The Arctic Tern Sterna paradisaea — a new inhabitant of the inshore archipelago

LARS VON HAARTMAN

v. HAARTMAN, L. 1982: The Arctic Tern Sterna paradisaea — a new inhabitant of the inshore archipelago. — Ornis Fennica 59:63—76.

Before World War II Arctic Terns were considered to breed exclusively in the offshore parts of the Finnish archipelago. The first pair breeding inshore was observed by the author in 1941 in his study area in SW Finland. The further development of the population was followed by continuous censusing of the area. From the 1950s on, the population increased and spread. In 1965-69 this process accelerated and Arctic Terns were found breeding on islets close to the mainland. The population growth still (1981) continues. It is suggested that chironomid catching has been a prerequisite for

It is suggested that chironomid catching has been a prerequisite for the invasion of the inshore archipelago by Arctic Terns. Either, a large chironomid population already existed in this part of the archipelago, representing a potential but long unexploited source of food. Or, as suggested by recent quantitative studies of the bottom fauna, chironomids have increased enormously as a consequence of eutrophication of the water.

The behaviour of chironomid-catching Arctic Terns is described. Terns feeding in this way were observed from shortly after their arrival until their departure from the area, maximum numbers being noted after the hatching of the young.

Arctic and Common Terns occupy different niches in the inshore archipelago. A slight increase in the population of the Common Tern took place simultaneously with the population increase of the Arctic Tern.

Lars von Haartman, Dept. of Zoology, Univ. of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland.

Dedication

Of all the teachers I have had, two stand out in my memory as especially inspiring, the schoolmistress who taught me art in the middle school, and a young university lecturer, who — in addition to all his other merits was an ornithologist. One essential feature they had in common was their enthusiasm. I remember as if it were yesterday the remark made by Pontus Palmgren, when as a freshman I told him about working in the archipelago of SW Finland. "Well", he said, "it is a fascinating region. One may find Arctic Terns and Great Crested Grebes nesting in almost the same area". As the result of a dramatic enlargement of the breeding habitat of the Arctic Tern, both species, today, do nest in the same area. This phenomenon and its causes are the subject of the present study, which is dedicated to my ornithology teacher on his 75th birthday.

The morphology of the Finnish archipelago

The archipelagos lying off Finland and Sweden in the Baltic Sea are unrivalled in the number of their islands. This applies especially to the SW archipelago of Finland, including the Aland islands (known as the



FIG. 1. Schematic representation of a Finnish archipelago. Left: archipelago typical of the S coast, right: typical of SW Finland. In the narrower archipelago the change from inshore to offshore archipelago is relatively regular and continuous, in the larger archipelago a large open-water area $(fj\ddot{a}rd)$ extends deep into the middle parts of the archipelago, bringing irregularity into the structure of the archipelago. For discussion see text.

"Archipelago Sea"), and its continuation, the Swedish "Archipelago of Stockholm" or Swedish "Archipelago Sea", from which it is divided by the narrow Sea of Aland. The number of islands and islets in this twin archipelago well exceeds 30,000.

Going from the coast in southern Finland toward the open sea, one witnesses a series of geographical and biogeographical changes, somewhat reminiscent of those seen on the ascent of a tall mountain or, on a larger scale, when travelling e.g. from S Scandinavia to Lapland.

The physiographical and biological gradients observed in the archipelago are the direct or indirect outcome of its peneplain gradually sloping downward until it is submerged in the Baltic. Familiar as these changes are to every Finn, they are extremely difficult to convey to a foreigner; our archipelago is unique. Fig. 1 gives a schematic view of what the archipelago may be like.

Close to the coast of the mainland, there is a broad spectrum of islands, varying greatly in size and nature, from small barren rocks to wooded islands several tens of kilometres in length and bearing farms and forest. The waters separating the islands are shallow and narrow. The water is opaque, and almost all the shores are surrounded by reeds. The wave action is moderate, so that small rocks and islets may bear vegetation. As one approaches the open sea, the islands become smaller and more barren, the separating waters deeper and wider. The water becomes transparent and the reeds disappear. Surf, wind and lack of soil influence the vegetation. Wooded islands become rarer, and the trees crippled. The extreme offshore archipelago consists of barren skerries with little or no vegetation.

The first systematic study of these basic features was carried out by Häyrén (1900, 1948). In the archipelago of Tammisaari/ Ekenäs off the south coast of Finland, in addition to the mainland, he distinguished four different zones, more or less parallel to the coast. This division was followed by Sundström (1927), who was the first to map the zones and the distribution of the archipelago birds. The narrower archipelago SW of Helsinki was divided by Bergman (1939) into three zones. In the Stockholm archipelago Wibeck (1939, 1957) discerned a Razorbill Alca torda, an Eider Somateria mollissima, and a Velvet Scoter Melanitta nigra zone, coinciding to some extent with du Rietz's (1923) treeless zone, zone of deciduous forest and zone of needle forest. A narrow strip along the mainland was not included and may, perhaps, be added as a fourth (Podiceps cristatus?) zone. In its narrower parts, the Stockholm archipelago lacks one zone, the Eider or deciduous marine forest zone.

In the large SW archipelago of Finland the zonation is unusually complex. Large islands located far from the mainland interrupt the regular sequence of zones, acting as gigantic breakwaters and wind-breaks, and giving rise to a kind of secondary inshore archipelago. Here and there, again, large open waters, known as fjärds, penetrate deep into the inner parts of the archipelago. With respect to the bird fauna and the vegetation they form a kind of exclave of the offshore archipelago. In a strict sense, they do not form a zone, as they break the sequence of parallel zones. For this kind of archipelago I have created the name *fjärd* archipelago or "zone" (v. Haartman 1945). The entire archipelago of SW Finland is more a mosaic of different archipelago types than a set of homogeneous belts.

Recently Granö (1981) has reviewed the historical and philosophical background of the zone concept, taking as his starting-points geography and botany. The neglect of the bird fauna in this context is perhaps due to the diminutive size of birds in comparison to geological formations and the vegetation. But birds are perfect biological indicators, probably more sensitive than any plants. Further, thanks to the examples of Sundström (1927), and even more of Palmgren (1930), the occurrence of the archipelago birds has been viewed from a quantitative standpoint for half a century, ornithology thus being methodologically far ahead of botany.

In the present publication I will use the simplest possible division of the archipelago, into an inshore and an offshore archipelago. In the area studied by me, the transition from the one to the other is unusually dramatic. It takes place through the narrow inlet of Palva, known from the sea battle in the reign of Charles XII. Here, suddenly, the inshore waters open into the wide Iniö *fjärd* (Iniön aukko). Towards the south, the archipelago slowly changes into a more offshore type, but the area studied by me may safely be characterized as inshore.

A bipartite division of the archipelago is, of course, a simplification, but it is sufficient in the present context. A basically similar division was used by Fabricius (1937).

Census method

Terns were censused from about 20 May to the beginning of July, exceptionally to mid-July. Either the maximal numbers of terns swarming over the breeding place were counted and halved to obtain the pair number, or the nests were counted. Nest counting was preferred when (1) the island was small and the possible nest sites were easily surveyed, (2) the number of terns was large, (3) Arctic and Common Terns bred together, in which case it may be difficult to census them separately by sight (cp. Suomalainen 1939). Both methods should give numbers slightly below the correct ones. If an islet was censused repeatedly in the same season, which was often the case, the maximum number observed was chosen. This, again, tends to give a slightly too high result, as replacement clutches will be treated as separate pairs.

In the following text, time is generally divided into lustra. If an island was not censused during a certain period, the average number of the preceding and following 5 years was used, but this procedure was necessary only in exceptional cases.

Spread of the Arctic Tern

In 1945 the following nine species were considered typical of the offshore archipelago of SW Finland, including the fjärd archipelago (v. Haartman 1945, but the species determination corrected for *Anthus*, and *Alca* included):

| Arenaria interpres | Stercorarius parasiticus |
|--------------------|--------------------------|
| Larus marinus | Alca torda |
| L. argentatus | Cepphus grylle |
| Sterna caspia | Anthus spinoletta |
| S. paradisaea | 1 |

Seven of these species were not found breeding in the inshore area censused by me, but single pairs of the Great Black-backed Gull and the Arctic Tern occurred there even then. Their distribution was similar to that of the arch-type of Eklund's (1937, 1958) "skerry plants" (Schärenpflanzen), Cochlearia danica, which was found on five islets in inshore Velkua, far from the open sea and large fjärds, where it is thought by botanists to be typical.

No less than four of these nine species have recently invaded the inshore archipelago. The Turnstone is still scarce and has not bred on islets



FIG. 2—5. Spread of the Arctic Tern in an inshore part of the archipelago of SW Finland (parishes Merimasku, Askainen, Velkua) during three decades. Smallest islet not mapped. Thick line: mainland. As the same pair may have bred on several islands during a decade, the map to some extent exaggerates pair numbers, cp. Fig. 6. Size of dots indicates pair number.

adjacent to the mainland. The Herring Gull has become abundant and ubiquitous in the Baltic archipelago and now breeds in my inshore archipelago in colonies and single pairs. The Great Black-Backed Gull is still relatively scarce in the inshore archipelago and not particularly abundant in the offshore one either. Finally, the Arctic Tern (= AT) has spread to the inshore archipelago in a spectacular way.

In 1941 the first record of the AT breeding inshore was made on the treeless point of a small wooded island, Loukeenkari S of Hautaluoto (or Hautluoto or Haukluoto) in Velkua (v. Haartman 1945). Since then, the AT has alternately nested and been absent from this island. In 1980 it still nested there. Among the other species found breeding on the island was the Kestrel *Falco tinnunculus*, a somewhat unexpected neighbour of the tern.

The spread of the AT can be followed from Figs. 2-7. Only from the mid-1950s on were there signs of a true population increase. The ATs still bred within a nautical mile of their first breeding site, but they now colonized several islets. In 1965-69 the growth of the population accelerated markedly, new areas were occupied and the first pairs settled with-



in a few hundred metres of the mainland. The population is still (1981) growing rapidly.

Today, the AT breeds as far inshore as possible. In 1971 a pair even occupied a point on the mainland at Lemsjöholm, and held this territory for almost a fortnight, disappearing, however, before the end of May, either because of the rising water level or because of immaturity. In the inshore area non-breeding but territorial ATs were strikingly numerous, as could be expected in a growing population with a presumably large recruitment of young individuals. In 1978 a pair of ATs was found at the Naantali fjärd (Naantalin aukko), an inshore water surrounded by mainland and two large islands, and connected with somewhat more open waters only through three inlets, no



wider than rivers. I wonder whether these ATs ever see open water during their breeding season. In this respect they could equally well breed on a lake of moderate size.

Most breeding places of the AT in the inshore archipelago consist of treeless islets. ATs often breed together with Common Terns Sterna hirundo but smaller monospecific colonies of ATs occur far inshore. A minority of the breeding places of both terns were on wooded islands, though less often than with the Common Gull Larus canus. With the terns as with the Common Gull (v. Haartman 1980), NW points were preferred. During the glacial periods these were on the side attacked by the ice cap and they are, consequently, well polished, offering few crevices where trees can take root.

Climate change versus eutrophication as a cause of the spread of the Arctic Tern

The climate theory, en vogue in Finornithology from 1936 for nish about quarter of a century onwards, could apparently apply to the in-shore spread of the AT. Since the thirties, there has been a slight decline in the average temperatures. Summer temperatures are higher inshore than offshore, and so the inshore areas could form a climatic borderland for arctic species (Ekman 1922). There is, however, no evidence that ATs ever nested in the inshore archipelago during the cool 19th century. Moreover, the climate theory becomes absurd, if we look at the four species which have recently invaded the same inshore archipelago as the AT, but from the opposite direction, so to speak, i.e. from eutrophic lakes and sea bays. These species are:

| Aythya ferina | Acrocephalus scirpaceus |
|---------------|-------------------------|
| Fulica atra | Emberiza schoeniclus |

The three first-mentioned species are southerly members of the Finnish bird fauna and could not possibly be favoured by recrudescence of low temperature. All four are, however, favoured by eutrophication as this promotes the growth of reeds. As eutrophication is brought about by man, these species fit into the theory that man-made changes in nature, and not climatic fluctuations, form the main cause of the recent changes in the bird fauna of North Europe (v. Haartman 1973).

It is, indeed, surprising to find the AT breeding on the same islet as the Pochard, which nests in the reeds along the shore or in crevices with some vegetation as does the Tufted Duck Aythya fuligula. It is also

strange to search for nests of the AT to the accompaniment of the song of nearby Reed Warblers or the Thrush Nightingale *Luscinia luscinia*, another newcomer in the area.

Chironomids as food of the Arctic Tern

The role of food in the ecology of the AT has repeatedly attracted attention. Kullenberg (1947) found a close correlation between the local productivity of the oceans and the migratory routes of the AT. Poor feeding conditions were observed to retard laying and reduce clutch size in the species (Boecker 1967, Lemmetyinen 1973b). In a comprehensive study of the food of the AT in the SW archipelago Finland, Lemmetyinen (1973b) of found that its staple diet consisted of Three-Spined Sticklebacks Gasterosteus aculeatus. Insects were taken frequently, but only a single AT had eaten chironomids, no less than c. 300 being found in its alimentary canal. Later Lemmetyinen (1976:637) observed that "when insect swarms (especialchironomids and Hymenoptera lv species) were abundant, Arctic Terns were also seen to catch them above small eutrophic lakes and bays but seldom fished there."

Recently Mikkola (1980) published two observations of terns catching chironomids in inshore waters of the Gulf of Finland. In the one case there were c. 30 ATs, in the other a few Common Terns. Chironomid catching by Common Terns was recently observed in Sweden, too (Vuorinen 1980).

Although my studies in the archipelago commenced in the mid-1930s, no chironomid catching was observed in terns until 1965. Since then, the



F10. 6. Average annual numbers of pairs of Arctic (_____) and Common (---) Terns during lustra in two areas in the inshore archipelago of SW Finland (parishes Merimasku, Askainen, Velkua). Above: larger area (c. 90 km², limits indicated by the names Livonsaari, Hautaluoto, Yllänpää, Kuusluoto, Vuchiluoto, also including a few islands in Musta-aukko). Below: smaller area (c. 1 km², consisting of 9 woodless islets W of Teersalo, Velkua).



FIG. 7. Number of pairs of Arctic Terns as percentage of corresponding number of Common Terns in the areas treated in Fig. 6, inshore archipelago of SW Finland.



FIG. 8. Catching swoop of Arctic Tern. Wavy line = active flight, straight line: gliding. Cp. text.

phenomenon has been noted down every year (except when I obviously considered it to be too commonplace), in some years repeatedly, e.g. on 6 days in 1970 and on 4 in 1975, not to mention 1980 and 1981, when this report was prepared. The maximum numbers of terns observed feeding in this way have increased:

| 196569 | 20 |
|---------|-----|
| 1970-74 | 70 |
| 1975—79 | 100 |

The vast majority of the chironomid-catching terns were ATs, though Common Terns were occasionally seen among them, and in 1981 a few terns were seen at a distance catching chironomids after all the ATs had probably disappeared. Other species, seen catching chironomids together with the AT were Black-headed Gulls Larus ridibundus, perhaps a few Common Gulls. Swallows Hirundo rustica, a few House Martins Delichon urbica, and Sand Martins Riparia riparia. Swifts Apus apus were seen catching chironomids fairly often and in numbers up to c. 10. The Swifts flew rapidly at an altitude of c. 1 m, now and then flying down to about 10 cm from the water and up again.

When catching chironomids (Fig. 8), the terns fly to and fro seemingly haphazardly, but obviously remaining over a more or less circumscribed area where the prey is abundant. The altitude of the terns varies around 2 m. At short intervals they perform a "catching swoop", gliding down on spread, immobile wings, and when almost touching the water, turn the bill straight down. The tip of the bill may actually touch the water, as shown by ipples at the surface when the sea is calm. Then, with wings still spread and immobile, the tern regains some height until, losing momentum, it changes to active flight and returns to its original altitude. On close distance one sees the tern opening and closing its bill to catch its minute prey.

The flight of a huge number of terns, continuously interrupted by stereotyped catching swoops, is a striking spectacle, which in my notebooks appears under the name "chironomid ballet". It is not surprising that the AT is the main performer in this ballet. Thanks to its longer tail feathers and lower weight it is likely to be better adapted than the Common Tern for the swift manoeuvres of the chironomid ballet (cp. e.g. Welty 1975:449 and Rüppell 1980: diagram p. 143). In the Finnish bird fauna the Swallow, the Long-tailed Skua Stercorarius longicaudus and the occasionally visiting Bee-eater Merops apiaster are other examples of this elegantly moving "catcher" type of bird. The Common Tern is c. 14 % heavier than the Arctic (v. Haartman et al. 1963-72), and its broods tend to be larger, which may make the pursuit of small insects unprofitable for this species.

Mikkola (1980) assumes that the terns catch chironomid pupae rather than imagines. The pupa rises from the bottom and floats at the water surface while the imago struggles to free itself. This would, undoubtedly, be a suitable moment for a predator to strike. However, the eclosion and departure of the imago takes only about a minute. Further, according to Palmén (1955), chironomids mainly hatch after sunset. Only arctic and spring chironomids show another rhythm, adapted to the optimal daily temperatures (Kureck 1980). Under these circumstances, it is difficult to see how terns in June and July could feed mainly or exclusively on pupae. Chironomid hunting was seen by me from 11 a.m. (only occasional investigations before noon!) to 10 p.m., with maximum numbers noted between 3 and 9 p.m.

For creatures flying so elegantly as ATs, chironomid imagines should not be difficult to catch when they are resting on the water or in flight. I have repeatedly caught flying chironomids with my bare hand, though hampered by reduced mobility of several finger joints and by farsightedness. But if terns mainly take imagines, they certainly prefer those close to or on the surface, as the catching swoops are always directed toward the water. The question could, of course, easily be solved by sacrificing a single tern, but after a lifetime spent with living creatures I would rather be mistaken than kill a tern.

At times ATs may catch insects, probably chironomids, above tree tops close to the shore. I have seen this behaviour after sunset. The terns flew in the same "staggering" way as do gulls catching swarming ants.

Chironomids were mainly caught by the terns above relatively shallow water (depth to a few m) with a muddy bottom. The largest numbers of terns were seen along the navigable channel leading from the cities of Turku and Naantali westward through the parishes of Merimasku (A), Askainen and Velkua (B), but they were also observed outside eutrophic bays. In 1980, I caught a number of chironomids flying or swimming in areas frequented by flocks of ATs. The species were determined by Dr. Bernhard Lindeberg.

| Time and place | Species or Genus | No. and sex |
|---------------------------------------|--|--|
| 26 June, A 29 June, A 9 July, B | Chironomus sp. Procladius sp. Chironomus plumosus Chironomus ?plumosus Microchironomus tener | 10500000000000000000000000000000000000 |

Microchironomus tener is a dwarf, and probably does not play any important role as food for the AT. Chironomus plumosus was the species observed by Mikkola (1980) to be taken by ATs on the S coast of Finland. It is abundant practically throughout the time that the AT is

present in Finland (Palmén & Aho 1966). The first observation of chironomid hunting stems from 15 May 1981, the last observations from 15 July 1981 and from 21 and 22 July 1980, in both years just before the disappearance of the AT from the area. Maximal numbers of terns catching chironomids were recorded from 11 June (at the time when the young hatch) to the end of the month. In 1980 the first fledgling was seen performing catching swoops on 9 July, when it cannot have been fledged for very long. According to Lehtonen (1981) young Common Terns show their first catching attempts at an age of 28-32 days (fledging age 22-24 days).

Such small objects as midges will have to be caught in copious numbers¹) to satisfy the needs of the adult terns and their broods. The frequency of catching swoops averaged no less than c. 7 per minute. In 12 cases single birds were observed for c. 1 minute and the swoops recorded. In the following table the figures have been recalculated as numbers per minute (A = catching swoops/min., B = birds observed):

A 3 4 5 6 7 8 9 10 11 12...19 B 1 - 3 2 - 2 1 1 - 1 1

Seven swoops per minute equals over 400 in the hour. This explains the large number of chironomids which may be found in a single tern (cp. p. 69). It also explains why the AT in the inshore archipelago is able to feed mainly on these minute creatures.

Have chironomid numbers increased?

Have the chironomids long constituted a large potential source of nutrition, an unexploited bonanza in the inshore waters, or have their numbers only recently sky-rocketed, enabling the AT to invade this new habitat?

The second alternative is at least possible. Chironomids are characteristic of eutrophic waters (e.g. Thienemann 1931, Leppäkoski 1975, Bonsdorff 1981). The recent eutrophication of the coastal waters of the Baltic is well known, and locally constitutes a serious problem. Changes indicative of eutrophication in the vegetation of my study area were mentioned in the paragraph "Climate change versus eutrophication".

The eutrophication of the coastal waters is brought about by several factors. Modern farming and forestry use enormous amounts of artificial manure, some of which inevitably ends up in the sea. Waste waters from human settlements may play a role, especially as the number of summer houses has increased rapidly in the inshore archipelago, though generally they do not seem to discharge sewage to the sea. The traffic of small motor boats, which has increased a hundredor thousandfold during the last 50 years, probably contributes by emulsifying organic compounds in the water. It is perhaps no accident that large numbers of terns catching chironomids were seen along the navigable channel from Turku and Naantali to the NW parts of the "Archipelago Sea". Factories do not exist in the study area, but a new source of eutrophication seems to be pisciculture, started during recent years. Our knowledge of the sources of eutrophication is probably far from complete. A factor of some importance may be that reeds

¹) According to a recent publication by Johansson (1981), the bird fauna of an area in Lapland survived a prolonged snow-weather, living on midges emerging in unusually large numbers.

have grown copiously, and that their decay promotes further spread and growth of reeds — a vicious circle.

Unfortunately, the study of bottom faunas has lagged behind the bird censuses in the archipelago. In the Turku-Naantali area data are available on the chironomid population from 1975 on. They show a considerable increase in the numbers and biomass of the chironomids. The following data on the important Chironomus *plumosus* stem from the *fjärd* of Naantali (Naantalin aukko), just east of my study area (data from Juuti & Leppäkoski 1976 and Rajasilta & Vuorinen 1981). The numbers had increased at all the sample sites, though there were indications of lessening pollution in parts of the Naantali fjärd:

| No. of sample site | | 1 | | | |
|--------------------|------------|----------|------|------|------|
| Yea | ır . | | | 1975 | 1979 |
| No. | of C_{i} | plumosus | ĩ | 188 | 477 |
| 9 | Ð | 2 | 2 | 1 | 9 |
| 1975 | 1979 | 1975 | 1979 | 1975 | 1979 |
| 5 | 91 | | 510 | 78 | 92 |

It may seem strange that artificial forest manuring could contribute to the growth of a tern population. But in ecologic causal chains are often complex.

Ecological niches of Arctic and Common Terns

As Common Terns seldom catch chironomids, the two similar tern species occupy different niches with respect to food. Whether this is an indispensable condition of their peaceful coexistence in the inshore archipelago, cannot be decided. The applicability of the somewhat hackneyed competitive exclusion principle (two species cannot compete for the same food) and Gause's rule (two species cannot compete for the same food, unless there is a predator causing strong fluctuations in their populations) is still debatable, probably because competition in nature never involves so few species, but takes place against a "background" of diffuse competition. Lemmetyinen (1973b, 1976) also found a considerable difference in food between the two terns, whereas Boecker (1967) found less, and Pearson (1968) no difference.

As is well known (e.g. Bergman 1937, Suomalainen 1939), the two terns also show different preferences with respect to nest sites. The crevices used for nesting by the AT in my study area had without exception short or no vegetation, according with the extremely short legs of the species, in the same manner as the chironomid hunting accords with its prolonged tail feathers, small broods and light weight. It does not seem likely that lack of breeding sites restricts population size in the Arctic and Common Terns. The different nest sites chosen by the two species can, therefore, hardly be a consequence of mutual competition, unless this has taken place under different conditions than those prevailing in the SW archipelago of Finland.

The population development of the two terns (Fig. 6) does not indicate any competition. The population explosion of the AT in the inshore archipelago took place simultaneously with some slight increase in numbers of the Common Tern.

Clutch size

Overpopulation in territorial species may cause failure to breed in the surplus or its exodus into inferior habitats (discussion in v. Haartman 1972). The AT is known to have become more numerous in some offshore areas (v. Haartman et al. 1963—72). Is it a surplus which has now invaded the inshore archipelago?

My incomplete observations do not confirm any population increase in the AT in the $fj\ddot{a}rd$ archipelago outside my inshore study area. A kind of population pressure could have been exerted by Herring Gulls occupying some of the breeding sites of the AT. At any rate, the inshore archipelago does not seem to be suboptimal for the AT at present.

The clutch size may throw some light on the food supplies available in different habitats. Lemmetyinen (1973a) found that the clutch size in his "middle zone" was larger than in his "outer zone", both situated not far from my study area. He considered that this difference was probably caused by the adverse food situation in his outshore archipelago during the egg-laying time.

As annual differences in clutch size were negligible (Lemmetyinen op. cit.), I have lumped the data available from my inshore archipelago from 1979—1981 in the following table. Only some of the clutches (A) were established to be complete by applying the "water test" to the eggs or by checking the clutch repeatedly. The other clutches (B) were assumed to be complete, since they were found well after the main laying time on nest sites that had obviously not been plundered.

Clutch size

| A B | 1 4 7 | 2 26 52 | 3 6 13 | N 36 72 | Mean 2.06 2.08 |
|--------|-------------|---------------|--------------|---------------|----------------------|
| Total | 11 | 78 | 19 | 108 | 2.07 |

My average, 2.07 ± 0.1 , should be compared with Lemmetyinen's average for his middle archipelago, 2.03 ± 0.02 , and for his offshore archipelago, $1.6\pm$ 0.05 (N 140) and in another set $1.6\pm$ 0.08 (N 56). The difference between the inshore and offshore archipelagos is large (0.5 eggs = $31^{\circ}/_{\circ}$) and statistically significant, indicating that the inshore archipelago represents the ecological optimum. I have no exact data on the success of broods in the inshore archipelago, but my general impression is that it is good.

A circumstance which must be remembered in connection with population increase in archipelago birds, is that plundering of birds' nests by man has practically been abandoned in the postwar period. As the Common Tern population has increased only slightly, I would not, however, ascribe decisive importance to this factor.

Acknowledgements. So many ornithologists have helped me on excursions, that I cannot mention them all by name. One of them, Mr Rauli Lumio, has accompanied me one or several times every year for about a decade. Dr. Bernhard Lindeberg kindly determined the chironomids, E. Bonsdorff, M. A., gave me references about the development of the chironomid fauna in the archipelago of Turku.

Selostus: Lapintiira, uusi sisäsaariston asukas

Ennen 1940-luvun alkua lapintiiraa pidettiin yksinomaan ulkosaariston pesimälintuna Suomen rannikolla. Kirjoittajan tutkimusalueella lounaissaaristossa se kuului levinneisyydeltään samaan ryhmään kuin esim. karikukko, merilokki, räyskä, ruokki ja riskilä. Ensimmäinen lapintiirapari tavattiin pesivänä sisäsaaristossa 1941 (kuva 2). Kanta alkoi selvästi runsastua ja levitä sisäraaristoon 1950-luvun keskivaiheilla (kuva 3), ja kasvu nopeutui vielä 1960luvun jälkipuoliskolla (kuva 4); 1970-luvulla (kuva 5) laji pesi jo kaikkialla alueen sisäsaaristossa, yksi pari (1978) jopa avomerestä täysin eristyneessä Naantalin aukossa. Pesimäpaikkoina ovat enimmäkseen puuttomat pikkukarit, harvemmin metsäsaarten puuttomat, mannerjäätikön sileiksi hiomat luoteiskärjet. Kannan kasvu, verrattuna alueella melko vakaana pysyneeseen kalatiirakantaan, on esitetty kuvissa 6 ja 7.

Tekijän käsityksen mukaan surviaissääskien pyynti on ollut edellytyksenä sisissaariston valtaukseen. Vaikka tutkimukset alueella alkoivat jo 1930-luvun puolivälissä, ensimmäiset sääskiä pyytävät lapintiirat havaittiin vasta 1965. Sen jälkeen tiirojen on todettu käyttävän tätä ruokailutapaa vuosi vuodelta yhä yleisemmin ja suuremmin joukoin toukokuun puolivälistä heinäkuun lopulle, eniten poikasten kuoriutumisen jälkeen. Tiirojen pyyntitekniikkaa on kuvattu (ks. kuvaa 8).

Varmaa vastausta ei ole siihen, ovatko surviaissääsket olleet kauan käyttämättömänä ravintovarana vai onko niiden määrä tavattomasti kasvanut ja siten avannut lapintiiralle mahdollisuuden levitä sisäsaaristoon. Jälkimmäinen vaihtoehto tuntuu todennäköiseltä, koska rannikkovedet ovat suuresti rehevöityneet ihmistoiminnan tuloksena. Naantalin aukon pohjanäytteet vuodesta 1975 eteenpäin osoittavatkin Chironomus plumosus-lajin huomattavaa runsastumista.

Kala- ja lapintiiran jonkin verran erilaiset ravinto- ja pesäpaikkavaatimukset tutkimusalueella eivät tunnu johtuvan keskinäisestä kilpailusta. Sisäsaaristo ei myöskään näytä edustavan suboptimaalista ympäristöä lapintiiralle, vaan suurempi pesyekoko ulkosaaristoon verrattuna viittaa pikemmin päinvastaiseen. Leviämistä saariston sisäosiin ei täten voida selittää johtuvaksi ylitiheydestä ulkoluodoilla.

References

- BERGMAN, G. 1939: Untersuchungen über die Vogelfauna in einem Schärengebiet westlich von Helsingfors. — Acta Zool Fennica 29:1—134.
- BOECKER, M. 1967: Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flussseeschwalbe (Sterna hirundo L.) und der Küstenseeschwalbe (Sterna paradisaea Pont.). — Bonn. Zool. Beitr. 18:15—126.
- BONSDORFF, E. 1981: Pohjaeläimistön kehitys Raisionlahdessa 1976–1979. – Lounais-Suomen Vesisuojeluyhdistys r.y. 48:83 –94.
- Du RIETZ, E. 1923: Det uppländska skärgårdshavet och dess framtid. — Sveriges Natur.
- DU RIETZ, E. 1925: Die Hauptzüge der

Vegetation des äusseren Schärenhofs von Stockholm. — Svensk Botanisk Tidskr. 19.

- EKLUND, O. 1937: Klimabedingte Artenareale. — Acta Soc. Fauna Flora Fennica 60: 309—326.
- EKLUND, O. 1958: Die Gefässpflanzenflora beiderseits Skiftet im Schärenarchipel Südwestfinnlands. — Bidrag t. Känned. Finl. Natur o. Folk 1—324+XVIII pp.
- EKMAN, S. 1922: Djurvärldens utbredningshistoria på Skandinaviska halvön. — Stockholm.
- FABRICIUS, E. 1937: Några iakttagelser rörande viggens, Nyroca fuligula (L.), beroende av måsfåglarna såsom häckfågel i skärgården. — Ornis Fennica 14:115 ---125.
- GRANÖ, O. 1981: The zone concept applied to the Finnish coast in the light of scientific traditions. — Fennia 159:63 —68.
- V. HAARTMAN, L. 1945: Zur Ekologie der Wasser- und Ufervögel im Schärenmeer Südwest-Finnlands. — Acta Zool. Fennica 44:1—120 + VIII.
 V. HAARTMAN, L. 1972: Influence of territory
- v. HAARTMAN, L. 1972: Influence of territory upon structure and dynamics of bird populations. — Population Ecology of Migratory Birds. Bureau of Sport Fisheries and Wildlife Research Report 2: 101—111.
- v. HAARTMAN, L. 1973: Changes in the breeding bird fauna of North Europe and their causes. — Breeding Biology of Birds. Nat. Acad. Sci. Washington D.C.:448 —481.
- v. HAARTMAN, L. 1980: Nest sites of the Common Gull Larus canus in relation to the ice age geology and other factors. — Ornis Fennica 57:11—16.
- v. HAARTMAN, L., O. HILDÉN, P. LINKOLA, P. SUOMALAINEN & R. TENOVUO 1963—72: Pohjolan linnut värikuvin. — Helsinki.
- HÄYRÉN, E. 1900: Längszonerna i Ekenäs skärgård. — Geogr. Fören. Tidskr. 12:222 —234.
- HÄYRÉN, E. 1948: Skärgårdens längszoner. Skärgårdsboken utgiven av Nordenskiöld-Samfundet i Finland: 242—256. — Helsingfors.
- JOHANSSON, S. K-J. 1981: Myggkläckning räddar fågelpopulationen i sommarens snöoväder. — Vår Fågelvärld 40:502 —503.
- JUUTI, T. & E. LEPPÄNEN 1976: Pohjaeläimistön tila Turun-Naantalin merialueella 1970–1975. – Lounais-Suomen vesisuojeluyhdistys r.y. Julkaisu 30:1–13 + 7 pp.

- KURECK, A. 1980: Circadian eclosion rhythm in Chironomus Thummi: Ecological adjustment to different temperature levels and the role of temperature cycles. — In D. A. MURRAY (ed.): Chironomidae, ecology, systematics, cytology and physiology, pp. 73—79.
- LEHTONEN, L. 1981: Kalatiiran Sterna hirundo poikasvaiheen saalistuksesta ja ravintobiologiasta Järvi-Suomessa. — Ornis Fennica 58:29—40.
- LEMMETYINEN, R. 1973a: Clutch size and timing of breeding in the Arctic Tern in the Finnish archipelago. — Ornis Fennica 50:18—28.
- LEMMETYINEN, R. 1973b: Feeding ecology of Sterna paradisaea Pontopp. and S. hirundo L., in the archipelago of southwestern Finland. — Ann. Zool. Fennici 10: 507—525.
- LEMMETYINEN, R. 1976: Feeding segregation in the Arctic and Common Terns in Southern Finland. — Auk 93:636—640.
- LEPPÄKOSKI, E. 1975: Assessment of pollution on the basis of macrozoobenthos in marine and brackish-water environments. — Acta Acad. Aboensis B 35:1—90.
- MIKKOLA, K. 1980: Lapin- ja kalatiirat pyydystävät kuoriutuvia surviaissääskiä (Diptera, Chironomidae). — Ornis Fennica 57:42.
- PALMÉN, E. 1955: Diel periodicity of pupal emergence in natural populations of some Chironomidae (Diptera). — Ann. Zool. Soc. Vanamo 17:1—30.
- PALMÉN, E. & L. AHO 1966: Studies on the ecology and phenology of the Chironomidae (Dipt.) of the Northern Baltic. 2. — Ann. Zool. Fennici 3:217—244.
- PALMGREN, P. 1930: Quantitative Untersuchungen der Vogelfauna Südfinnlands,

mit besonderer Berücksichtigung Ålands. — Acta Zool. Fennica 7:1–218.

- PEARSON, T. H. 1968: The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. — J. Anim. Ecol. 37:521—552.
- RAJASILTA, M. & I. VUORINEN 1981: Pohjaeläimistö merialueella Naantali—Turku— Parainen v. 1979. — Lounais-Suomen vesisuojeluyhdistys r.y. 48:57—82.
- Rüppell, G. 1980: Vogelflug. Reinbek bei Hamburg.
- SUOMALAINEN, H. 1939: Über die Brutbiologie der Küstenseeschwalbe, Sterna macrura Naum., in ihrem Verhältnis zu derjenigen der Flussseeschwalbe, Sterna hirundo, in den Schären des Finnischen Meerbusens. — Ann. Soc. Vanamo 6:16—21.
- SUNDSTRÖM, C. E. 1927: Ökologisch-Geographische Studien über die Vogelfauna der Gegend von Ekenäs. — Acta Zool. Fennica 3:1—170+13.
- THIENEMANN, A. 1931: Tropische Seen und Seetypenlehre. — Arch. Hydrobiol. 22, Suppl. 9:1—763.
 WELTY, J. C. 1975: The life of birds. — Phila-
- WELTY, J. C. 1975: The life of birds. Philadelphia, London, Toronto, 2nd ed.
 WIBECK, E. 1939: Sjöfågelslivet i Stockholms
- WIBECK, E. 1939: Sjöfågelslivet i Stockholms skärgård. Redogörelse för Sv. Jägarf. f. Stockholms stad o. län sjöfågelinventering 1937–1939. – Stockholm.
- WIBECK, E. 1957: Stockholms skärgård, vårt största sportfiskeområde. Dess landskapliga natur och fågelliv. — Fiske 6:1—19.
- VUORINEN, J. 1980: Jakt på puppor av fjädermygga (Diptera, Chironomidae) observerad hos fisktärna (Sterna hirundo). — Fåglar i Norrköpingstrakten 1:17—18.

Received February 1982