feathers prevents efficient catching of ducklings.

The present paper is based on field records made during 52 successive seasons, mainly on the S coast of Finland.

Acknowledgement. The language was corrected by Mrs Anna Damström, M.A.

References

Ahlqvist, H. & Fabricius, E. 1938: Die Vögel das äusseren Schärenhofes zwischen Tvärminne und Jussarö. — Ornis Fennica 15:21—32.

Andersson, M., Götmark, F. & Wiklund, C. G. 1981: Food information in the Black-headed Gull, Larus ridibundus. — Behav. Ecol. Sociobiol. 9: 199—202.

Andersson, Å. 1965: Havsruten (Larus marinus) som häckfågel i Skåne, Meddelanden från Skånes Ornitologiska Förening 1965:1—5.

—»— 1968 a: Gråtrutens näringsekologi och inverkan på kustfågelfaunan med särskild hänsyn till ejdern. — — Thesis. Zool. Institute, Univ. of Lund, Sweden. 103 pp.

—»— 1968 b: Gråtrutarna på Hallands Väderö och deras grannar. — Skånes Natur 56: 100—109.

—»— 1970: Food Habits and Predation of an Inland-Breeding Population of the Herring Gull Larus argentatus in Southern Sweden. — Ornis Scand. 1:75—81.

Andersson, Å. & Staav, R. 1980: Den häckande kustfågelfaunan i Stockholms län 1974—1975. — Natur i Stockholms län. 4 Kustfågelfauna. Stockholms läns landsting.

Aumees, L. 1967: Lääne-Saaremaa merelaidude linnustikust. (The bird fauna of the maritime islets off the West coast of Saaremaa island). — Eesti Meresaarte Linnustik 32—42. Tartu.

Barth, E. K. 1966: Mantle colour as a taxonomic feature in Larus argentatus and Larus fuscus. — Nytt Mag. Zool. 13:56—82.

—»— 1975: Taxonomy of Larus argentatus and fuscus in north-western Europe. — Ornis Scand. 6: 49—63.

Belopolskii, L. O. 1961: Ecology of the sea colony birds of the Barents Sea. — Jerusalem. (Orig. edition Moscow-Leningrad 1957).

Berg, B. 1918: Stora Karlsö. — Stockholm.

Bergman, G. 1939: Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. — Acta Zool. Fennica 23: 1—134.

—»— 1946: Kvantitativa data över fågelfaunan i några begränsade skärgårdsområden i södra Finland. — Ornis Fennica 23: 26—31.

—»— 1957: Das Porkalagebiet als biologisches Experimentalfeld. Über die Veränderungen der Säugetier- und Vogelfauna des Gebietes während seiner Verpachtung an die Sovietunion nebst biologischen Beobachtungen nach der Wiedervereinigung — Acta Soc. Fauna Flora Fennica 74: 1—52.

—»— 1960: Über neue Futtergewohnheiten der Möwen an den Küsten Finnlands. — Ornis Fennica 37: 11—28.

—»— 1965: Trutarnas konkurrensförhållanden, födobehov och relation till andra skärgårdsfåglar. — Zool. Revy 27: 58—77.

Bergman, G.,Fabricius, E. & v. Haartman, L. 1940: En preliminär undersökning över silltrutens, Larus f. fuscus L., och gråtrutens L. a. argentatus Pont., näringsbiologi, särskilt ur jaktvårdssynpunkt. (Zusammenf.: Eine vorläufige Untersuchung über die Nahrungsbiologie von Larus f. fuscus und Larus a. argentatus, mit besonderer Berücksichtigung ihrer Bedeutung für die Pflege der jagdbaren Seevögel.) — Ornis Fennica 17: 33—41.

Blomqvist, R. & Tenovuo R. 1980: Merihanhen pesimisestä Saaristomeren luoteisosassa. (The nesting of the Greylag Goose Anser anser in the northwestern Archipelago Sea.) — Suomen Riista 28: 25—29.

Burger, J. & Lesser, F. 1978: Selection of colony sites and nest sites by Common Terns Sterna hirundo in Ocean Country, New Jersey. — Ibis 120: 433—499.

—»— 1980: Nest site selection in an expanding population of Herring Gulls. — J. Field Ornithol. (Bird-Banding) 51: 270—280.

Burger, J. & Shisler, J. 1980: The process of colony formation in Herring Gulls Larus argentatus in New Jersey. — Ibis 122: 15—26.

Chabrzyk, G. & Coulson, C.J. 1976: Survival and recruitment in the Herring Gull Larus argentatus. — J. Anim. Ecol. 45: 187—203.

Coulson, J. 1968: Difference in the quality of birds nesting in the centre and on the edges of a colony. — Nature 217: 478—479.

Dawis, J.W.F. & Dunn, E.K. 1976: Intraspecific predation and colonial breeding in Lesser Black-backed Gulls Larus fuscus. — Ibis 118: 65—77.

Drury, W.H. Jr. & Smith, W.J. 1968: Defence of feeding areas by adult Herring Gulls and intrusion by young. — Evolution 22: 193—201.

Duncan, N. 1978: The effects of culling Herring Gulls (Larus argentatus) on recruitment and population dynamics. —J. Appl. Ecol. 15: 697—713.

Erwing, R.M., Galli, J. & Burger J. 1981: Colony size dynamics and habit use in Atlantic coast seabirds. — Auk 98: 550—556.

Ewald, P.W., Hunt G.L. & Warner M. 1980: Territory size in Western Gulls: importance of intrusion pressure, defence investments, and vegetation structure. — Ecology 61: 80—87.

Fisher, J. 1963: Evolution and bird sociality. — In: Huxley, J. et al. (eds.), Evolution as a process. 71—83. New York.

Forssgren, K. 1981: The kleptoparasitic behaviour of the Arctic Skua Stercorarius parasiticus and the Lesser Black-Backed Gull Larus fuscus with the Caspian Tern Hydroprogne caspia. — Memoranda Soc. Fauna Flora Fennica. 57: 5; repr. 1980.

Gillet, W.H., Hayward, J. L. Jr. & Stout, J. F. 1975: Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. — Condor 77: 492—495.

Goethe, F. 1937: Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (Larus a. argentatus Pontopp.) auf der Vogelinsel Memmertsand. — J. Ornithol. 85: 1—119.

—»— 1956: Die Silbermöwe. — Neue Brehm-Bücherei 102. Wittenberg.

—»— 1960: Felsenbrütertum und weitere beachtenswerte Tendenzen bei der Silbermöwe. — Proc. 12 Int. Ornithol. Congr. Helsinki 1958: 252—258.

—»— 1975: Zur Biologie der Heringsmöwe Larus fuscus unter besonderer Berücksichtigung ethologischer Aspekte. I. Nahrung und Nahrungserwerb. — Ornis Fennica 52: 5—12.

Grenmyr, U. & Sundin, J.A. 1981: Fågelfaunan vid Västerbottenskusten — förändringar sedan 1930-talet. (Summary: The bird fauna of the Västerbotten coast

— changes since the 1930's). — Vår Fågelvärld 40: 91—104.
Grenquist, P. 1938: Die Nistvogelfauna des Vogelschutzgebietes Klåvskär auf Åland. — Ann. Univ. Turkuensis (A) 6:9: 1—40.
—»— 1942. Vogelbestandsaufnahmen in der Meereszone des Schärenhofs Südwest-Finnlands. — Ornis Fennica 19: 45—61.
—»— 1965: Changes in abundance of some duck and sea-bird populations off the coast of Finland 1949—1963. — Finnish Came Res. 27: 1—114.
von Haartman, L. 1945: Zur Biologie der Wasser- und Ufervögel im Schärenmeer Südwestfinnlands. — Acta Zool. Fennica 44: 1—120.
—»— 1948: Fågelbeståndet på några utskär vid Karlö (Hailuoto) sommaren 1947. — Memor. Soc. Fauna Flora Fennica 24: 61—64.
von Haartman, L. Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R., 1963—1967: Pohjolan linnut värikuvin. — Helsinki.
Haftorn, S. 1971: Norges fugler. — Oslo, Bergen, Tromsö.
Hand, J.L. 1980: Human disturbance in Western Gull Larus occidentalis livens colonies and possible amplification by intraspecific predation. — Biol. Conserv. 18: 59—63.
Hario, M. 1981: Harmaalokin vaikutus selkälokin poikastuottoon. (Summary: Impact of the herring gull on the breeding of the lesser black-backed gull.) — Lintumies 16: 24—29.
Harris, M.P. 1964: Aspects of the breeding biology of the gulls Larus argentatus, L. fuscus, and L. marinus. — Ibis 106: 432—456.
—»— 1970: Rates and causes of increase of some British gull populations. — Bird Study 17: 325—335.
Hatch, J.J. 1970: Predation and piracy by gulls at a ternery in Maine. — Auk 87: 244—254.
Hildén, O. 1964: Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. — Ann. Zool. Fennici 1: 153—277.
—»— 1965: Habitat selection in birds. A review. — Ann. Zool. Fennici 2: 53—75.
—»— 1983: Changes in the seabird popultions in Finland. — Proc. VI Finnish-Estonian Ornithol. Congr. 1979, in press.
Hildén, O., Hurme, T. & Taxell C.G. 1978: Häckfågelstudier och sträckobservationer på Valsörarna. — Österbotten 1978: 1—115.
Holmgren, E. 1871: Handbok i Zoologi. II. Skandinaviens Foglar. — Stockholm.
Horn, H.S. 1968: The adaptive significance of colonial nesting in the Brewe's blackbird (Euphagus cyanocephalus). — Ecology 49: 682—694.
Hörnfelt, B. 1981: Gråtrutens ekologi och metoder som prövats för skötsel av måsfågelbestånd. En litteraturgenomgång. — Statens Naturvårdsverk PM 1434. Solna.
Hortling, I. 1929—31: Ornitologisk handbok. — Helsingfors.
Hunt, G.L. 1972: Influence of food distribution and human disturbance on the reproductive succes of Herring Gulls. — Ecology 53: 1051—1061.
Karlin, A. 1980: Kalatiiran suopesinnästä Suomessa (Summary: The nesting of Common Tern on the peatlands in Finland.) — Lintumies 15: 35—37.
Karpovich, V.N. & Tatarinkova, I.P. 1968: Number dynamics of Great Black-backed and Herring Gulls at the islands on Murman coast and their influence on the efficiency of the reproduction of Common Eider. — The Common Eider (Somateria mollissima L.) in the USSR. Proc. of a conference, Estonia May 1966 (Edit. E. Kumari) pp. 85—104. (Russian with Eng. summary).
Kastepöld, E. 1972: Matsalu riikliku looduskaitseala Väinamere ja kesklahe saarte haudelinnustikust 1972. A. (On the breeding population of the islands located in the Väinamere (Moonsund)). — Loodusvaatlusi 1972: 11—16.
Kihlman, J. & Larsson, L. 1974: On the importance of refuse dumps as food source for wintering Herring Gulls Larus argentatus Pont. — Ornis Scand. 5: 63—70.
Kilpi, M., 1980: Harmaalokki — saariston lintuyhteisön musta lammas? (Summary: The Herring Gull — a pest in the archipelago?). — Lintumies 15: 102—107.
Kilpi, M., Puntti, H. & Toivonen, J. 1980: Numbers of gulls on the northern coast of the Gulf of Finland. — Ornis Fennica 57: 153—160.
Koskimies, J. 1952: Observations on the development of mobility in young Common Gulls, Larus canus L., and Lesser Blackbacked Gulls, L. fuscus. — Ornis Fennica 29: 83—87.
Kosonen, L. & Mäkinen, R. 1978: (Harmaalokin pesintä rakennuksissa). (Summary: Herring Gulls nesting on a building.) — Ornis Fennica 55: 87.
Krebs, J.R. 1974: Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (Ardea herodias). — Behaviour 51: 99—134.
Kumari, A. 1967: Lindude levikust ja arvukusest Väinamere saartel. (Distribution and numbers of the bird populations of the islets in the Väinameri (Muhu sound)). — Eesti Meresaarte Linnustik: 61—84. Tartu.
Kumari, E. 1976: The increase in the number of the Common Gull Larus canus and its colonization of Estonian peat bogs in recent decades. — Ornis Fennica 53: 33—39.
Lack, D. 1968: Ecological adaptations for breeding in birds. — London.
Lemmetyinen, R. 1980: Vesi- ja lokkilintujen kannanmuutoksista Gullkronan selällä, Turun saaristossa vuosina 1948—1977. (Changes in the numbers of gulls and waterfowl of southwestern Finland in 1948—1977. — Suomen Riista 28: 42—48.
Linkola, P. 1976: Merilokki Larus marinus leviämässä järvialueelle. (Summary: The Great Black-backed Gull spreading into the Finnish Lake District.) — Lintumies 11: 122.
Loman, J. & Tamm, S. 1980: Do roosts serve as "information centers" for crows and ravens? — Amer. Naturalist 115: 285—289.
Lönnberg, E. 1929: — in: von Wright, M. & von Wright, F., Svenska fåglar. Med text av professor Einar Lönnberg. III. Stockholm.
Mathiasson, S. 1964: Gråtrut och gråtrutsbekämpning. — Zool. Revy 26: 41—51.
McNicholl, K.M. 1975: Larid site tenacity and group adherence in relation to habitat. — Auk 95: 98—104.
Monaghan, P. 1979: Aspects of the breeding biology of the Herring Gulls Larus argentatus in urban colonies. — Ibis 121: 475—481.
Monaghan, P. & Coulson, J.C. 1977: Status of the large gulls nesting on buildings. — Bird Study 24: 89—104.
Munro, J. & Bédard, J. 1977: Gull predation and créching behaviour in the Common Eider. — J. Anim. Ecol. 46: 799—810.
Nieminen, J. & Tolvanen, J. 1979: Merilokki Larus marinus pesivänä Vanajanselällä. (Summary: the Great Blackbacked Gull nesting in the Finnish Lake district.) — Lintumies 14: 37—38.
Nordberg, S. 1932: Die Entwicklung des Seevogelbestandes in einen Vogelschutzgebiete auf Åland 1918—1932. — Ornis Fennica 9: 89—122.
—»— 1950: Researches on the bird fauna of the marine zone in the Åland archipelago. — Acta Zool. Fennica 63: 1—62.
Paavolainen, E. 1957: Die Vogelfauna des äusseren Schärenhofes im östlichen Teil des Finnischen Meerbusens. I. Quantitative Ubersicht. — Ann. Zool. Soc. Zool. Bot. Fenn. 'Vanamo' 18 (5): 1—51.

Palmgren, R. 1913: Helsingfors-traktens fågelfauna. — Acta Soc. Fauna Flora Fennica. 38: 1—224.
Paludan, K. 1951: Contributions to the breeding biology of Larus argentatus and Larus fuscus. — Vidensk. Medd. Dansk Naturh. Foren. 114: 1—128.
Parsons, J. 1971: Cannibalism in Herring Gulls. — Brit. Birds 64: 528—537.
Parsons, J. 1976: Nesting density and breeding success in the Herring Gull Larus argentatus. — Ibis 118: 537—546.
Richter, R. 1938: Beobachtungen an einer gemischten Kolonie von Silbermöwen (Larus a. argentatus Pont.) und Heeingsmöwen (Larus fuscus graellsii Brehm) — J. Ornithol. 86: 366—373.
Risberg, L., Aspenberg, P. & Erikson, L. 1976: Häckfågelfaunan längs Gästriklandskusten — förändringar under de senaste årtiondena. — Vår Fågelvärld 35:195—212.
Robert, C.H. 1975: Effects of human disturbance on the breeding success of gulls. — Condor 77: 492—495.
Salomonsen, F. 1979a: Ornithological and Ecological Studies in S.W. Greenland (59° 46—62° 27 N. Lat.) — København.
—»— 1979b: Marine Birds in the Danish Monarchy and Their Conservation. — In: Bartoneck, J.C. & Nettleship, D.N. (eds.), Conservation of Marine Birds of Northern North America. US. Dept. Int. Fish Serv. Wildl. Res. Repo. 11, pp. 267—287.
Spaans, A.L. 1971: On the feeding ecology of the Herring Gull Larus argentatus Pont, in the northern part of the Netherlands. — Ardea 79: 1—188.
Staav, R. 1979: Dispersal of Caspian Terns Sterna caspia in the Baltic. — Ornis Fennica 56: 13—17.
Sternberg, T. 1982a: The size of the breeding Eider population of the Baltic in the early 1980s. — Ornis Fennica 59: 135—140.
—»— 1982 b: Djurvärlden. — In: Lindgren, L. & Stjernberg, T. (eds.), Skärgårdshavets nationalpark. Manuscr.
Taxell, C.-G. 1934: Fågelfaunan på Valsörarna i Vasa skärgård. — Ornis Fennica. 11: 5—13.
Thomas, G.J. 1972: A rewiew of gull damage and management methods at nature reserves. — Biol. Conservation 4: 117—127.
Tinbergen, N. 1953: The Herring Gull's world. — London.
Took, G.E. 1955: Nesting of Herring Gulls on rooftops in Dover. — Brit. Birds 48: 88.
Väisänen, R.A. & Järvinen, O. 1977: Dynamics of protected communities in a Finnish archipelago. — J. Anim. Ecol. 46: 891—908.
Valovirta, E. 1931: Signilskärin linnustosta. (Zusammenfassung: Die Vogelfauna auf den Signilskär-Inseln im Ålands-Archipel.) — Ornis Fennica 7: 88—102.
Ward, P. & Zahavi, A. 1973: The importance of certain assemblages of birds as "information centres" for food finding. — Ibis 115:517—534.
Verbeek, N.A.M. 1977: Interactions between herring and lesser black-backed gulls feeding on refuge. — Auk 94: 726—735.
Vickholm, M. 1982: Lintujen esiintyminen ja torjunta Helsinki-Vantaan lentoasemalla. — Ilmailuhallituksen PM. Helsinki.
von Wright, M. & Palmén, J.A. 1873: Finlands Foglar. — Helsingfors.

Received 26.IV.1982
Printed 10.XII.1982