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Terns and gulls as features of habitat recognition for birds nesting in their colonies.

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The tendency of many ducks, grebes and shorebirds (*Aythya fuligula, Podiceps nigricollis* and *Arenaria interpres* are particularly characteristic examples) to nest in the breeding colonies of terns and gulls (notably *Sterna hirundo, S. macrura, Larus ridibundus,* and *L. canus*) is one of the most discussed problems of recent Fennoscandian waterfowl research (e.g. NYSTRÖM 1927, OLSONI 1928, FABRICIUS 1937, v. HAARTMAN 1937, 1945, 1948, BERGMAN 1939, 1941, 1946, DURANGO 1940, 1945, 1947, 1954, NORDBERG 1950, KOSKIMIES and ROUTAMO 1953, RAITASUO 1953). In spite of the interest aroused by this phenomenon, there is no satisfactory agreement about its causalities and biological significance.

Two main theories have been put forward in explanation of the phenomenon during recent years. One, which may be called the »protection theory», assumes that the ducks, grebes and shorebirds are attracted to the tern and gull colonies because of the safety and protection they, through their aggressivity, afford against predators during the breeding season. Of the writers mentioned OLSONI, FABRICIUS and DURANGO, clearly give their support to this idea.

The »protection theory» is based on a certain amount of observational evidence (e.g. OLSONI 1928, SWANBERG 1932, FABRICIUS 1937, BERGMAN 1939, SALOMONSEN 1942, DURANGO 1945, ROSENBERG 1946, OLSSON 1951), which seems to show that the nests of the associated breeders really are better protected, against crows in particular, within tern and gull colonies than outside them. Because of its biological reasonableness and factual support, this idea has gained fairly wide acceptance (e.g. PALMGREN 1953, p. 120).

A basically different explanation has been offered by v. HAARTMAN (1937, 1945). He considers that the formation of these heterotypic colonies is brought about by a purely social attraction of the ducks (notably *Aythya fuligula)* towards the larids. v. HAARTMAN does not, however, absolutely reject the idea of a protective value of this nesting habit, and he even refers to the possibility that protection through the larids may act as a selection factor favouring the social reaction of the ducks towards the larids. In a later paper (v. HAARTMAN 1948), however, he takes a rather critical attitude towards the protection theory. BERGMAN (1941, 1946), another supporter of this »companion theory», likewise explains the phenomenon as being based on a social reaction, agreeing in principle with v. HAARTMAN. He clearly disagrees with the protection theory. RAITASUO (1953) again, discussing the phenomenon as exhibited by *Aythya fuligula,* emphatically disagrees with the protection theory and maintains that this communal nesting is based on some kind of social misreaction, i.e. on the social attraction effected by substitute companions (larids) in absence of conspecific social companions.

RAITASUO (op.c.) has proceeded one step further and attempted to analyse the releasers of the social reaction assumed to be exhibited by these ducks. His idea that the contrast pattern of black and white in the larids releases a social misreaction in the tufted ducks, which exhibit a somewhat similar contrast pattern dos not perhaps seem very plausible (cf. e.g. DURANGO 1954) and in any case can be applied to no other species than the tufted duck.

The difference of outlook behind the two main lines of thought is striking. The »protection theory» emphasizes the biological significance of the phenomenon, the »companion theory» (including the »misreaction hypothesis» of RAITASUO), again, its releasing system. Even is spite of rather emphatic differences of opinion (most recently RAITASUO 1953 and DURANGO 1954) it seems that the contradiction between the two viewpoints is only ostensible and that they may be harmoniously combined.

In the author's opinion, the tendency of the ducks, grebes and shorebirds to associate with terns and gulls in their breeding colonies may be regarded as a special case of normal habitat selection. Here, as in all cases of breeding habitat selection, the basic biological »interest» is the best possible survival of the offspring (eggs and young). The actual selection of the breeding habitat, however, is guided by certain immediate features of recognition in the potential breeding environment (LACK 1949, SVÄRDSON 1949, DURANGO 1953). In a biologically adapted situation an instinctive reaction to such recognition marks, in themselves perhaps completely irrelevant from the point of view of survival of the species, leads in average conditions to the selection of a habitat of the highest survival value to the species in question.

In the present case, it seems logical to suppose that the protection by the larids is the fundamental biological cause of the inclination of the birds mentioned to nest within their colonies. Insofar as this habit has survival value for these nesting associates, environmental selection favours any reasonable reactions which lead to communal nesting. One very obvious method of attaining this biological end would be a positive reaction to the larids themselves. It thus seems that *the larids* (through optic and/or acoustic stimuli) *form a part of the releasing features of habitat recognition in the ducks, grebes and shorebirds nesting in their colonies.* The reaction of these »alien» birds is seemingly identical with sociability (in the sence of need for companionship) but compared with it, of more secondary origin.

In an earlier paper (KOSKIMIES and ROUTAMO 1953) the author has presented this same idea concerning the response of *Melanitta fusca* to larids in the outermost archipelago. A hypothesis was put forward that »die Gegenwart der Lariden ist ein wesentlicher Teil in dem Eigenschaftskomplex, auf welchen der Vogel bei der Wahl des Nistplatzes reagiert. Das Fehlen der Lariden führt dazu, dass das fragliche Nistgebiet nicht alle für einen idealen Nistplatz characteristischen Merkmale aufweist, und seine »Auslösungskraft» ist schwächer» (p. 50).

Although habitat recognition in animals is evidently guided by basically innate reactions (e.g. LACK 1949, SVÄRDSON 1949), the innate component of the releasing mechanism is probably very broad and is adapted to guide the selection of specific habitats rather vaguely. Otherwise, the ability of most bird species to breed in habitats differing widely in structural details (e.g. SVÄRDSON op.c., DURANGO 1953) can hardly be understood. Yet the permanently much stricter habitat requirements of individual birds and local populations suggest that the broad innate mechanism of *specific* habitat recognition may be supplemented by additional features of habitat recognition acquired during the early life of an individual, to form a more definite mechanism of *individual* habitat recognition (cf. also DURAN-

GO 1947). This supplementing of the mechanism of habitat selection would be comparable in principle to the well-known process of imprinting, by means of which young animals through individual experience refine the vague innate recognition marks of their parents (and other species companions).

The nesting of ducks, grebes and shorebirds in the larid colonies as a result of a reaction to the presence of larids probably represents a case of a refined habitat recognition system acquired through imprinting in local populations.

It is probable that the imprinting to the presence of larids takes place during the period when the young birds are developing in these characteristic surroundings. In this way, the habit of breeding in gull colonies, once acquired as a result of perhaps more or less accidental breeding in such surroundings, will be perpetuated in following generations (cf. the analogous case of acquiring a »new» breeding habitat by *Apus apus;* KOSKIMIES 1956). Admittedly, this hypothesis might perhaps be thought to explain the spread of such a habit in local populations even without assuming it to have definite survival value, not, however, its preponderance over nesting without larids. The fact that the breeding of many of the birds dealt with (notably *Aythya fuligula* and *Podiceps nigricollis)* is in many areas almost exclusively bound to the presence of larids, strongly suggests that this habit has a definite survival value as compared with breeding outside the larid colonies, and thus supports the idea of a »protection» component in its causalities.

In an earlier paper (KOSKIMIES 1955) the author, following the ideas originally presented by BAKER (1938), has emphasized the necessity of distinguishing between the two levels of biological causal factors in cases involving the study of biological adaptations. The *ultimate causal factors* characteristically represent a certain biological survival »interest», which, through the action of environmental selection, guides evolution towards adaptations, the immediate releasers (the *proximate causal factors)* of which may be quite independent of the original biological »interest». There are numerous well-established examples of how this line of reasoning has led to a clear understanding of biological phenomena with seemingly contradictory evidence of causal relations (e.g. BAKER op.c., LACK 1949, 1954, KOSKIMIES op.c.).

In the present case, the biological (ultimate) cause of the phenomenon in question is the breeding-season protection of the ducks, grebes and shorebirds offered by this habit, while its immediate (proximate) cause is the releasing effect of the larids.

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Selostus: **Tiirat ja lokit niiden kolonioissa pesivien lintujen pesimisympäristön valintaa ohjaavina tunnuksina.** Monien sorsalintujen, uikkujen ja kahlaajien selväpiirteinen taipumus pesiä lokkilintukolonioissa on pyritty selittämään toisaalta niiden siellä nauttimaan pesimisaikaiseen suojaan vedoten, toisaalta vain niiden luontaisen seurallisuuden ilmauksena. Näiden kahden ajatussuunnan ristiriitaisuutta on kirjoittajan käsityksen mukaan aiheettomasti korostettu. On todennäköistä, että lokkilintujen aggressiivisuuden aikaansaama suoja petoja, etenkin varista vastaan on siksi huomattava, että luonnon valinta on suosinut lokkilintuihin kohdistuvan »sosiaalisen» reagoinnin kehittymistä niiden kolonioissa nykyisin pesivien »vieraiden» lajien kannoissa. Ilmiö on näinollen epäilemättä tulkittava normaalin elinympäristönvalinnan erikoistapaukseksi. Tässä kuten kaikessa pesimisympäristön valinnassa, luonnon valinta suosii sellaisten biologisesti sinänsä ehkä aivan epäolennaistenkin piirteiden sisältymistä pesimisympäristön valintaa ohjaaviin tunnusmerkkeihin, jotka johtavat jälkeläisten elinkykyisyyden kannalta edullisimman pesimisympäristön valintaan.

On luultavaa, että lokkilintuja luonnehtivien näkö- ja/tai kuuloärsykepiirteiden sisältyminen po. »vieraiden» lintujen ympäristönvalintaa ohjaaviin tunnusmerkkeihin on tapahtunut ekologisen »kokeilun» (tai sattuman) tietä. Sen siirtyminen seuraaville sukupolville on taas todennäköisimmin tapahtunut poikaskehityksen aikana muodostuneen tottumisen (leimautumisen) tuloksena.

Viirretjokisuun ja läheisen saariston pesimälinnusto vv. 1954—55.

TEUVO HAHL-MARJOKORPI

Alue on tyypillistä Keski-Pohjanmaan rannikkoa ja siihen liittyvää saaristoa huomaamattomasti alenevine maastoineen ja mataline rannikkovesineen. Se sijaitsee Lohtajan ja Himangan kk:n välillä, Vaattajan niemestä pohjoiseen n. 64° 5′ N, ja 23° 30′ E.

Oheisessa taulukossa esitetyt arviot on suoritettu seuraavilla ala-alueilla, jotka käsittävät tutkitun alueen pääosan. Muilta lajiluettelossa mainituilta paikoilta on vain hajahavaintoja.

Syrni (jäljempänä S, ala 10 ha) on mantereen laaja, lietteinen tulvaniittyalue kiviriuttoineen ja pienine metsäsaarekkeineen. Erittäin hyvä muuttohavaintopaikka. — Kannuskari-niminen niemi (KK, 7 ha) on rannoiltaan riuttainen, kuten kaikki seuraavatkin, sisäosat korpea tai VT- ja CT-männikköä. Lampi lähellä kärkeä. — Viirretjokisuu (V, 2 ha). Tulvaniittyjen ja lepikoiden ympäröimä riuttainen alue. Joki mutainen ja matala, *Scirpus lacuster* muodostaa siinä tiheitä kasvustoja. — Kalliokari (K, 7 ha). Kallioinen ja sekametsäinen