Population trends and selection of nest-sites in *Larus argentatus* and *L. fuscus* on the Finnish coast

Mikael Kilpi

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This report presents the trends in populations of the Herring Gull *L. argentatus* and the Lesser Black-backed Gull *L. fuscus* on the Finnish coast. In most areas *L. fuscus* increased up to c. 1960, after which it declined. *L. argentatus* has increased in all areas during the last few decades. Invading *L. argentatus* seem to select colonies of *L. fuscus*, which results in the formation of mixed colonies. Initially, *L. argentatus* nests on open cliffs and *L. fuscus* in more sheltered habitats. With increasing density, *L. argentatus* starts using other habitats, eventually excluding *L. fuscus*. The mixed colonies are thus unstable. The exclusion of *L. fuscus* is a matter of unknown density-dependent factors, but other factors are also involved in the decline of *L. fuscus* on the Finnish coast.

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Introduction

In northwestern Europe, three large *Larus* gulls breed sympatrically: the Great Black-backed Gull *L. marinus*, the Herring Gull *L. argentatus* and the Lesser Black-backed Gull *L. fuscus*. All three species breed along the Finnish coast, and the two smaller species, *L. argentatus* and *L. fuscus*, often form mixed colonies (Kilpi et al. 1980, Bergman 1982). In 1930—1940, when *L. argentatus* began to increase in the Finnish archipelago, *L. fuscus* and the Common Gull *L. canus* were the most abundant gull species in coastal areas (Bergman 1939). According to a recent survey of gull populations in the Gulf of Finland, *L. argentatus* has increased dramatically, while *L. fuscus* has decreased (Kilpi et al. 1980).

The interactions between *L. argentatus* and *L. f. fuscus* in the Finnish archipelago are not fully understood. Most Finnish studies report that the two species differ in nest-site selection (Bergman 1939, Väisänen & Järvinen 1977a). *L. argentatus* typically nests in open habitats, while *L. fuscus* prefers to nest in the shelter of vegetation. Since the 1960s, most *L. fuscus* colonies in the Gulf of Finland have been rapidly invaded by *L. argentatus* (Bergman 1965). Territorial clashes between the large *L. argentatus* and small *L. fuscus* may be expected to end in the defeat of *L. fuscus*, since dominance and body size are related in birds (Burger et al. 1979, Götmark 1982).

In this paper I try to elucidate the following subjects with the aid of many earlier studies and my own data from recent years:

— the population trends from 1930 to 1980 for *L. argentatus* and *L. fuscus* along the Finnish coast
— colony-site and nest-site selection in the two species
— evidence of competition between the two species.

Material

The main references and study areas used in this report are presented in Table 1 and Fig. 1. Unpublished field data of my own were collected in Hanko in 1976—82, and in Helsinki in 1979—81. The latter area covers all of Bergman's (1939, 1965, 1982) study areas.

Results

Population trends. L. argentatus has increased from 1930 to 1980 in each of the seven study areas (a—g). In most areas *L. fuscus* increased roughly between 1940 and 1960, but later decreased (Fig. 2). In the Gulf of Finland *L. fuscus* has decreased from peak numbers (c. 1800 pairs) in the late 1950s to some 1400 pairs in 1980. In the late 1950s *L. argentatus* numbered c. 1500 breeding pairs; in 1980 there were some 12 000 pairs (Kilpi et al. 1980, Kilpi, unpubl.). The largest colonies of *L. argentatus* in the Gulf of Finland contain more than 400 pairs on a single islet; in other coastal areas the colonies seldom exceed 100 pairs.

The total population in the Archipelago Sea (including study areas e and d) has not been censused adequately, but it is probably about 5000 pairs (see Bergman 1982). In the Gulf of Bothnia the population is sparse. At Valassaaret (study area f) the largest colony in 1978 was c. 20 pairs,

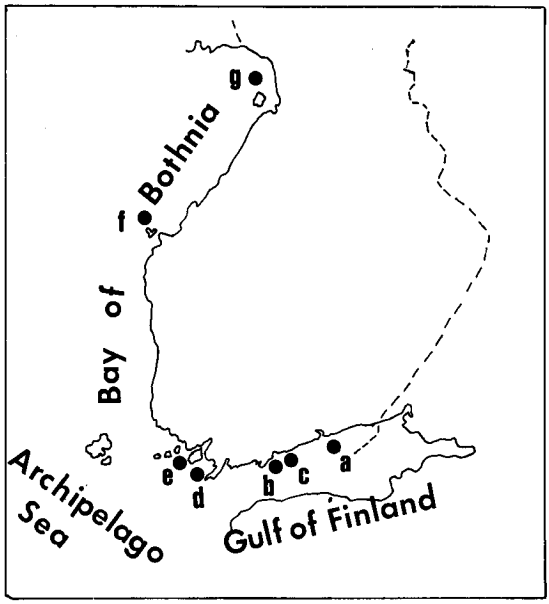

Fig. 1. Location of the study areas, abbreviations as in Table 1.

and the total population 70 pairs (Hildén et al. 1978). Of the total *L. argentatus* population breeding along the coast of Finland, probably more than half breeds in the gulf of Finland.

Only a few *L. fuscus* colonies contain more than 50 pairs (Bergman 1982). In the Gulf of Finland, the size of the *L. fuscus* population is only 10 % of that of *L. argentatus*. In the Archipelago Sea the number of breeding *L. fuscus* may be in the range of 2000—3000 pairs (Bergman 1982), i.e. about half of the *L. argentatus* population. Along the coast of the Gulf of Bothnia, *L. fuscus* still most probably outnumbers *L. argentatus*.

Colony-site selection among invading Herring Gulls. In the islet group of Krunnit, the first breeding pair of *L. argentatus* settled in 1949. Ten years later eight of nine pairs nested in colonies

Table 1. The study areas and data sources, abbreviations as in Fig. 1.

Area	Symbol on Fig. 1	Total no. of study islands	Source
Aspskär	a	6	Grenquist 1965 Hario 1979
Kirkkonummi	b	100	Bergman 1939, 1965
Helsinki	c	200	Kilpi 1980, Kilpi et al. 1980, this study
Hanko	d	100	This study
Trollö	e	100	Lemmetyinen 1963, 1980
Valassaaret	f	60	Hildén et al. 1978
Krunnit	g	22	Väisänen & Järvinen 1977 a, b

of *L. fuscus* (Väisänen & Järvinen 1977). Solitary *L. argentatus* may breed without connection with other gulls (Bergman 1982, own observations), but in newly invaded areas it seems that assemblages of more than 5 breeding pairs (here defined as a colony) form in existing colonies of *L. fuscus* (Table 2). Some of the colonies used in the initial stage of the invasion were mixed colonies of *L. fuscus* and *L. canus* (one in Kirkkonummi, one in Krunnit). In Hanko two *L. argentatus* colonies formed in pure colonies of *L. canus*. Newly established *L. argentatus* colonies may grow very rapidly (Fig. 3).

Nest-site selection and morphology of the nesting islets. Both *L. argentatus* and *L. fuscus* typically nest on fairly small treeless islets, usually less than 2 ha in size. The colony islets of Hanko all share at least three characteristics: (1) an elevated bare granite cliff; (2) a low-lying meadow, sometimes with *Juniperus, Prunus* and *Alnus* bushes and stones (0.1—1 m in diameter), and (3) a stony beach. Fig. 4 gives an example of such an islet; the two species are here well segregated, *L. argen-*

Table 2. The occurrence of *L. argentatus* colonies in existing *L. fuscus* colonies shortly after the invasion of four areas by the former species.

Area Year	No. of *L. fuscus* colonies	Size range (pairs)	*L. fuscus* colonies occupied by >5 pairs of *L. argentatus*	% of all *L. argentatus* in area, no. of pairs in brackets	Years since invasion*
Krunnit 1970	4	33—85	3	86.1 (72)	10 yr
Trollö 1977	4	4—77	(3)	92.0 (195)	15 yr
Hanko 1978	12	5—20	10	98.0 (220)	15 yr
Kirkkonummi 1937	6	6—57	4	91.3 (127)	10 yr

* The approximate time elapsed since the appearance of a colony of *L. argentatus* with more than 5 pairs.

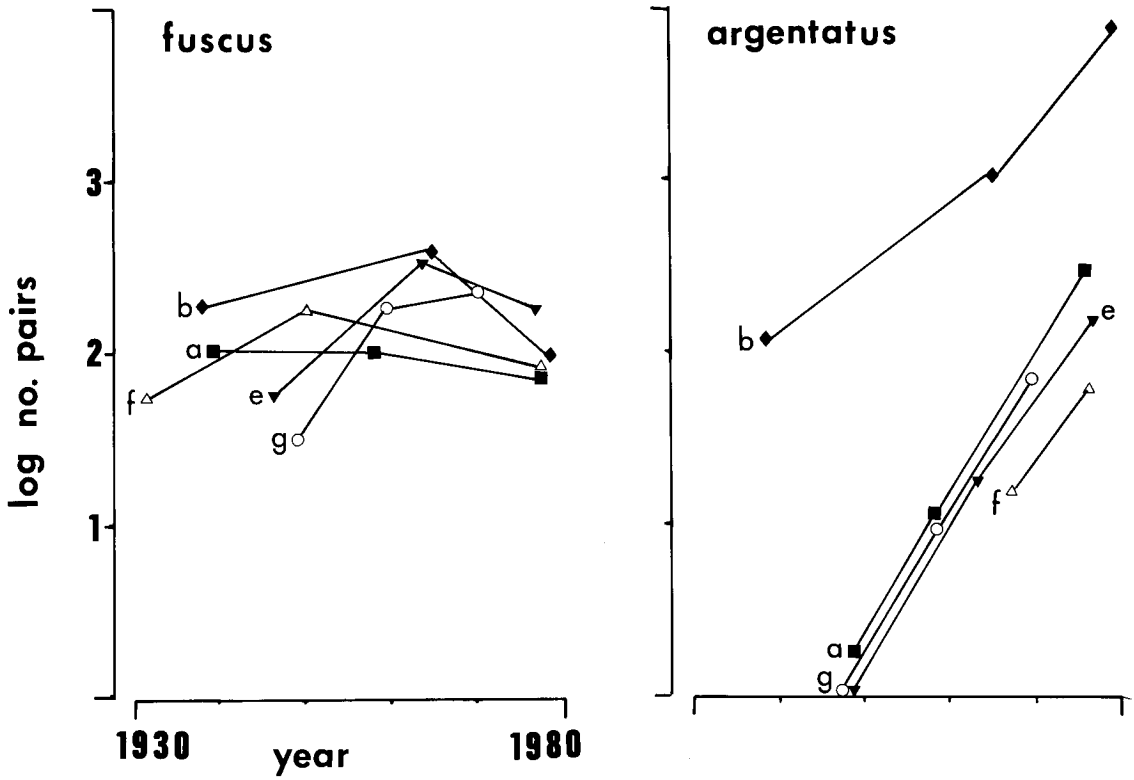

Fig. 2. Population changes in *L. fuscus* and *L. argentatus* in the study areas, abbreviations as in Fig. 1.

tatus nesting on the cliff and *L. fuscus* on the stony shore and under bushes. Table 3 gives the main nesting habitats of the colonies in Hanko and Helsinki. In Hanko *L. argentatus* typically uses exposed sites, while *L. fuscus* uses more sheltered sites.

In the Gulf of Bothnia the islets are composed of stones of different sizes. Väisänen & Järvinen (1977a) found *L. fuscus* mainly on grassy skerries, an islet type resembling that preferred by the species in the Gulf of Finland (Bergman 1939). *L. argentatus* used more open habitats than *L. fuscus*, segregation being obvious (Väisänen & Järvinen 1977a).

One problem in assessing the nest-site preferences of *L. fuscus* is that the situation before the increase of the Herring Gull is not sufficiently known. In Hanko no changes in nest-site selection were noted on islets invaded by *L. argentatus* between 1976 and 1981. *L. fuscus* thus seems to use sheltered nest-sites even when *L. argentatus* is absent. The two cases in Helsinki in which *L. fuscus* nested on open beaches (Table 3) may be due to the fact that these beaches are the only habitats left unexploited by *L. argentatus* on these islets. There are also observations of a change in the location of nests of *L. fuscus* on an islet (Table 4).

The collapse of L. fuscus colonies. Table 5 shows the fate of the four largest *L. fuscus* colonies

Table 3. Habitats of main part of colony in Hanko (1978 data) and Helsinki (1979 data). The nests of *L. argentatus* in the Helsinki colonies were distributed over a wide range of sites, and were not concentrated in any particular habitat.

Area	Species	Location of main part of colony (No. of cases)				
		Cliff	Bush	Beach	Meadow	Open beach
Hanko	*L. fuscus*	0	6	6	0	0
	L. argentatus	10	0	0	0	0
Helsinki	*L. fuscus*	0	3	3	1	2

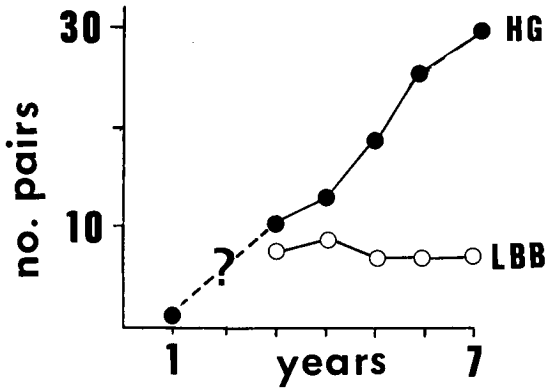

Fig. 3. Growth of a colony of *L. argentatus* (HG) compared with that of *L. fuscus* (LBB) in Hanko. The first Herring Gull pair settled in 1976 (year 1).

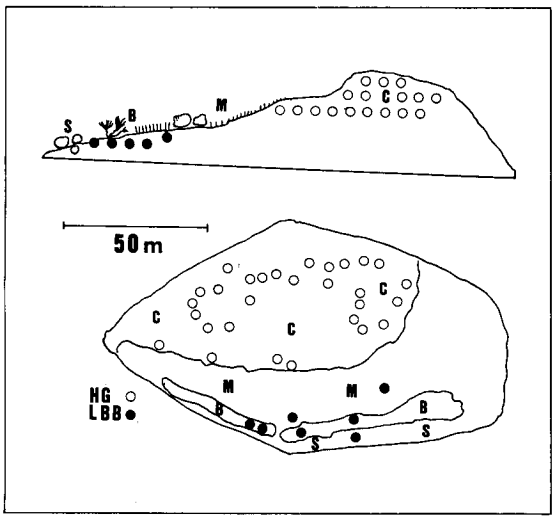

Fig. 4. A mixed colony in Hanko. The main habitats on the islet are indicated (S = stony beach, B = bushy area, M = meadow and C = cliff). The distribution of the nests of both species seven years after the first pair of *L. argentatus* settled. The location of *L. fuscus* nests did not change in the period 1978—82. The height of the islet is not drawn to scale with the width.

known to Bergman (1939) in Kirkkonummi. These may be the only documented cases of colony collapse probably caused by intruding *L. argentatus* on the Finnish coast. Bergman (1982) states that *L. fuscus* was forced to abandon outer islets, and that new colonies formed closer to the mainland. These colonies have now also been invaded by *L. argentatus,* and *L. fuscus* is declining on them. In a very large part of the Gulf of Finland there are no pure *L. fuscus* colonies left. The rate of the decline of *L. fuscus* is greatest in Kirkkonummi, which has the densest *L. argentatus* population on the Finnish coast (Kilpi et al. 1980).

Discussion

Status of the populations. The Herring Gulls on the coast of Finland have been very successful during the last 50 years (Kilpi et al. 1980) and success has been the general rule over the entire breeding range of this species during this century (Burger 1979). Their increase, often considered the result of man's activities, has been believed to have a profound effect upon other coastal birds (Drury 1973—74). The large *L. argentatus* can be a serious threat to other, smaller larids, due to both predation and competition for nest sites (Bergman 1982, Burger 1979).

Kilpi et al. (1980) have previously reported that *L. f. fuscus* is declining in the Gulf of Finland. According to the data compiled here, *L. f. fuscus* is decreasing in most coastal areas of Finland. This trend is in contrast to the increase of the species in other areas. The race *L, f. graellsii* seems to be increasing in the British Isles (Brown 1967, Davis & Dunn 1976), and Götmark (1982) has reported an increase in SW Sweden *(L. f. intermedius).*

The reason for the decline in Finnish *L. f. fuscus* are not known, but several factors are probably involved. I argue that one reason in some areas is selection of *L. fuscus* colonies by breeding *L. argentatus,* which subsequently causes competition for nest sites. However, *L. fuscus* is also declining in areas where *L. argentatus* is still scarce (e.g. Valassaaret), so additional factors must be involved. In many areas along the south coast,

Table 4. Change in the location of nests of *L. fuscus* during the increase of a *L. argentatus* population on an islet.

Year	Nest-site of *L. fuscus* Open N	Open %	Concealed N	Concealed %	Pairs of *L. argentatus*	References
1942	48	(74 %)	17	(26 %)	15	Bergman 1965
1965	22	(22 %)	76	(78 %)	147	Bergman 1965
1979	0	(0 %)	8	(100 %)	314	Kilpi 1980, unpubl.

L. fuscus has been observed to have very low reproductive output (Hario 1981, own data), but the reasons for this are speculative.

Colony selection and competition for nest-sites. Gulls have deferred maturity. Chabrzyk & Coulson (1976) found that in a British colony of *L. argentatus,* the mean age for the breeding début was 5.25 years. Both species treated here are migratory but young age-classes will return in several summers to the breeding area before breeding (Kilpi & Saurola, unpubl.). As non-breeders the gulls familiarize themselves with potential breeding sites, and local opportunities for feeding. The stimulus to settle on a particular islet must come either from the physiognomy of the islet, or from the presence of other larids. Many species of larids tend to breed in existing colonies of other larids (Buckley & Buckley 1980). *L. argentatus* invading new areas along the Finnish coast evidently prefers to settle in colonies of *L. fuscus.* At the start of the invasion, there is an abundance of topographically suitable islets, yet *L. fuscus* islets are selected. This implies that *L. argentatus* selects the breeding colony during its pre-breeding life, since breeding adults return to the colonies considerably earlier than *L. fuscus* (Kilpi & Saurola, unpubl.). As the *L. argentatus* population expands, other islets are also used, and the birds may prefer to breed among conspecifics.

In New Jersey, Burger (1977) found that in newly established *L. argentatus* colonies there was an initial preference for dry elevated areas as nest sites. Such areas were restricted, and as a colony grew, other habitats were used as well. This broadening of nest site selection led to direct competition for space between *L. argentatus* and the Laughing Gull *L. atricilla* breeding on the same islands. *L. atricilla* is a considerably smaller species, and exclusion occurred (Burger 1979). There is a considerable difference in size between *L. argentatus* and *L. fuscus* breeding on the Finnish coast. The average weight of a male *L. fuscus* is c. 30 % smaller ($\bar{x}$=819 g) than that of a male *L. argentatus* ($\bar{x}$ = 1210 g, data in both cases from Barth 1967). Thus, at least theoretically, *L. fuscus* may be expected to lose in territorial clashes, since body size and dominance are related in birds (Burger et al. 1979). The situation is further aggravated by the fact that most of the *L. fuscus* adults do not return from the winter quarters before the bulk of the breeding *L. argentatus* have completed their clutches (Kilpi & Saurola, unpubl.).

On her study islands, Burger (1980) found that *L. argentatus* defended territories up to 100 m^2 in area. In one colony in Kirkkonummi (see Table 4), the space available for the two species in 1937 was 263 m^2, and in 1979 it was only 47 m^2. On this particular islet the decline of the *L. fuscus* population began roughly when the density of *L. argentatus* approached 1 pair/100 m^2 (Fig. 5). Since the physiognomy of the islets shared by the two species along the south coast of Finland does not seem to vary very much, this density may be used to predict whether there is serious nestsite competition between the two species.

Table 5. Fate of the four largest *L. fuscus* colonies in Kirkkonummi.

Species	Number of pairs		
	1937	1965	1979*
L. fuscus	52	100	8
L. argentatus	5	147	314
L. fuscus	27	. .	0
L. argentatus	42	. .	425
L. fuscus	49	. .	0
L. argentatus	58	. .	356
L. fuscus	45	. .	0
L. argentatus	4	. .	800

* Data collected by Kilpi and Puntti & Toivonen from nest counts, see Kilpi (1980), other data according to Bergman (1939, 1965).

The main issue concerning the exclusion of *L. fuscus* is whether *L. argentatus* broadens its nest site selection as the number of pairs on a shared islet increases. This is clearly the case, though quantifications of habitat use are not yet available. For example, in an old colony near Helsinki, I found *L. argentatus'* nests in all but one available habitat type, including cliff, meadow, rocky shore, bushes and a sandy ridge. The only habitat not used for nesting was a very exposed beach of small stones, where there was a small cluster of *L. fuscus* nests.

Thus, it seems that on the Finnish coast, *L. argentatus* is expelling *L. fuscus* by first selecting colonies of the latter species for breeding, and later occupying habitats originally used by *L. fus-*

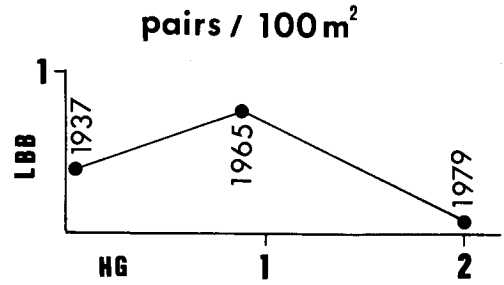

Fig. 5. Density of *L. fuscus* (LBB) plotted against density of *L. argentatus* (HG) on an islet in Kirkkonummi.

cus as nest sites. This exclusion is no doubt facilitated by the early arrival and larger body size of *L. argentatus*.

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Selostus: **Suomen rannikkoalueen harmaa- ja selkälokkikannan kehitys ja lajien pesäpaikanvalinta**

Artikkelissa käsitellään harmaa- ja selkälokin rannikkokantojen kehitystä viime vuosikymmeninä. Useimmilla tutkituilla alueilla selkälokki runsastui aina 1960-luvulle, jonka jälkeen kannat ovat taantuneet. Harmaalokki sen sijaan on runsastunut koko rannikkoalueella.

Tietyn alueen valtauksen alkuvaiheessa harmaalokki tuntuu hakeutuvan jo olemassaoleviin selkälokkiyhdyskuntiin pesimään. Näin syntyneissä sekayhdyskunnissa harmaalokki aluksi suosii luodon tai saaren avoimia, kallioisia osia pesimäympäristönä. Selkälokki pesii enemmän kasviston suojassa. Kun harmaalokkiparien määrä sekayhdyskunnassa lisääntyy, alkavat ne pesiä myös selkälokin käyttämässä ympäristössä. Tämä johtaa kilpailuun pesimäpaikoista, ja harmaalokki todennäköisesti aina vetää pidemmän korren suuremman kokonsa ja aikaisemman saapumisensa ansiosta. Sekayhdyskunnat ovat näin ollen epävakaita, ja ennen pitkää selkälokki häviää niistä. Selkälokin häviämisnopeus riippuu toistaiseksi tuntemattomista, tiheydestä riippuvista seikoista (harmaalokin reviirikoko, saalistuspaine). Koska selkälokkikannat taantuvat myös sellaisilla alueilla, missä harmaalokkeja on vähän, vaikuttavat myös muut tekijät kannankehitykseen.

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