

Review

Differences in ecological properties in the herring gull (*Larus argentatus*) as a basis for explaining and predicting colonization events — A case history in retrospect

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Herring gull colonization of the Fennoscandian-Baltian area by the taxonomically and chorologically separate elements, *cachinnans* and *argentatus*, is evaluated in the light of their ecologies. The colonization events within the area consist of several consecutive occurrences during periods of large-scale temporal dimensions. Such characteristics as the ecological tenacity determining habitat selection and the invasion ability vs. inability to occupy certain kinds of habitats — both determined by the past history of the pertinent populations — were considered essential in the distributional dynamics of *cachinnans* and *argentatus*. These components formed the conceptual basis for hypotheses generating testable predictions of future colonization events.

1. Introduction

The suggestion that the yellow-legged element of the herring gull *Larus argentatus* in the Fennoscandian-Baltian area derives its origin from the southeastern populations around the Caspian Sea populated by the yellow-legged *cachinnans* group was not new when presented by me (Voipio 1954) several decades ago. However, viewed in retrospect, my suggestion at that time was actually based on holistic evidence attained not only from morphology (taxonomy) and distribution history (chorology), but also from the ecology of the

yellow-legged (*cachinnans*) and the pink-legged or flesh-coloured (*argentatus*) element.

Returning to the problem of *cachinnans* and *argentatus* now, I will not focus in the first place on the problem of taxonomy of the species in terms of subspecific differentiation and genealogy, nor on the division into two separate species, *argentatus* and *cachinnans*, as suggested by Haffer (1982). Rather, I am considering the expansion and colonization of these two large taxonomically and chorologically separate elements on the basis of their ecologies to discover the factors determining their fates within the

Fennoscandian-Baltian area. On the basis of this analysis I venture to assess — be it in retrospect — the power of the hypotheses generated for predicting the future dispersal and colonization events of the two elements within the area.

The history of opinions upon the existence of the yellow-legged herring gulls on the shores of Northern Europe originated when Pallas (1811) wrote about *cachinnans*: “Abundat in mari Caspio; majoribusque fluminibus Rossiae illuc et ad mare glaciale tendentibus, nec non in magnis Sibiriae lagubus, presertim Baicale” (p. 318). It is thus only natural that the herring gulls with yellow legs recorded by the Russian and other ornithologists on their journeys in the northern regions of the Eurasian continent were considered representatives of the species *Larus cachinnans*. And, as the north Russian and northwest Siberian dark-backed gulls with yellow legs were later regarded as another species, it is no wonder that the light-backed gulls with yellow legs recorded from the Gulf of Finland, the large inland lakes of Onega and Ladoga, and also from the White Sea, were considered *Larus cachinnans*.

The interest in the occurrence of the yellow-legged birds in the Baltian area actually arose in the beginning of the 1920s when Lönnberg (1921) reported this form in the archipelago off the eastern coast of Sweden in 1919. He suggested that *cachinnans* (considered a subspecies by him) had extended from the Southeast through the Baltic as far as the Swedish coast. Hartert (1923:85, Nachtrag I) took this claim seriously and pointed out that this form occurs also in Estonia. He expressed astonishment at how it could have escaped the notice of the Swedish ornithologists and asked whether the appearance of the yellow legs, in fact, was a consequence of a — then — recent expansion of *cachinnans* from the Southeast.

The first Finnish ornithologist addressing the problem of the yellow-legged herring gulls was Hortling (1928). Though he, indeed, considered them representatives of the species *cachinnans*, he later (Hortling 1930), seemingly after having been acquainted with the publication by Pleske (1928), adopted the view that the yellow-legged birds originated from the White Sea and hybridize with the pink-legged western form on the Baltic. He thus comes to the conclusion that this race, prob-

ably representing the form *Larus argentatus omissus* from the White Sea, had invaded south-westward, colonizing the Finnish inland and the coasts of the Baltic Sea.

The myth (Barth 1975) of the existence of the subspecies *omissus* thereby originated. It was based on an unsatisfactory description by Pleske (1928) who — as expressed by Lönnberg (1932) — gave a short preliminary description of it in advance of the description proper to be presented later by Sushkin. It was never described, however. Though the name *omissus* could thus well have been rejected and regarded (as I myself would decidedly recommend, see also Voipio 1954:40) as *nomen nudum*, it has continually appeared in the *Larus argentatus* systematics.

2. Status of the two elements breeding within the Fennoscandian-Baltian area from the 1800s until about the 1920s

To acquire a reliable picture of the population changes within a large geographical area, a reasonable choice of starting (or zero) point with respect to which one can compare later dispersal and colonization events must be made. The only basis for this would be some sort of steady state of long duration for the focal population, documented in the faunistic records available in the literature of past decades. A certain defectiveness notwithstanding, this source appears sufficiently reliable for my purpose. I shall survey the information on the occurrences, within the Fennoscandian-Baltian area, of the two elements, *argentatus* and *cachinnans*, separately. In speaking of *argentatus* and *cachinnans* elements, I refrain from treating them as taxons of any taxonomic category.

I am well aware of the cautious attitude towards my method of using only the colour of the legs as a criterion for determining the affinity of the populations to one or another distributional element (see, e.g., Mierauskas et al. 1991). It is a fact, however, that there are distinct and extensively distributed populations also among the *argentatus* group, the members of which are always yellow-legged in contrast to the other, likewise widely distributed, populations contain-

ing birds with flesh-coloured legs only. No one believes that this difference would be based on mere environmental factors. Though we know that a more or less yellowish tint occasionally occurs among birds of populations with regularly flesh-coloured legs and even in individuals of some other gull species such as *marinus*, and that the yellow colour, likewise occasionally, can fade away in single individuals, e.g. of the species *fuscus* (see, e.g. Barnes 1953, Barth 1968), there are positive indications, direct and indirect, of the hereditary determination of this colouration within the *argentatus-fuscus* complex (see, e.g. Voous 1946, Voipio 1954:27, 1968:76–77). Generally, therefore, the colour of the legs can, if not must, be considered an indicator of the populations belonging to one or another element or possessing characteristics based on hybridization.

2.1. Occurrence of the *argentatus* element

In the literature of the 1800s and the early 1900s, it has been stated unanimously that the breeding populations all over the Fennoscandian-Baltian marine environments of the herring gulls were composed of the *argentatus* element only (Nilsson 1858, Wright & Palmén 1873, Mela & Kivirikko 1909). This was still the case according to the handbooks published decades later (Kivirikko 1927, 1940, Hortling 1929/31).

The colonization of the coasts exclusively by the pink-legged gulls seems to hold good also for the western marine areas of the Baltic, including the Swedish east coast, until the date of the above mentioned report by Lönnberg (1921). The south and west coast of Sweden, too, has always been considered an area colonized by the *argentatus* element only (Olsson 1958, Løppenthin 1967). It is also noteworthy that it is this element which eventually colonized the great inland lakes of southern Sweden at some remote time, the oldest records relating to the 1870s (Lindroth 1946).

Finally, the whole of the Scandinavian west coast, so far as the literature is concerned (Hartert 1912, Løvenskiold 1947, etc.), has been considered an area populated by the *argentatus* element, and the same holds true, with some reservation (of which see below), also for the coast of the Arctic Ocean from North Norway as far east as

the Murman coast. It is to be noted, in this context, that no yellow-legged birds were seen among the hundreds of nesting birds on the coast of Vardö and Petsamo in the late 1920s and early 1930s, in spite of intentional searching for yellow-legged birds (Lönnberg 1932, 1933, Hortling & Baker 1932, Hortling 1937). The same also holds true for the later observations made by Ottow (1949) on the arctic coast in 1942 and 1943. Within the area stretching from the Tanafjord in North Norway in the West to the Litsafjord on the western Murman coast in the East, all of the breeding birds were representatives of the pink-coloured element only.

As for the abundance ratios, it can be ascertained that in all of the faunistic sources available from the 1800s and early 1900s the population sizes of the *argentatus* type on the Baltic coast have been said to be moderate at most, in contrast to the situation prevailing on the North Sea and the arctic coast of Fennoscandia with their large colonies of the *argentatus* element. This situation seems to have continued until the first two or three decades of the 1900s at least, as inferred from the information given, e.g. by Mela & Kivirikko (1909), Kivirikko (1927) and Hortling (1929/31). Hortling also pointed out that the herring gull did not breed on the coasts of the Baltic states and that it only irregularly bred on the German shores of the Baltic. The last statement accords with the information given by Brandt (1941) according to which the species was not included in Gross & Transehe's catalogue of 1929 of the Vertebrates of the Baltian area and with the statement by Kumari (1954) and Lepiksaar & Zastrov (1963) according to whose papers the species — if not of the yellow-legged element already (see later) — breeds in small numbers only on the marine islands off the Baltian coast.

This phase of the low population number evidently lasted until about the turn of the 1920s and 1930s, when the habit of breeding sparsely in solitary pairs came to an end and was gradually replaced by colonial breeding due either to the intrinsic growth of pertinent population or, rather, to the invasion from elsewhere, presumably from the west (Kilpi 1988). The survey by Kilpi amply confirms this picture outlined above. It appears that while the populations of the herring

gull were already rapidly increasing on the shores of the North Sea (Netherlands, Germany) during the early decades of this century, the sparse settlement of the species breeding in solitary pairs (not forming large colonies) on the Gulf of Finland and on the shores of the southwestern-southern areas of the Baltic (in the Bornholm area, coasts of Germany and Poland) still continued until the early 1930s (see, e.g. Paludan 1951). The same appears to have been the case regarding the Swedish east coast as well as the great lakes of Sweden populated by the *argentatus* type.

To sum up, we can thus speak, for part of the pink-legged element, of a long period of stability prevailing in the Baltic after its primary colonization in the remote past and consider it, or its historically documented end phase in the 1900s, the zero or starting point in respect of which the dispersal and colonization events of the later time can be compared.

2.2. Occurrence of the *cachinnans* element

The early records, in our faunistic handbooks, of the occurrence of the yellow-legged element in the Fennoscandian-Baltian area refer, in addition to the Finnish inland lakes and mires, to the Murman coast and the White Sea (Kivirikko 1927, Hortling 1929/31). The existence of a yellow-legged race ("*omissus*") on the shores of the White Sea and on the Murman coast, when brought to general knowledge (Pleske 1928, Hortling 1930, Lönnberg 1932, Buturlin & Dementiev 1934, Hartert 1932–38), caused a lively discussion about its implications. Lönnberg (1932), in particular, gives an account of how Sushkin informed him personally about the herring gulls with sometimes yellow, sometimes pink, legs breeding on the White Sea and the Murman coast. Hartert (1938) informs us, in turn, that Stegmann sent him a series of breeding yellow-legged herring gulls from the White Sea. Observations and reports mentioned led to the suggestion that the boundary on the arctic coast between the two elements must have been located, at that time, somewhere to the East of Petsamo (Hortling 1937) and, as it appeared later on (Dementiev 1941), in the eastern part of the Murman coast (see also Voipio 1954:19).

Viewed against such a history of early opinions upon the existence of the yellow-legged element in the White Sea and on the Murman coast, the statement by Bianki (1977), several decades later, that there are no yellow-legged herring gulls breeding in the White Sea appears problematic. Or do we have to interpret the situation by suggesting a lengthy continued spreading of the pink-legged element at the expense of the yellow-legged form? If this is the case, it would fit well, as an analogy, with my view upon the colonization history of the two elements in the Baltic Sea where the more aggressive *argentatus* seems to have displaced the yellow-legged element for a long interval.

Awareness of the circumstances prevailing in Fennoscandian-Baltian area has been later completed by records elucidating the problem of the duration of the settlement of the yellow-legged herring gulls on the Estonian and Latvian inland lakes and mires. Although the records of the appearance of this element there mainly relate to rather recent new colonizations (Brandt 1941, Berzins 1946, Kumari 1954, Taurinš 1961, Lepiksaar & Zastrov 1963, Onno 1966), it is known that many of the habitats under consideration, according to the knowledge of the local inhabitants, have been settled for decades before the 1920s, i.e. as far back as the 1800s, or as long ago as within the last few hundred years (Lepiksaar & Zastrov 1963, Onno 1966). The possibility of a duration of centuries or even of thousands of years in regard to the settlement of these habitats thus cannot be ruled out. Mierauskas et al. (1991) emphatically stress the ancient settlement of the yellow-legged herring gulls on the raised bogs of inland Baltia in Latvia.

The same seems to hold true for the yellow-legged element of inland Finland (Hytönen 1934, Voipio 1954). While there are no records, in old Finnish handbooks, of the breeding of the herring gull on the great Finnish lakes (Wright & Palmén 1873, Mela 1882, Mela & Kivirikko 1909), there are many reports of the species having been either occasionally observed or regularly encountered on the large Vuoksi lake system and also on some other lakes of southern Finland as long ago as the 1800s. This, of course, points to the possibility that the herring gull has bred rarely here and there on the Great Saimaa lake system

(Vuoksi) since ancient times. The first records of nesting there come from the end of the 1920s and the first half of the 1930s (Voipio 1954), presumably as a sign of the commencement of a new colonization of the yellow-legged element contemporaneously with that on the Baltian area as described above. Knowledge of the circumstances on the mires of southern Finland accords with this. While the majority (58%) of the mires were not known to be colonized until the 1920s (3) and 1930s (14), seven have already been colonized in the 1800s (Hytönen 1934).

Although the yellow-legged herring gulls were unknown on the marine habitats of the Baltic Sea, some scattered observations from its easternmost parts notwithstanding, there is a report (Flach 1953) of a colony of the yellow-legged gulls breeding on the Stora Karlsö off Gotland as early as 1865. The significance of this interesting observation lies in that, in accordance with the very old existence of this element on the Finnish and Baltian inland lakes and mires, it points to the ancient presence of the element also on the Baltic Sea. This presumably represents an isolated remnant of the very remote primary colonization of the Fennoscandian-Baltian area by the yellow-legged element.

This naturally raises the question of which of the two colonizations, that of the yellow-legged element or that of the pink-legged one, occurred first. My preliminary suggestion (Voipio 1954:21) was that the former was the first. The early statements by Nilsson (1858) and Wright & Palmén (1873) that the flesh-coloured legs of the marine *argentatus* gulls often possess a yellowish tint on their legs are interesting. Together with the above mentioned report by Flach (1953) they seem to support my suggestion. That is, if the pink-legged element really invaded the Baltic Sea after the primary colonization of the yellow-legged element, this yellowish tint of the feet (or often of their webs only) can reasonably be interpreted as a remnant characteristic of the old yellow-legged herring gull population assimilated with the pink-legged element intruding into there from the West.

As for the abundance ratios, the first records (Buturlin 1911, Koch 1911, Lönnberg 1921, Hortling 1930) of the yellow-legged birds on the Baltian area refer to a few isolated individuals and somewhat predate the once so sensational

report by Lönnberg (1921) from the Swedish east coast in 1919. These scattered appearances of the yellow-legged herring gulls are an indication of the commencement of the movements of this element in the eastern Baltian area (see also Voipio 1954, 1968, 1972), which eventually turned out to be a strong expansion of the *cachinnans* element resulting in several new colonizations on the peat bogs or mires and inland lakes during the first quarter of this century and onwards (Voipio 1954, 1972). It appears that all these colonizations were related to birds genuinely breeding in colonies. Further, as has been pointed out by Bergman (1939), the new colonists of *cachinnans* type on the archipelago off the Finnish south coast comprised about 10 percent of the population as a consequence of only a few pairs of *cachinnans* which had invaded the archipelago in the 1920s when the settlement of the pink-legged element there was small.

We can thus conclude (see Voipio 1954:17) that, while the herring gulls with yellow legs have occurred in the Fennoscandian-Baltian area since the remote past, their apparent scarcity on the inland habitats and even their absence over much of the Baltic Sea until the early decades of this century indicates that a long lasting stable stage of even thousands of years' duration prevailed there between the primary yellow-leg colonization of the area and the new invasion taking place from the early decades of this century onwards.

2.3. Conclusions

From all of the knowledge available, the following picture of the history of the herring gull in the Fennoscandian-Baltian area emerges. The primary colonization of the Baltic Sea and the nearby inland mires and lakes of inland Baltia and Finland took place by the yellow-legged element invading from the Southeast and extending as far North as to the districts around the White Sea in the remote past during the so-called climatic optimum of the Littorina time. Later on, during the cooler and moister subatlantic phase (Voipio 1954, Løppenthin 1967), another expansion, but now by the pink-legged element, oc-

curred from the West or Southwest. It reached the Norwegian and Swedish coasts (eventually also including the Swedish lakes) and the coasts of the Arctic Ocean as far as the western Murman, where it confronted the *cachinnans*-element inhabiting the eastern Murman coast. In the South, it reached the Baltic Sea up to its eastern parts.

After these two primary colonizations, a period of presumably thousands of years of comparative stability commenced. The pink-legged type bred in large colonies on the arctic coast in the North and in a sparse settlement of birds breeding in single pairs on the Baltic, whereas the inland mires and lakes were populated by the yellow-legged element genuinely breeding in colonies. This phase continued until the early decades of the 1900s, at which time the stable phase became disturbed by a new expansion of the *cachinnans*-element from the Southeast. This resulted in several new colonies on peat bogs and lakes in the Baltian countries and Finland during the ensuing decades. It appears that the early phase of this colonization of the yellow-legged herring gulls occurred at a time when the herring gulls represented by the pink-legged element were still rare in the maritime environments of the Baltic, if not absent from these, thus approximately coinciding with the zero point fixed above for the pink-legged element.

The pink-legged population off the south coast of Finland was then increased by a small proportion of the yellow-legged immigrants and has since been (though with decreasing proportion or even with total disappearance later) polymorphic for leg colour. The majority of the yellow-legged gulls of this expansion settled on the inland habitats, however, presumably according to their habitat preference.

The general view outlined above is the same as that once presented by me (Voipio 1954). The vicissitudes of both of these elements have been depicted in Fig. 1. The primary expansion of the *cachinnans*-element is to be seen there by a broken line leading from the Aralo-Caspian districts into the Fennoscandian-Baltian area. The dotted line, in turn, indicates the primary invasion of the *argentatus* element, on the one hand, as far as the eastern Murman coast where it met the yellow-legged element, and up to the Baltic where it displaced *cachinnans* for a long period to come,

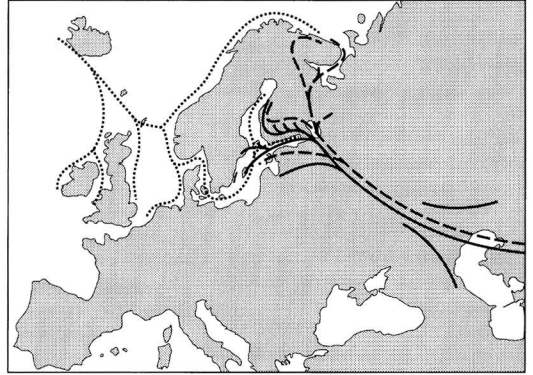


Fig. 1. Colonization of the herring gull in Northern Europe. pink-legged element; - - - yellow-legged element (first colonization); — yellow-legged element (second colonization). (Modified after Voipio 1954).

on the other. Finally, the solid line depicts the new expansion of the *cachinnans* element from the Southeast to the eastern part of the southern Fennoscandia and the Baltian countries during this century.

3. Expansions and colonizations of the herring gull — A problem of ecological biogeography

Finnish biogeographical studies have generally “tended to be descriptive rather than focusing on the causative ecological processes” (Ranta & Järvinen 1987:161). This emphasizes the need for another look, viz. “the study of biogeographical patterns in relation to ecological processes causing these patterns”. In addition to such processes as stochastic demography and interspecific interactions, Ranta and Järvinen enumerate dispersal and the ecology of colonization which, of course, are central from our point of view. I will now proceed to examine the dispersal to, and the colonization of, the different habitats by the herring gull along these lines. For this purpose, I inevitably meet problems considered years ago, i.e. at a time when the then recent (new) emergence of the yellow-legged herring

gulls in the Finnish inland areas called for an explanation of its causes (Voipio 1954).

The following four primary questions were thus asked (Voipio 1954:8–9):

- 1) Why is it that the inland lakes in Finland are colonized by the yellow-legged herring gulls alone, whereas the Swedish lakes contain pink-legged birds only?
- 2) Why is it that the mires in Sweden have remained unsettled despite the increasing colonization of the inland area, whereas the colonization of mires is a characteristic feature of Finland and of certain Baltian areas?
- 3) Why is it that the greatly increased populations on the archipelago of the Gulf of Finland have not been capable of colonizing the inland, whereas the colonization of the Swedish inland lakes advanced effectively?
- 4) Why is it that the herring gulls of both the *cachinnans* and *argentatus* type occur together in the marine habitats, whereas on the inland habitats with few exceptions (extensive mires near the sea coast), one is replaced by the other, only yellow-legged birds breeding there?

Today, these same questions must be presented, more appropriately, in the past tense because there have been considerable changes (particularly in respect of the conditions referred to in question 3 and 4) in the circumstances during the subsequent decades. This, however, by no means nullifies the conclusion drawn from the events described above.

3.1. Ecological tenacity as a factor determining the habitat selection of the herring gulls

In regard to question 1), it is worth remembering that the northwestern outposts of the distribution of the yellow-legged element are principally located within the Finnish area. Particular importance has been attached to the fact that, within that area, the pink-legged and yellow-legged gulls replace each other ecologically. Attention to the alternative of breeding either on the marine coasts (*argentatus*) or on the swampy shores of the nearby lakes only ("*omissus*") was formerly

focussed on the circumstances prevailing on the coast of the Arctic Ocean. Such a phenomenon was considered, in the literature (e.g., Stresemann 1943, Mayr 1949), a classic example of ecological tenacity acting as an isolating mechanism between the groups. The observations by Ottow (1949) are particularly interesting. It appeared not only that the swampy inland lakes on the tundra of the district of Petsamo were colonized by the yellow-legged gulls ("*omissus*") alone but also that the yellow-legged herring gulls had never been observed on the marine coast during the breeding season. The ecological replacement there thus concerned both the breeding habitat and the feeding habitat. This is not all, however. The geographical extent of the ecological replacement appearing within the species was, in fact, considerably larger because of the colonization of the inland lakes and mires by the yellow-legged birds only. The area within which the difference in the habitat selection makes its appearance thus encompasses not only the districts of the marine arctic coasts in the North, but also inland Finland and Baltia in the South.

On the basis of the facts presented, it therefore seems legitimate to consider the yellow-legged inland colonizers representatives of an ecological type of its own which rather tenaciously adheres to the inland habitats in some way or other. It is quite possible that the oncoming great increase during the 1900s of the populations inhabiting mires and lakes was based, in part, on the intrinsic growth of the local populations themselves. This would explain the situation only in part, however. The conspicuously strong increase of the yellow-legged birds in these habitats during the subsequent decades presupposes a much more abundant source population than the one breeding in the colonies of inland Finland. It is also hardly conceivable that the new colonists on the Baltic mires and on the shores of the Baltic Sea up to the east coast of Sweden in the 1920s could have been derived from the limited inland colonies, nor from the yellow-legged populations breeding on the White Sea. If the latter, often offered explanation, had occurred, the increase of the White Sea populations adapted to the marine environment through their existence there for millennia, should have occurred also on the coasts of northern Scandinavia (Norway, Petsamo) which, however, did not occur.

As has been pointed out by Peitzmeier (1942) and Stresemann (1943), in those cases, in particular, where the groups behave differently within an individual species, a more or less noticeable influence of the ecological tenacity is to be taken into consideration. Or, in other words, one can expect that the specific features in the ecology of the groups to a great extent are connected with the specific climatic and vegetational characteristics of the area of the distribution origin. The herring gull, it is true, is a rather flexible species ecologically, for which the exceedingly different ecological conditions within the different parts of its distribution area provide evidence. It must be pointed out, however, that the herring gull, as a colonizer of inland mires and lakes and rivers, is widely distributed within large parts of southeastern Europe and southwestern Asia which, in terms of distribution history, are much older than Fennoscandia. It is very noteworthy that all populations breeding there contain yellow-legged individuals only. To be overparticular, yellow-legged populations occur also in the extreme North, but these are all colonizers of the marine coasts and are, moreover, so much darker on the mantle that they cannot be considered close relatives of the Fennoscandian yellow-legged herring gulls.

Considered against the ecological (and morphological) background outlined above, the only reasonable hypothesis thus was, and still is, that the yellow-legged colonizers of the inland lakes and mires had invaded there from the Southeast. This appeared the more probable as the area of the yellow-legged element extends to the upper courses of the east Baltian rivers near the headwaters of the great Russian rivers Dnieper and Volga and to the watercourse of the Volga itself, and because of the long-range migrations of the yellow-legged gulls from the Ponto-Caspian area along the great Russian rivers northwards turned out to increase in intensity (e.g., Ogilvie 1954, Keve & Pátkai 1955, Voipio 1968, see also Goethe 1982).

It may be difficult to understand, at first sight, why not only the inland lakes but, particularly, also the raised bogs, were preferred by the yellow-legged gulls. The derivation of the nesting habit on mires from the southeastern populations does

not necessarily offer any special difficulty, however. The physiognomy of the mires rather indicates that, in regard to the elements of the landscape, the mires also correspond well with the habitat requirements of the species elsewhere under mainland conditions. Quite obviously, the numerous ponds of the extensive mires and the large system of ponds within the confines of an individual peat bog are analogous in many respects to the conditions prevailing in the steppe areas and on the lower courses of the great rivers characterized by shallow waters with numerous islets covered with grass and reeds.

To conclude: question 1) about why two elements, the yellow-legged and pink-legged ones, have colonized inland lakes each in its own quarters within the Fennoscandian-Baltian area, can be explained only in terms of their ecological biogeography outlined above. It also becomes comprehensible why the border between the yellow-legged and pink-legged gulls as colonizers of the inland lakes is so steep in Fennoscandia. The Finnish and Baltian inland waters lie at the northwestern end of the distribution route along the great eastern European streams, whereas the Baltic Sea has effectively acted against continuous spreading of the yellow-legged element towards the West.

3.2. Differences in the colonizing ability due to separate distribution histories of the groups

In the case of question 2) the answer is to be found in the different ecological behaviour of the separate elements. It appears that the southeastern yellow-legged populations only are originally found as colonizers of mires. This thus holds true also for those mires which have been colonized, due to the increase of the nearby marine populations, by the pink-legged element later, and of which the peat-bog *Sahne-mosse* on the Finnish west coast is a well documented example. The absence of mire colonists in Sweden is thus a consequence of the inability of the pink-legged element to settle down in such habitats. This thus basically depends on historical circumstances. The *argentatus*-element invading from the West

typically belongs to the ecological group of colonizers on the rocky shores of the Atlantic Ocean not inclined to settle down on swampy sites inland.

The appearance and the ensuing increase in the relative abundance of the yellow-legged element also on the marine habitats of the Baltic observed around the middle of the 1930s, in turn, cannot be considered particularly strange because the inhabitants of continental Asia once colonized the coasts of the Mediterranean area. It is quite conceivable that some of the yellow-legged herring gulls, at the termination of their expansion into the Baltian area, colonized the sea shores whereas others, perseveringly holding on to their habitat preference, colonized the inland habitats further. The former, by their intrusion into the new habitats on the Baltic Sea, came to breed together with the pink-legged herring gulls and thereby confined themselves to these new habitats through factors strengthening the philopatry. If this had not taken place, the strongly increased population of the archipelago in the Gulf of Finland would have been capable of colonizing the inland areas, as a result of which the populations there would have become dimorphic in respect of leg colour. This was not the case, however, at the time we are considering here, in contrast to the circumstances prevailing at present when the dimorphic element of the strongly increasing population of the Finnish archipelago, indeed in accordance with the prediction by Olsson (1958: 154), has eventually colonized a large part of inland Finland during the subsequent three or four decades. This fact notwithstanding, the remaining questions 3) and 4) presented above have received a reasonable answer.

4. Analysis of the theory of colonization of the Fennoscandian-Baltian area

As the colonization events within the area under consideration represent successive occurrences during a period of large-scale temporal dimension, the basis of the theory inevitably consists of several hypotheses proposed for explaining the consecutive events separately.

4.1. Hypothesis I

As has been suggested rather unanimously (but compare, e.g. Barth 1968), the centre of the differentiation of the yellow-legged element of the herring gull is to be found on the Aralo-Caspian-Black Sea area colonized by populations varyingly defined by the taxonomists either as subspecies *ponticus*, *cachinnans* and *barabensis* of the species *argentatus* or, in accordance with some earlier taxonomists, as belonging to a separate species *cachinnans* (Haffer 1982). The vicissitudes of the *cachinnans* element have thus supposedly been closely associated with the changes in the physical conditions, particularly climatic ones, with accompanying fluctuations in the water-level of the inland seas, lakes and rivers of the steppe zone (for particulars referring to the remote past, see, e.g., Flint 1947, Voipio 1954). Here was the basis for the hypothesis (Voipio 1954:16) according to which the periods of drought brought out in the Aralo-Caspian region (and in the nearby districts of Southwest Asia) acted as a thrushing factor in the distribution dynamics of the species. The period of the so-called climatic optimum, particularly, characterized by an extreme drought effectively acting for the shrinking of the extensive inland seas and also for the reduction or even disappearance of the numerous shallow steppe lakes, gave a definitive push for emigrations of the herring gulls in different directions, including towards the Northwest.

As a corollary of hypothesis I, it was proposed further (Voipio 1954:17) that owing to the ecological behaviour, particularly due to habitat preference, the mires and lakes as well as the swampy lakes on the tundra were the principal outposts of the dispersal towards the Baltian and eastern Fennoscandian area, not primarily the Baltic Sea. It is even probable, on these grounds, that this element did not obtain too firm a foothold on the marine habitats in contrast to inland, where it presumably appeared as a true colonial breeder.

4.2. Hypothesis II

The new wave of colonization of the yellow-legged herring gulls commenced at the begin-

ning of, and increased in strength during the first half of, this century. Occurring at a moment when the pink-legged herring gull populations on the Baltic were still in a stable stage with relatively sparse populations of solitary breeding pairs, this expansion was immediately noticed in many quarters and called for an explanation.

The temporal coincidence of this new phase of immigration with the areal growth of the desert, the disappearance of many steppe lakes, and the general lowering of the water-level on the Aralo-Caspian area (Kalela 1940, Voipio 1954:24) led to the second hypothesis suggesting that this new colonization wave of the yellow-legged element on the Baltian area in the 1900s was caused by drought bringing about an escape of birds from the hostile conditions through emigration — as an analogy to the primary colonization during the climatic optimum of the postglacial.

How extremely devastating this new climatic phase of drought really must have been is only too apparent in the far-reaching plans (later abandoned) of the Russians as early as the 1940s for changing the course of the great Siberian rivers towards the Aralo-Caspian area to prevent it from drying up to a far too dangerous extent (Voipio 1954:25; see also Schüz (1959) for the conditions prevailing around the southern Caspian Sea).

4.3. Hypothesis III

It has been generally agreed that the Fenno-scandian pink-legged element of the herring gull is to be considered a terminal link of the *smithsonianus* – *argenteus* – *argentatus* series of the Atlantic group. As has been pointed out above, it seems that this element has not immigrated into the Baltic until the subatlantic climatic phase, i.e. thousands of years later than the yellow-legged element. This led to the following hypothesis (Voipio 1954:20).

The supposedly sparse population of the yellow-legged herring gulls, having settled down on the coasts of the Baltic Sea during the warm atlantic phase, was forced to make room for the invasion of the western pink-legged element. As an oceanic element, the pink-legged gulls got the

upper hand and displaced the yellow-legged ones, if not simply settled down as pioneers on the empty (rocky) habitats available. This is the more probable as this climatic phase implied a simultaneous moistening of the climate on the steppe areas manifested in the general rise of the water level on the Aralo-Caspian region (Flint 1947) which, in turn, tended to reduce or even stop the emigration of the gulls from the area.

The hypothesis receives support from the fact that the feet of the otherwise pink-legged birds breeding on the shores of the Gulf of Finland before the turn of the century commonly exhibited a yellowish tint, probably as a remnant of the characteristics of the old ancient population of the herring gulls assimilated by the western pink-legged intruders shown to be genetically the dominant type in respect of leg colour (see Voous 1946).

4.4. Assessing the predictive power of the hypotheses presented

To examine whether the hypotheses presented fulfil the requirement of possessing the power of prediction, I shall consider my hypothesis I first. The (second) colonization events of the yellow-legged gulls occurring on the Baltic from the Southeast after the turn of this century, in fact, can be interpreted as a validation of the prediction of events derived from the occurrences during the warm postglacial climatic optimum. Continuing the deduction on the same lines, one can postulate that my hypothesis II upon the source of the yellow-legged element appearing on the Baltic area during this century in turn generates the following prediction:

If the living conditions of the Aralo-Caspian yellow-legged herring gulls for one reason or another turn out to be intolerable or unbearable, the ensuing emigration to be expected from that area will probably lead to a rise in the relative frequency of the yellow-legged individuals within the Baltian herring gull populations.

As has been stated by Kilpi (pers. comm.) and Mierauskas et al. (1991), the numbers of the yellow-legged birds, after having been reduced considerably during the second half of the century,

indeed have experienced a perceptible rise in abundance during the last few decades (or even years?). Being clearly contrary, though swinging back and forth occasionally, to the long continued course of events, it requires an explanation. The thrilling question arises of whether there are again circumstances acting as an agent for a certain amount of emigration from the old source area in the Aralo-Caspian region? The answer seems to be in the affirmative. Articles in the world's press offered a very interesting first hand piece of evidence (document). They report an extremely rapidly advancing drying up of the Caspian Sea as well and, particularly, of the Aral Sea, principally due to adverse impact on water conditions through the cotton industry wasting the water of the great rivers of Syr-Darja and Amu-Darja, causing them to completely dry up during the summer and leading to the disappearance of the Aral Sea itself. How alarming the situation *de facto* is at present has recently been reported by Rich (1991). This has inevitably brought about a serious deterioration of large parts of the natural habitats of the herring gulls, presumably with consequent emigration towards less hostile districts.

To conclude, it appears, first, that my hypotheses I and II fulfil the requirement of possessing the power of prediction of probable outcomes under certain conditions and, second, that the predictions presented have been validated.

Finally, as regards hypothesis III upon the original immigration of the pink-legged element from the West to the Baltic during the subatlantic climatic phase (a suggestion already based on taxonomic evidence considered reliable in the 1930s, e.g. by Geyr von Schweppenburg 1938), the following prediction can be made:

If the conditions for living within the original source areas of the pink-legged element in the West turn out to become exceptionally advantageous, the ensuing great population growth will lead to a new emigration toward the Northeast (eventually reaching the Eastern Baltic) and manifest itself in specific characteristics, be they ecological or morphological or both, of the new colonists on the freshly occupied breeding sites.

This is indeed what seems to have occurred. In this case too, therefore, nature has given us an answer to the questions how and why? As has

been emphasized by Hario (1986), Kilpi & Hario (1986) and Kilpi (1988), a perceptible change in the population status of the herring gull on the Gulf of Finland took place at about the turn of the 1920s and 1930s. It referred to the start of a continuous increase of the population that included the following decades, initially presumably due to the invasion of the pink-legged element from the West. Contrary to the former sparse population breeding in solitary pairs only, this new immigration wave contained birds that were genuine colonial breeders. The temporal coincidence of the population growth in the Baltic area with the population changes on the coasts of the North Sea and Britain already indicates that the colonization here originates from the West. This view gains support from the fact that this new element of pink-legged birds seems to be affiliated with the populations of the North Sea and Britain, except in regard to the expressly ecological characteristic of coastal colonial breeding, but however also in respect of its wing-tip pattern (Kilpi & Hario 1986).

It is possible that municipal land-fills and commercial fishing reaching very great proportions, particularly in the North Sea area, have been the main cause of the change. How sensitively the populations really are in regard to the feeding conditions, is excellently reflected, on a smaller scale, by the opposite events which took place on the Eastern Baltic after the 1950s. As stated by Mierauskas et al. (1991:17), the coastal gulls (i.e., the pink-legged element) reached their largest numbers on the Eastern Baltic in the 1950s and 1960s, but as the amount of fish caught in the littoral zone sharply decreased after 1960, they started occupying inland waters.

While such a change advances comparatively rapidly in these more limited areas, this event, however, recalls, as an analogy, the temporally more continual and extensive evasion of the yellow-legged element from the Aralo-Caspian area which, particularly in regard to the latter case, was due to the deterioration of both the feeding and the breeding conditions of the species.

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