

Single-breeding versus colonial breeding in the Caspian Tern *Hydroprogne caspia*, the Common Tern *Sterna hirundo* and the Arctic Tern *Sterna paradisaea*

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The Baltic population of the Caspian Tern, c. 2300 pairs, tends to breed either in single pairs (146 of 204 recorded localities) or in dense colonies (around 50 islets with 9—164 pairs). The pronounced sociability is partly an adaptation to coastal regions where suitable breeding localities are scarce and the Caspian Tern and other larids are forced to gather on the few localities available. The first Caspian Terns arriving in the Baltic archipelagoes were single pairs. They could not find any colonies of conspecifics and accepted colonies of other larids as substitutes.

Single-breeding pairs defend their whole islet against conspecifics, preventing other single pairs from joining them. In this way single-breeding has been preserved for centuries in the Baltic. The difference in aggressiveness between single-breeders and colonial breeders is obviously related to differences in conditioning and imprinting of the young: in colonies they constantly live close to numerous conspecifics, whereas the young of the single-breeders hardly see any foreign conspecifics but many other larids. Earlier, only single-breeders occurred in the Baltic archipelagoes, but around 1880 a colony from Sleswig (North Sea) moved into the Baltic and settled south of Stockholm. It increased and divided into several colonies, situated in Sweden, Finland and Estonia. Since the colonies attract single pairs, the single-breeding system has begun to vanish from the vicinity of the colonies. Even the colonies of Caspian Terns settle only on islets occupied by other larids, including conspecifics.

In the Common and Arctic Tern the few single pairs do not prevent other single pairs from joining them. Their colonies are not very dense and fighting at territory borders is infrequent. The conditions for conditioning to conspecifics is almost identical for all young. Therefore, offspring of single pairs do not develop any especial aggressiveness towards conspecifics which would preserve the single-breeding. The mutual attraction between the Common and Arctic Tern frequently cause breeding in the same locality. Single pairs of these terns occur only in particularly attractive environments. For breeding in less suitable environments both species need the additional stimulus offered by a colony of terns, but they do not accept other larids as substitutes.

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Introduction

The Baltic population of the Caspian Tern *Hydroprogne caspia* shows a pro-

nounced tendency to breed either in single pairs or in dense colonies. Horting (1929—31) pointed out that the single pairs nesting in Finland are at-

tracted to colonies of other larids, but this sociability is also displayed by colonies of Caspian Terns. Both single-breeders and colonies occur in outer archipelagoes in the whole Baltic area. Single pairs also occur in the North American population (Godfrey 1966), but in other parts of the wide range they have been reported only occasionally.

This article will discuss the reasons for the segregation into single-breeding pairs and colonial breeders, and deal briefly with single-breeding in the Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea*.

Material

The Caspian Tern material used consists of bird censuses made in the archipelagoes of Finland, Sweden and Estonia. The present size of the Baltic population is about 2300 pairs (Staav 1979). The proportion of single-breeders and the number of colonies of different sizes were determined from records published no later than 1978. The authors consulted were: Paavolainen 1950 and 1957, Aumees 1967, A. Kumari 1967, Nylund 1971, Staav et al. 1972, Soikkeli 1973a, Väisänen 1973, Väisänen & Järvinen 1977, and Hildén et al. 1978. I have also considered T. Stjernberg's unpublished survey made in SW Finland in 1977—78, information from ringing Caspian Terns in Finland and my own records from the S coast of Finland. Older studies and newer records have been used for examining site tenacity and the effect of colonies on the occurrence of single pairs. The study was also largely based on experience obtained during my fifty summers spent in the archipelago of Esbo and Kyrkslätt SW of Helsinki, and during my studies on the behaviour of the Caspian Tern (Bergman 1953).

For the Common Tern and the Arctic Tern I have used the pair numbers given in the studies by Paavolainen (1950, 1957) and Väisänen & Järvinen (1977), and my own censuses in Pernå (1945), Esbo (1937), Kyrkslätt (1979), the bird sanctuary Nothamn SE of Ekenäs (1938) and the islets of Tvärminne Zoological Station (1962). These regions were chosen because their clear-cut zoning (outer, middle and inner archipelago) and because the Common and Arctic Tern there have been censused separately.

Composition of the Baltic population of the Caspian Tern and stability of colonies of different sizes

The distribution of the Baltic localities by the number of pairs is shown in Fig. 1. Of the 204 breeding islets, 146 (75%) had single pairs, but around 92% of the population (in the late 1970s somewhat more) breeds in colonies of 9—164 pairs. The ratio of the numbers of islets supporting 1, 2 and 3 pairs is 146:7:1. Such a distribution cannot be accidental. There must be environmental and/or behavioural features preventing the formation of colonies of 2 or 3 pairs. In the Common Tern and the Arctic Tern the number of pairs breeding in such minute colonies is greater than the number of single pairs (see p. 148).

In the Caspian Tern, contrary to the situation in the Common and the Arctic Tern, islets occupied by 1 pair (or 2—3 pairs) have never turned into colonies through the addition of a few pairs each season, but a considerable number of pairs may suddenly appear and establish a colony on such an island. In all such cases studied, a corresponding reduction in the population was observed in the same season in the neighbourhood or elsewhere in the Baltic region. Such changes of breeding locality (deserting flights, Cullen 1958) are evidently often caused by disturbance (several own records 1942—68, Väisänen 1973, Staav & Forssgren in litt. 1976, Staav 1979).

All Caspian Terns prefer small, low, flat, rocky or gravel islets without trees or bushes, in most cases less than 2 ha in area and situated in a physiognomically marine landscape. When a colony settles in a new area it is not particularly attracted to islets where single pairs of Caspian Terns are breeding (for reasons, see p. 145), but larger colonies

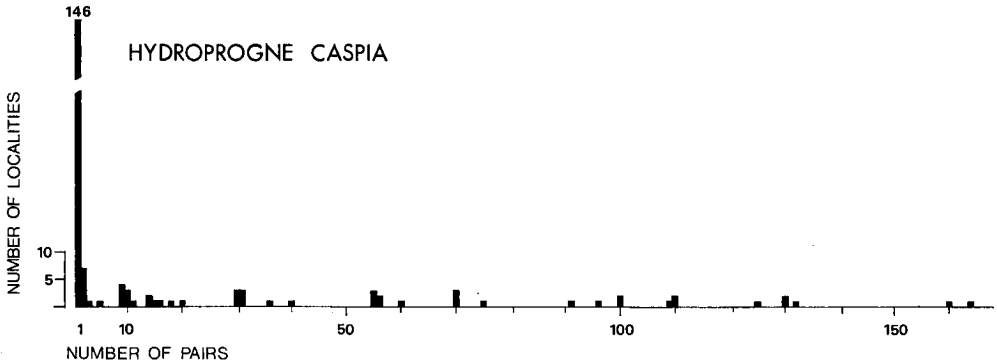


FIG. 1. The Caspian Tern *Hydroprogne caspia*. Frequency of different colony-sizes and single-breeding pairs in the Baltic population.

have a strong "collecting" effect on conspecifics (see p. 146). Evidence of shifts of numerous birds from one colony to another is provided by the sharp fluctuations in colony size, mentioned in almost all descriptions of the occurrence of Caspian Tern colonies in the archipelagoes of Sweden and Finland.

Colonies of 4—8 pairs may be considered unusual and less stable than large colonies. The instability of small colonies had already been noted by Holm (1945). Colonies of this size have occurred almost exclusively in areas where breeding has repeatedly been disturbed and therefore appear to be remnants of larger colonies. I have found nine published records of such colonies, but the present material contained only one (5 pairs, Staav et al. 1972, on an islet where a larger colony had bred in the previous season). There is no record from undisturbed areas in Finland of colonies of 4—8 pairs breeding on the same islet in two consecutive seasons. The small colonies observed in Kyrkslätt in 1935—38 (Bergman 1939, Tab. 7) obviously all resulted from disturbance of a larger colony during the egg-laying period.

Colonies of about 9—15 pairs seem to have greater site tenacity than the smallest ones. In several cases such colonies have bred in the same locality during at least three consecutive seasons. Larger colonies tend to breed many seasons on the same islets. This may be due to the fact that many of the birds leave the colony during the day to fish and so avoid possible disturbance. When they return to the islet, they behave in a normal way and are numerous enough to prevent disturbed birds from deserting the locality.

Many islets are known as traditional breeding localities of single pairs, and the same pairs probably often breed several seasons on the same islets. If the old pair disappears a new pair sooner or later replaces it. The stability of single-breeding pairs is also dealt with on p. 146.

History of the Caspian Tern in the Baltic Sea area

The history has been reviewed by Väisänen (1973), but some additional facts contributing to explain single-breeding may be mentioned here. In the 17th and 18th century some islets off the coast of Sweden were already known as

breeding localities for Caspian Terns (Lönnerberg 1929, Wibeck 1939), but no colonies had been recorded. Some names of islets in Sweden and Finland show that the species occurred even earlier than is shown by scientific records. During the main part of the 19th century, colonial breeding of the Caspian Tern in the North Sea and Baltic Sea areas appears to have been restricted to the island Sylt in Sleswig (a colony of at least 200 pairs). At the very beginning of the 19th century there was also a colony on the Baltic coast of Germany, on a reef off the mouth of the River Oder (Naumann 1897—1905), but the locality was destroyed by storms. During the last third of the century human disturbance caused the gradual disappearance of the Sylt colony. The desertion of the Sylt locality undoubtedly led to the establishment of the first colony in Sweden and thus initiated colonial breeding in the archipelagoes of the Baltic area. The first reliable record of a colony in Sweden — off Hartsö in Södermanland — is from 1894, but a colony was probably already breeding on a nearby islet some 20 years earlier (Jägerskiöld & Kolthoff 1926, Rosenius 1942).

The first colony in the southern archipelagoes of Finland appeared in 1925 (about 25 pairs on the islet Espskärskubb in Kyrkslätt 25 km SW of Helsinki, G. Saurén pers. comm.), and this was obviously also the result of desertion of some other locality. In 1927 the colony bred on Juktisgrund 5 km away (Kreüger 1928). All the breeding localities used later by colonies in Kyrkslätt have been situated less than 8 km from this islet. In the northernmost part of the Gulf of Bothnia colonial breeding was recorded as early as 1908 and 1909 (about 10 pairs on the islet Tasanenletto in the Krunnit group, the Merikallio Archives/Väisänen 1973). The colony of 21 pairs recorded in 1923 off Kalix, 50 km NW of the Krunnit group, may at least partly have originated from the Krunnit area. The development of the colony-breeding population in Finland and Sweden has been followed since the 1930s. Around 1935 the whole Baltic population may not have exceeded 500 pairs.

Since about 1955 the Caspian Terns have suffered from the sharp increase of the Herring Gull *Larus argentatus*, especially in the western half of the Finnish south coast. In Kyrkslätt all the islets occupied by colonies of Caspian Terns during at least one season between 1925 and 1970 (Flatgadden, Lökhäll, Espskärskubb, Rönnbuskskubb, Tratten, Tunnan, Juktisgrund, Tirgrund, Engelsmansgrund and Lergrund) have been invaded by numerous Herring Gulls. At the same time the number of colonial Caspian Terns in Kyrkslätt has dropped from c. 200 to about 30 pairs. Sixty pairs bred on Lill-Salgrund in 1971—77, but in 1976 and

1977 almost all their young were eaten by Herring Gulls and in 1978 the colony consisted of about 30 pairs and had shifted c. 1 km to the islet Pargrunten. There it was able to produce about one fledgling per pair. At Hamngrund in Ingå, 60 km SW of Helsinki, Herring Gulls occupied the nesting area of a Caspian Tern colony (15—60 pairs), forcing the terns to breed among low bushes. By 1980 there was only c. 10 pairs left and no young fledged. Staav (1979) mentions severe damage done by Herring Gulls in a Caspian Tern colony in Småland, SE Sweden. In the archipelago off Stockholm the kleptoparasitic behaviour of Lesser Black-backed Gulls *Larus fuscus* towards fish-carrying adult Caspian Terns caused starvation and increased mortality of the young (Forssgren 1980).

Between about 1930 and 1970, some increase was observed in the number of single pairs. One of the reasons for this was the creation of many new sanctuaries (Staav et al. 1972), another was the discontinuance of egg-collecting. Before the increase of the Herring Gull, the nesting success of single pairs was at least as good as that of the pairs breeding in large colonies: in 16 single pairs the mean number of fledged or almost fledged young was 1.8 (my own records from the Gulf of Finland 1933—62). In two colonies in SW Finland the nesting success was about 1.5 fledglings per pair (Soikkeli 1973a).

In the colony-breeding Caspian Terns formation of new pairs occurs mostly on the common ground of the breeding locality (many own observations on Lökhäll 1949—51, Bergman 1953; cf. the function of the "clubs" of Herring Gulls, Tinbergen 1953), and probably never in the wintering area (Staav 1979), while single-breeders probably mostly form pairs at the future nesting site. I have one record of such behaviour on Lill-Salgrund 1964.

However, several circumstances (see p. 148) show that young hatched in colonies prefer to breed in colonies, and it is unlikely that single-breeders are often recruited from the much more numerous offspring of the colonies. During the period that the colonial population has risen from around 300 to almost 2000, the single pairs have only increased by some ten.

Why do both colonies and single pairs of Caspian Terns breed exclusively in colonies of other larids?

In most parts of the wide range of the Caspian Tern the number of suitable breeding islets is very restricted and

these must be shared with several other colonial species as well. The tendency to breed in dense single-species groups among other larids is presumably at least partly a consequence of adaptation to this situation. In the geologically very young archipelagoes of the tideless Baltic, there is an abundance of low, flat, isolated islets, but the species shows no special ethological adaptation to such a region. Its sociability remains so strong, that both the single pairs and the colonial breeders accept only localities occupied by other larids.

The Baltic archipelagoes have evidently been colonized by single pairs of Caspian Terns, arriving occasionally from elsewhere, probably from the North Sea. Since they did not find any colonies of conspecifics, they joined colonies of other larids. However, when another single pair is already breeding in a colony of larids, the new single pairs evidently do not join this pair but prefer another larid colony on another island. Thus single pairs use other larids as substitutes for colonies of conspecifics and, although a somewhat defective adaptation to the archipelago environment, this behaviour is one of the reasons why single-breeding has been successful and prevailed for generations and centuries. If adaptation were better, the Caspian Tern would be less dependent on colonies of other larids, and the single pairs would frequently join to form their own colonies. Since flocks of the species rest independently of other larids during the pre-egg-laying period in spring (see p. 146), the even may be able to establish breeding colonies on unoccupied islands, but as far as is known, this has never occurred in Finland, Sweden or Estonia.

Hildén (1958, 1965) points out, that when single pairs and small colonies of the Little Gull

Larus minutus — a species of eutrophic lakes and marshes — are settling in the archipelago, they need the stimulus of colonies of terns or Black-headed Gulls *Larus ridibundus*, which thus substitute for conspecifics. In the outer archipelago the Black-headed Gull also needs a corresponding stimulus. However, these species have never shown any tendency to develop a single-breeding population dependent on colonies of other species. Their pairs and small colonies have subsequently disappeared or in some cases the Black-headed Gull has developed real colonies. I should like to stress that there is no sharp border between the behavioural reactions of non-colonial species (such as the Turnstone *Arenaria interpres* and Tufted Duck *Aythya fuligula*) preferring breeding among larids, and the behaviour of social larids accepting colonies of other larids as substitutes. All birds breeding in or close to a colony of larids utilize the reactions of the other birds for information on the situation in the surroundings and the shelter offered by the colony against predators. These advantages probably strengthen the tendency of species such as the Caspian Tern, Little Gull and Black-headed Gull to breed in colonies of other larids. The information and shelter provided by a substitute colony may be almost identical to that provided by conspecifics.

The strong attraction of the Caspian Tern to colonies of other larids sometimes results in acceptance of islets clearly different from the normal breeding localities of the species. Such localities are Gaddarna and Enbusken in Kyrkslätt (occupied by single pairs in the 1950s) and Adgrund (off Ekenäs, with 60—95 pairs in the 1950s and 1960s, the colony was destroyed and abandoned in 1968). These skerries (area 2—3 ha) bear abundant bushes and some trees, but they harboured considerable colonies of Lesser Black-backed Gulls and some Herring Gulls and Common Gulls *Larus canus*. Only once I have seen a pair of Caspian Terns choose a nest site from which no other larids were visible (islet S of Berghamn, Houtskär, nest in 1946 on shore below steep 10-m rock; some other larids were breeding 100 m away at the opposite end of the islet).

Other evidence of the sociability of the Caspian Tern

At least in the breeding area, single Caspian Terns hardly ever rest in such localities where no other larids are resting. Bengt Berg (1919) mentioned

that the Caspian Tern never alights to rest during its long fishing tours (cf. also Soikkeli 1973b). Flocks of Caspian Terns rest more frequently. In Kyrkslätt resting in flocks occurs during the pre-egg-laying period on reefs and low shores close to the preferred fishing waters in the innermost archipelago. Later, flocks of birds that have lost their eggs may spend several days and nights there. In July-August families and flocks rest in the innermost archipelago and in lakes, preferring localities with other larids. Since single individuals and pairs avoid alighting and resting in localities where they cannot see any conspecifics or other larids they are unable to breed in such localities.

Single-breeding pairs of Caspian Tern do not desert the breeding locality as easily as do the colonies. This is evidently due to sociability: the other larids mostly stay on the islet, though often disturbed. None of the seven single pairs in Kyrkslätt 1933—43 deserted their islets, even when I visited them in the sensitive pre-laying period. Colonies of Caspian Terns may desert a locality although some pairs already have clutches of 3 eggs (Flatgadden 1942, desertion caused by hunters shooting waterfowl 400 m from the locality).

Why do single Caspian Tern pairs not join to form colonies?

What are the behavioural peculiarities that cause and preserve single-breeding? Besides the use of other larids as substitutes for conspecifics, I should like to stress two circumstances: (1) Single-breeders are aggressive towards conspecifics occasionally appearing around the breeding islets, and (2) during the period of territory establishment single pairs and small groups of

pairs are rather inconspicuous. I have recorded aggressive reactions of single pairs towards conspecifics at all their 7 nesting islets in Kyrkslätt in 1933—43. Although the pair remains within a small area (coloured white by their faeces), no larger than the normal territories of the colonial breeders, it reacts aggressively to conspecifics trying to alight on the island or flying over or beside it. A single pair trying to settle in an area will rather probably attempt to settle on an islet where another single pair is already established, because that islet is especially attractive in some way. But the aggressiveness of the established pair, already familiar with the islet, its birds and its surroundings, is generally enough to prevent the newcomers from settling there. They are unlikely to be successful unless especially strong and aggressive, or unless the old pair happens to be on a long fishing tour. Compared with the number of single pairs, the number of islets occupied by two pairs is very low. This shows that such a situation seldom occurs, or that the newcomers may sometimes drive away the old pair.

There is hardly any evidence that colonies of less than about 15 pairs attract solitary pairs breeding in their vicinity, but larger colonies appear to have an irresistible attraction for single pairs breeding within a radius of at least 5 km. Sooner or later such pairs disappear from the old localities and are not replaced. However, there is no indication that single pairs abandon already laid clutches when a colony appears in the vicinity.

The failure of small colonies to attract single-breeders seems to be due partly to their instability (see p. 143), partly to their inconspicuousness. Especially before their laying period, the majority of the birds go on long fishing tours every day, spending many hours

close to their fishing waters, and the birds staying "at home" are too few to gather in a flock at the "club". Conspicuous gatherings on common ground are typical in large colonies, and there are also many display flights between the "club" and the nesting sites and aerial displays extending as far as 5 km from the islet. The birds are also very noisy.

The disappearance of single pairs from the vicinity of colonies has been followed at the islet group Valsörarna (5×3 km), where three to five localities were abandoned in the same season as the colony appeared, and the last locality 4 years later (Hildén et al. 1978). In the Krunnit area (10×10 km) it took almost 10 years before all the single pairs had disappeared (Väisänen 1973). Between Helsinki and Tvärminne (about 110 km along the S coast of Finland) the number of single pairs has decreased from about 15 (my own records) to 6 (H. Puntti, T. Tallgren and J. Valste, pers. comm.). In the 1930s colonies bred only in the eastern part of the area; later considerable colonies appeared in its western half (Hamngrund, Adgrund, islets SE of Jussarö), but at the same time the colonial breeders of the eastern part diminished to about 30 pairs (see p. 144). In W Estonia, the appearance of two colonies was followed by a gradual decrease in the number of single pairs from about 10 (A. Kumari 1967) to only one (T. Kastepöld, pers. comm. 1980).

Väisänen (1973) states that the period 1908—46 in the Krunnit area was characterized by single-nesting pairs and formation of small colonies. It seems to me that the factors leading to colony formation, first at Krunnit and later in the adjacent Swedish archipelagoes were most probably egg-collecting, at those times a widespread custom among the coastal inhabitants, and the relative scarcity of suitable breeding localities. Repeated destruction of gulleries and terneries causes the birds to gather in undisturbed localities and try to breed or resume breeding there. Pairs of Caspian Terns may thus have followed other larids to new localities, become accustomed to the locality and to each other and begun to breed together. Or after the destruction of their nest they may have gathered in a non-breeding flock on some undisturbed islet on which they then began to breed in a colony. These low, partly sandy northern archipelagoes have been the only place where colonial breeding arose in the Baltic region. In all other parts of the Baltic, such breeding was

initiated by groups of individuals which had evidently bred in colonies elsewhere. However, the large colonies recorded after 1946 in the northernmost Gulf of Bothnia may partly have been built up by colonial breeders from other parts of the Baltic (v. Haartman 1948, Väisänen 1973).

In the future the increased number of colonies and more and more frequent disturbance by man, causing colonies to settle in new areas, will probably reduce the number of single pairs even in areas where they are still relatively numerous.

Differences in conditioning a possible explanation of the different types of breeding

In Caspian Tern colonies the distance between nests mostly ranges from 0.7 to 3.0 m. The young spend at least their first 10—14 days within the small breeding territories, in and around which they continuously see and hear many adults and young of the same species, they frequently fight with other young and even adults, and learn where the common grounds areas are situated. Thus, they see much of their conspecifics, but little of other larids, because these do not generally intrude into the area of the colony. If such intrusion occurs, it is mostly done by predatory Herring Gulls, towards which the terns behave aggressively. The situation is the same on islets where the young shift to common ground on the shore. Thus any tendency to react aggressively to conspecifics at greater distance than some metres disappears through conditioning. Aggressive pursuit of conspecifics in the air occurs only as a short continuation of a struggle started on the ground. The young of the colony-breeders become accustomed to live close together and to defending only a few square metres as their territory.

The life of single pairs and their young at the breeding locality lacks all

contacts with conspecifics outside the family. They never have to struggle with foreign conspecifics on the ground and there is no conditioning to seeing foreign conspecifics close to the breeding territory or on a common area on the shore. Instead, the single-breeders and their young are in closer contact with other terns and gulls than the colonial breeders. They are members of the mixed gull-tern society of their breeding islet, while the colony-breeders are mainly members of their own society. These differences may well result in differences in imprinting to conspecifics, or at least in conditioning to situations prevailing in the life of colony-breeders, but hardly occurring on islands with single-breeders or a few pairs. To some degree the young may be imprinted to other larids as well, at least as a feature of the breeding environment (cf. Koskimies 1957).

For birds which have earlier bred or been hatched in a colony the presence of a flock of conspecifics is an essential part of the environment, and presumably cannot easily be replaced by other gulls or terns. Convincing proof of this is provided by the instability of 4—8-pair colonies, the common shifts of part of a colony to another colony, and to some degree the fact that the number of single pairs does not increase in regions with large colonies.

Individuals that have never lived in a colony of conspecifics are satisfied by the environmental situation on islets with colonies of other larids, and since they have not been conditioned to seeing many nonaggressive conspecifics around the breeding territory, they tend to defend the whole islet against conspecifics. Thus single-breeding continues as long as no accidental factors force several single-breeders to gather on the same islet, or as long no stable colony appears in the vicinity.

The Common and Arctic Tern

There is a mutual attraction between these two species at the breeding localities. Therefore, in the following only pairs breeding in localities with no pair of the other species are considered single-breeders. However, in the summarizing Fig. 2, colonies containing a small number of additional pairs (proportion not greater than 1:5) of the other tern species are considered single-species colonies. The breeding islet is regarded colony unit though there sometimes occurs, even on small islets, segregation into clearly different groups: The Common Terns, for instance, gather on grassy areas, the Arctic Terns on gravel or flat rocks.

The material used (see p. 142) shows clearly that the Common and Arctic Tern do not prefer to breed in single pairs. Single-breeding occurs in both species, but the number of these solitary pairs is smaller than the sum of pairs breeding in groups of 2—3 pairs. In the areas considered about 18 % of the breeding localities of the Common Tern and 10 % of those of the Arctic Tern are occupied by single pairs. In New Jersey the proportion of localities with single-breeding Common Terns is even smaller, only 2.9 %; in the 34 localities with altogether 2830 pairs there were only 2 single pairs and one group of 2 and one of 3 pairs (Burger & Lesser 1978). In the Caspian Tern the proportion of localities with single pairs is 75 %.

The mutual attraction of the two species is shown clearly by the fact that in the inner parts of the Esbo-Kyrkslätt area the more marine Arctic Tern has been found nesting only in colonies of Common Terns, never in genuine single pairs. Conversely, the clearly less marine Common Tern never bred in genuine single pairs in the outermost

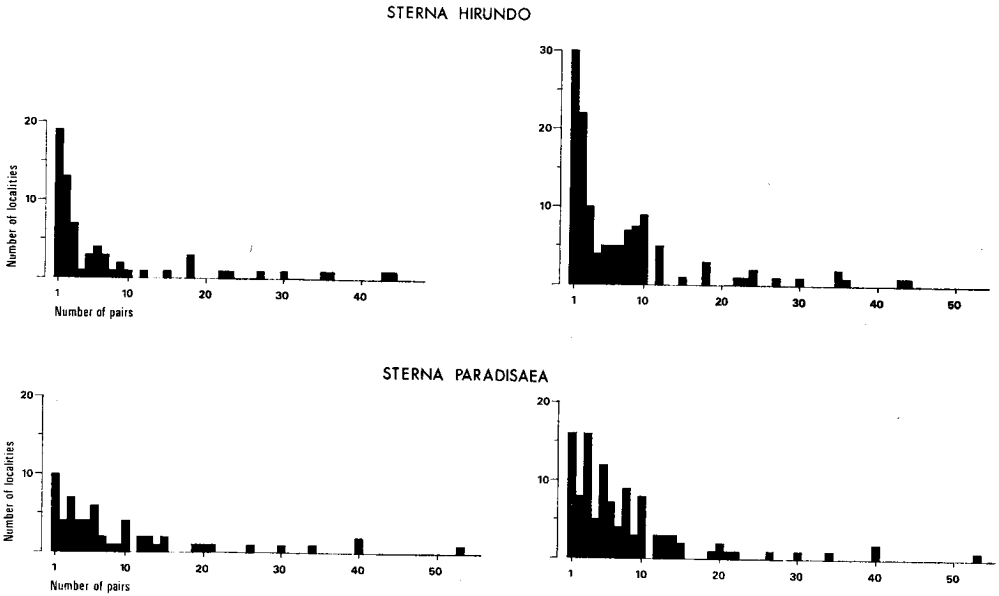


FIG. 2. The Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea*. Frequency of different colony-sizes and single-breeding pairs in some archipelago-areas in Finland. Left part: single-species localities (including localities with a few additional pairs of the other species. Right part: all localities.

archipelago, although colonies occurred on the outermost islets as well, even those where no Arctic Terns were breeding. Thus, as in the Black-headed Gull and in the irregularly occurring Little Gull (see p. 145), these terns need the additional stimulus provided by a colony of the other species to settle in localities which do not fully correspond to their habitat requirements. As the Common and Arctic Tern are very similar in both size and behaviour and their optimal habitats do not differ very much from each other, each species readily accepts colonies of the other as substitutes for its own colonies.

The Common and Arctic Tern avoid breeding within the colonies of gulls and Caspian Terns, though they commonly breed in separate groups on the same islands as long as there is no severe competition for space. The other

larids are bigger than these terns, and in many cases they nowadays interfere severely with them. The terns have often deserted islets invaded by colonies of Black-headed Gulls, Herring Gulls, or Caspian Terns, and single pairs of terns have never been recorded in typical colonies of these species. Thus, the Common and Arctic Tern do not accept colonies of the other larids commonly occurring in the archipelago as substitutes for their own colonies.

Neither Common nor Arctic Terns breed in very dense colonies. The distance between the nests in the terneries in Esbo and Kyrkslätt is generally 2–10 m, being smaller only when there is not enough space or sometimes when vegetation isolates the nest sites from each other. In New Jersey the distance between the nests in the Common Tern colonies is of the same order as in the

areas studied by me, though the mean size of the colonies there is about 10 times greater than in southern Finland (Burger & Lesser 1978). In most terneries watched by me fighting was infrequent and the pairs clearly separate in their own territories. This is at least partly due to their short legs, which make both young and adults rather immobile on the ground. Pursuit of predators in collective flight is infrequent; only birds of prey and owls may sometimes release such behaviour. In most cases not even crows or gulls stealing eggs or young on the ground are pursued collectively. Thus the life of the young of a single-breeding pair does not differ much from that of the young in a colony. Their conditioning or imprinting to conspecifics is hardly different. Normally, young terns do not come into close contact with other larids, which makes imprinting to the latter impossible.

The very low proportion of single-breeders and small colonies in New Jersey probably depends mainly on the great attraction of the large colonies, and the great site tenacity of the terns (Austin 1940, 1949, Onno 1965, A. Ling 1967). However, the possibility cannot be excluded that the young also become imprinted to the general features of the breeding locality. The occurrence of a large colony of conspecifics may be one such feature. This would be an additional explanation for the scarcity of single pairs and minute colonies in New Jersey. These circumstances explain why no preference for single-breeding or breeding in colonies of other larids develops in the Common and Arctic Tern.

In Esbo and Kyrkslätt single-breeding pairs of Common Terns and Arctic Terns occurred mainly when a colony had been destroyed or disturbed at the beginning of the egg-laying period.

Since the terns possess a strong *Orts-treue*, single-breeders settled mainly within less than 1 km of the old breeding locality. In some of these localities the number of pairs increased in the following seasons, but localities where the single pair did not succeed in its first breeding were all abandoned. Single-breeding thus acts indirectly as a method for the population to examine the fitness of new localities. The reason why some pairs, when disturbed, do not join undisturbed colonies in the vicinity is that the most suitable territories on these islets are already occupied, while there are abundant nearby skerries that fulfil the requirements of the terns.

Selostus: Räyskän, kalatiiran ja lapintiiran pesimisestä yksittäispareina ja yhdyskunnittain

Räyskä pesii yksittäispareina tai yhdyskunnittain, kun taas kala- ja lapintiiralla ei ole taipumusta pesiä nimenomaan yksittäispareina. Mistä tämä ero? Räyskä on aina 1800-luvun loppupuolelle asti Itämeren saaristoissa pesinyt pääosaltaan yksittäispareina eikä varsinaisia yhdyskuntia ollut lainkaan. Itämeren saaristot saivat ensimmäiset räyskäyhdyskuntansa Schleswigin Syltin saaren yhdyskunnan siirtyessä Södermanlandin saaristoon. Tästä koloniaspesintä Itämeren saaristoissa sai alkunsa. Vain Krunneilla tuntuu pieni yhdyskunta syntyneen erillisesti. Vaikka Itämeren räyskäkanta 1970-luvun alussa oli enentynyt n. 2000 pariksi ja yhdyskuntia oli jo n. 50, oli yksittäin pesiviä pareja edelleen lähes 150 (75 % pesimäpaikoista, 7.5 % kanasta, vrt. kuva 1).

Syyt yksittäispesimisen suhteelliseen runsauteen ovat todennäköisesti seuraavat. Räyskä on synnynnäisesti hyvin sosiaalinen. Kun yksittäiset yksilöt aikoinaan harhauuttuaan Itämeren saaristoon eivät löytäneet oman lajin yhdyskuntia, ne asettuivat pesimään muiden lokkilintujen joukkoon. Tällaisilla paikoilla räyskän poikaset eivät totu vieraisiin lajikumppaneihin ympärillään eivätkä myöskään räyskäyhdyskunnalle ominaiseen riittäisaan elämään. Yhdyskunnissaan räyskät puolustavat rajusti vain pientä pesimäpiiriä, mutta eivät paljoakaan reagoi etäämmällä oleviin lajikumppaneihin. Yksittäispareina

pesivät räyskät taasen suhtautuvat aggressiivisesti jopa pesimäluodon ohitse lentäviin lajikumppaneihin: nehän ovat varttuneet yhden räyskäparin luodolla. Yksittäisparien aggressiivisuus yleensä estää toisen parin asettumisen luodolle, joten yksittäispesintä jatkuu sukupolvesta toiseen. Yhdyskunnat vetävät kuitenkin puoleensa lähiseudun yksittäisparit.

Yksittäisparit ja ainakin Suomessa ja Ruotsissa yhdyskunnatkin asettuvat vain luodoille, joilla pesii muita lokkilintuja. Räyskän pesintä tiheissä yhdyskunnissa on sopeutuma alueille, joilla sopivia luotoja on hyvin niukasti. Räyskä ei pystyisi leviämään yksittäispareina maapallolla vain muutamassa paikassa esiintyviin tiheisiin mataliin saaristoihin, ellei sen sosiaalisuus olisi niin voimakas, että se hyväksyy toisten lokkilintujen yhdyskunnat oman lajinsa kolonioiden korvikkeeksi.

Kala- ja lapintiiroista Suomenlahdelta ja Perämereltä peräisin olevan aineiston mukaan 1—2 % pesii yksittäisparein. Kalatiirojen pesimäluodoista ovat n. 18 % yksittäisparien asuttamia, lapintiirojen luodoista n. 10 %. Kuvassa esitetään kummankin lajin parien jakauma. Vasemmalla ne pesimäpaikat, joilla laji esiintyy joko ainoana tiirana tai joissa toista tiiralajia on käsiteltävän lajin yhdyskunnan parimäärän lisäksi korkeintaan suhteessa 1:5. Oikealla kaikki pesimäluodot. Koska näiden tiiralajien pesimäpiirit ovat melko laajat, kaikki niiden poikaset elävät ympäristössä, missä kosketusta lajikumppaneihin on melko vähän. Pesintätapa siis tuskin vaikuttaa poikasten myöhempään aggressiivisuuteen eikä jatkuvasti yksittäispesintään johtavaa suhtautumista lajikumppaneihin synny. Molemmat lajit hyväksyvät toisen lajin sosiaaliseksi korvikkeeksi, mutta välttävät asettumista muiden, tiiraja häiritsevien lokkilintujen yhdyskuntien rajojen sisäpuolelle. Ympäristössä, joka ei täysin vastaa lajin vaatimuksia, on pesimään asettumisen ehtona jommankumman lajin läsnäolo: lapintiiira ei pesi yksittäispareina sisäsaaristossa, vaan asettuu siellä usein kalatiirojen yhdyskuntiin, ulkoluodoilta taas puuttuvat yksittäiset kalatiiraparit.

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