Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators

RISTO LEMMETYINEN
Department of Zoology, University of Turku

LEMMETYINEN, R. (Zool. Dept., Univ. of Turku, 20500 Turku 50, Finland) 1971. — *Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators.* Ornis Fenn. 48:13—24.

The frequency of attacks on a stuffed dummy, usually of a Great Black-backed Gull, made by Arctic Terns was compared with those made by Common Terns. Furthermore, the attacks made by pairs nesting solitarily were compared with attacks made by pairs nesting in colonies. The experiments showed that the same object had a different releasing effect depending on the phase of the nesting cycle. Terns reacted by attacking a dummy placed in their nesting territories immediately after arriving from migration but their reactions were quite slight before laying. The frequency of attacks increased very clearly after laying and throughout the whole incubation period. The attacks were most violent during the fledging period. There were no significant differences between Arctic and Common Terns in the frequency of attacks. However, the Arctic Tern was clearly more aggressive towards man. Attacks made on the dummy by pairs nesting solitarily or in colonies were equally numerous. Terns nesting solitarily were clearly able to protect their broods from nest predators just as well as terns in colonies. This was shown by means of experiments with hens' eggs, too.

In the author's opinion the losses of tern broods in colonies were caused by the fact that certain trees and shrubs which often grow in the nesting terrains of terns in Finnish archipelagos give effective shelter to predators, especially when they still have not developed definite feeding habits.

Heavy losses caused by nest predators have been observed among larids nesting on the ground. However, mechanisms to minimize these losses have been developed in the course of time. In order to protect their broods more effectively from predators Common and Arctic Terns *Sterna hirundo, S. paradisaea* commonly gather together during the nesting period at which time they also react very aggressively to nest predators (CULLEN 1960). DARLING (1938) has mentioned that the more densely a colony is inhabited, the more effective is the protection given by its members. Many persons have made experimental studies on anti-predator behaviour in colonies of gulls (TINBERGEN 1967). According to BERGMAN (1939) terns nesting solitarily are more aggressive towards nest predators than pairs nesting in colonies. LIND (1963) has observed that the same is true for the Sandwich Tern *Sterna sandvicensis.* BERGMAN (1939) also observed that the eggs of solitarily nesting terns escaped predators better than the eggs in colonies. In addition, the protection offered by tern and gull colonies for the Tufted Duck *Aythya fuligula* nests is quite inadequate (v. HAARTMAN 1945).

The Common Tern is generally regarded as a less aggressive species than the Arctic Tern (SUOMALAINEN 1939, TENOVUO 1963a, BOECKER 1967, V. HAARTMAN *et al.* 1967). When visiting the nest sites of terns it is very easy to observe that Arctic Terns are more active in their pursuit of man than Common Terns. If this is so with other predators, too, then the broods of the Common Terns should be more exposed to danger. However, according to MARKGREN (1960) birds react in different ways to different predators depending, among other things, on how dangerous the predator in question is.

These partly contradictory reports caused me to perform experimental studies on the attacking behaviour of terns using stuffed nest predators. I compared the frequencies of attacks made on the dummies by the Common Tern with those made by the Arctic Tern, as well as the attacks made by pairs nesting solitarily with those nesting in colonies. In addition, I made experiments to discover how effective the attacking behaviour is by locating ordinary hens' eggs in the territories of tern pairs.

Methods

Experiments were carried out mainly in the commune of Kustavi in the southwestern archipelago of Finland in 1966—69. Some of studies on the Common Terns were performed at Puulavesi, Lake District of Finland, in 1970.

I studied the behaviour of terns on their nests or in the immediate vicinity of chicks by using dummies of a stuffed Hooded Crow *Corvus corone,* a Raven *C. corax* and a Great Black-backed Gull *Larus marinus.* All these species nest in the study area and every one of them is known to prey on tern broods.

In order to obtain reliable observations it is useful to make experiments with dummies to which terns react as strongly as possible. On the other hand, when results are compared if different species have been used as dummies in different experiments, this may lead to errors. For the experiments I therefore chose a species to which terns would react quite strongly and which could be used for the whole series of experiments. Because of the considerable quantity of droppings from attacking terns the Raven was too black for experimental purposes. While my experiments showed that terns reacted more violently to the Black-backed Gull than the Hooded Crow, I chose the former species as the dummy in most of my experiments. However, at Puulavesi, where the Black-backed Gull does not occur as a nesting bird, only the Hooded Crow was used as a dummy.

I put a dummy no more than 10 metres (usually about 2—5 m) from the nest or chicks. In the case of experiments before laying the dummy was placed in territories known to have been settled the preceding year. The frequency of attacks on the dummy was measured by counting the number of swoops per minute during the first 16 minutes after the first swoop had been performed (although the time of 16 min. was chosen arbitrarily it had to be long enough for the purpose of this kind of experiment, cf. HINDE 1954). Only attacks which came within one metre or less of the dummy were taken into account. The mean number of attacks was calculated for each experiment and series of them were compared when the results were analysed.

With pairs nesting in colonies the nesting stage was calculated from the time the first pairs began to nest. Therefore all the experiments after the first chicks in a colony had hatched were labelled as fledging period experiments in spite of the fact that a great proportion of the pairs were still incubating. HINDE (1954, 1966) has shown that the response to predators wanes if experiments, especially with the same stimulus, are repeated at too short intervals. Because of this I took care not to repeat experiments with the same tern pairs or the same colony too frequently. The shortest intervals were two days in the case of four experiments.

Because terns paid hardly any attention to man when a dummy was in the territory, I considered it unnecessary with every experiment to leave an islet on which terns were nesting but I retreated to the shore in order to count the attacks from a sheltered place. Often — especially on small islets — I counted the swoops from a boat, anchored some thirty or forty metres from the islet.

The experiments were performed with 15 solitary pairs of the Arctic Tern and 10 Arctic Tern colonies and 7 solitarily nesting Common Terns and 7 colonies of Common Terns. The total time of all experiments was 32 h 16 min and the total number 121. The experiments were made at as evenly spaced intervals as possible during all the phases of the nesting cycle. The proportions for each species and for each different phase of the nesting cycle are given in Table 1. I have regarded terns living two or less together on the same islet and at a distance of about 100 m at least from other pairs as solitarily nesting pairs.

TABLE 1. Numbers of experiments carried out with Arctic and Common Terns at different phases of the nesting cycle at Kustavi and Puulavesi Lake.

	Solitary pairs		In Colonies	
	Arctic Tern	Common Tern	Arctic Tern	Common Tern
Before laying	12	10	5	2
During incubation	16	12	13	8
During chicks in nests	10	7	12	14
Total	38	29	30	24

Response during the experiment

The frequency of attacks varied from experiment to experiment. During a 16-min. experiment the frequency was usually the same throughout but in a few less aggressive pairs the intensity diminished towards the end of the experiment or attacks even ceased altogether. For this reason the degree of scatter in the results is high.

The differences in the mean number of attacks between various phases of the nesting cycle (Fig. 1) are statistically significant when results for the whole incubation period are combined (F-test, $P < 0.001$), in spite of very great individual scatter in the results.

Before laying the frequency of attacks was not even during experiments but the frequency decreased sharply during the first 6 minutes. On the other hand, during the fledging period attacks were very numerous and exceeded 40 per min. In this period the attack frequency increased during the first four minutes. This increase is not statistically significant (Mann-Whitney test). The attack frequency increased throughout the whole incubation period (Fig. 2). The experiments carried out during the first half of the incubation period therefore give quite different results from those of the latter half (Fig. 1). The number of attacks was most even in the 16-min. experiments during the first half of the period whereas it rose during the first minutes of experiments carried out during the second half of the period: it was reminiscent of the curve for the fledging period in Fig. 1.

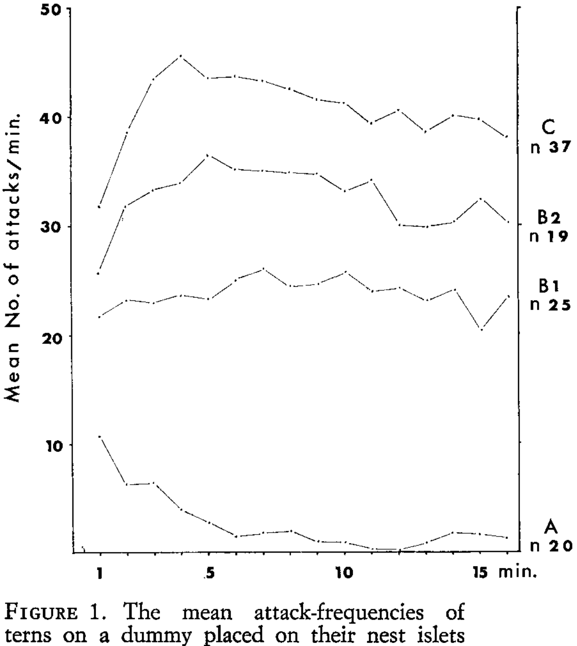

FIGURE 1. The mean attack-frequencies of terns on a dummy placed on their nest islets within the first 16 min. of experiments, before egg laying (line A), during the first half (line B1) and second half (line B2) of the incubation period and during the fledging period (line C). Experiments were carried out at Kustavi in 1966—68.

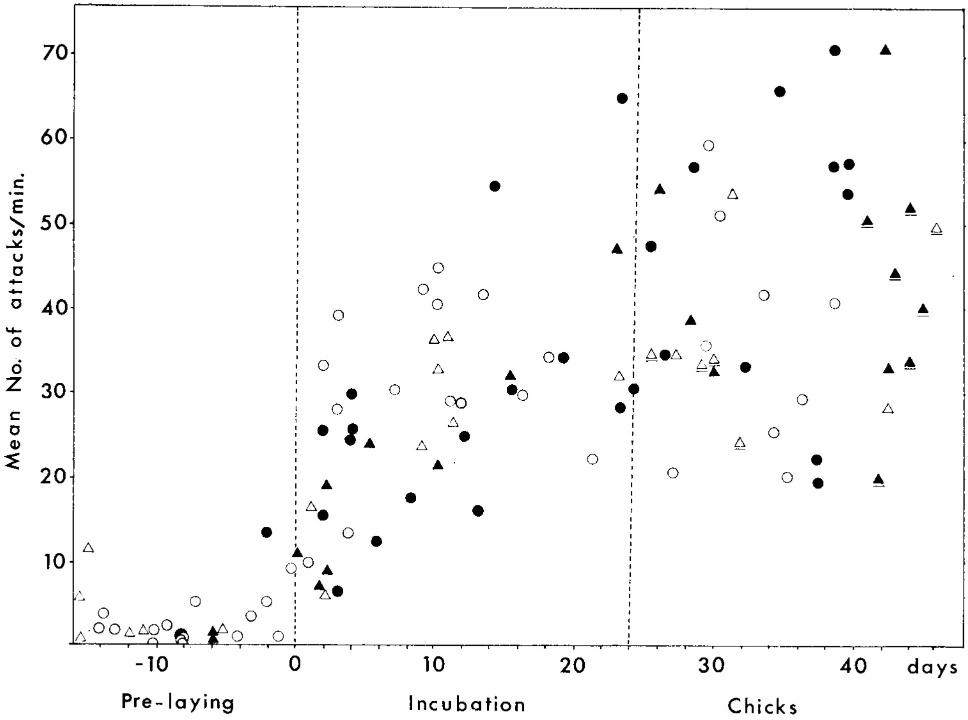

FIGURE 2. Numbers of attacks per min. on a dummy at different phases of the nesting cycle made by Arctic Terns nesting solitarily (○) and in colonies (●) at Kustavi and by Common Terns nesting solitarily (△ $\underline{\triangle}$) and in colonies (▲ $\underline{\blacktriangle}$) at Kustavi and at Puulavesi, respectively.

Attack-frequency during the nesting cycle

The general development of the attacking behaviour of terns during the nesting cycle is given in Fig. 2. In a territory which had been settled the previous year by Arctic Terns they reacted to a nest predator immediately after arriving from migration. 10 of the 11 experiments performed during the first week after arrival were positive. However, nest predators flying above an islet where nesting was taking place did not trigger off so strong a reaction at this stage. In order to make sure whether attacks before the laying period really were associated with the defence of their territory I carried out experiments on shores which were not used as nest sites. These control experiments lasted for many hours, and the stuffed gull being examined by several terns flying over, but I did not observe any attacks on the dummy. Most of the terns flew over without any reaction; a few of them gave a warning but did not remain to circle above the dummy.

The reactions to nest predators were slight before laying (Fig. 2). The mean number of attacks was generally less than two per min. The frequency of attacks increased very clearly after laying. During the whole incubation period the frequency further increased but the scatter in the results of different experiments became much greater.

Towards the end of the incubation period frequencies began to level off but maximum values were not reached until the chicks were born. At the same time the violence of attacks also increased but the difference between the incubation and fledging periods in the number of attacks striking the dummy was not significant. In the fledging period, however, it was quite often impossible to calculate the percentages of such attacks especially in experiments carried out in colonies where the attackers were more numerous. The greater aggressiveness of terns during the fledging period was proved by the fact that the maximum number of strikes made by solitarily nesting birds was then as high as 31 per min. (72 %) of all 28 experiments, but during the incubation period only 11 attacks per min. (30 %) of all 17 experiments. Aggressiveness towards man also increased. During the incubation period only one Arctic Tern struck me but, after hatching, birds of about ten pairs did so.

Comparison of attack-frequencies between Common and Arctic Terns

As mentioned above the Common Tern is regarded as a species less aggressive to nest predators than the Arctic Tern. Anyone who has visited Finnish terneries occupied by both species is willing to accept the opinion. Fig. 2, however, which shows the frequencies of attacks made by Arctic and Common Terns indicates that there are no significant differences between the species ($F = 0.61$, $f_1 = 1$, $f_2 = 35$ during the incubation period and $F = 0.96$ during the fledging period). A pair of Common Terns nesting solitarily were the most violent attackers of the whole series of experiment. Their attacks were so violent that one tern was, on one occasion, injured. In the experiments at Puulavesi the Common Terns completely destroyed the head of the dummy. In addition, as an attacker the Common Tern very often turned out to be at least as violent as the Arctic Tern and even more violent in many experiments where both tern species nested on the same small islet.

There was, however, a very pronounced difference between the species in their behaviour towards man. Usually the Common Tern only became alarmed or made a few half-hearted attacks and I was never struck on the head by this species. On the other hand, among Arctic Terns there were some pairs one parent of which at least struck me on the head and even, at times, drew blood.

It is probably this difference in behaviour towards man that has given rise to the supposition that the Common Tern is less aggressive; it has then been generalized to comprise all nest predators.

The attack-frequency of terns nesting solitarily and in colonies

There was no statistically significant difference in the numbers of attacks made on the dummy by terns nesting solitarily and by those in colonies ($F = 0.93$, $f_1 = 1$, $f_2 = 44$ during the incubation period and $F = 2.66$ during the fledging period) (Fig. 2). Therefore the nest defence aggressiveness of an individual attacker was notably greater among solitary birds, as the number of attackers, usually only 1—2 birds, was significantly smaller in territories of solitary pairs (Mann-Whitney $P < 0.001$).

In addition, the intensity of attacks made on humans walking on their nesting islets during the fledging period by solitarily nesting Arctic Terns was notably greater. Five of nine solitary pairs examined during the fledging period attacked me so violently that at least a few swoops struck my head, but only in three of ten colonies were such violent terns (1—3 birds in each) found. Considering the number of terns in the colonies, the difference in violent behaviour of terns nesting solitarily and in colonies was noticeable.

The greater attack-frequency of the solitary terns could be explained in two ways. Firstly, the difference may be caused by spontaneity of behaviour (LORENZ 1963). Much fewer opportunities arise among the pairs nesting solitarily to release aggression, as other members of the tern's own species are entirely lacking. When a nest predator approaches the nest the accumulated aggressions are released more violently than in colonies. Secondly, it is possible and perhaps more likely that selection eliminates from solitary pairs the less aggressive birds which nest more successfully in colonies.

On the other hand, e.g. KRUUK (1964) has emphasized that attacking behaviour is clearly more frequent and effective in colonies of Black-headed Gulls than in pairs nesting solitarily. This is caused by the fact that each parent gull attacks a predator over an area round its nest which is much larger than its territory. A predator which enters the colony is, therefore, attacked by many pairs. Most nests of Black-headed Gulls are situated less than 2 metres from the nest of the neighbouring pair (PATTERSON 1965). This is a much shorter distance than in Common and Arctic Terns. This may also be one cause why attacks in colonies of the terns in question are less frequent than in colonies of Black-headed Gull (cf. LIND 1963, TAVERNER 1965).

Effect of attack behaviour on the survival of eggs and young

As shown above the terns nesting solitarily attacked nest predators very frequently. To clarify the effects of attack behaviour on the nesting succes I estimated the survival of eggs and young in the colonies and in the territories of solitary pairs. The number of eggs in nests was checked at intervals of 1—4 days throughout the incubation period when the losses were relatively easy to observe. After hatching all the chicks were ringed, usually at the age of 0—2 days, when they still were in the immediate vicinity of the nest. The nest sites were visited at intervals of 1—3 days during the fledging period. I considered the age of 14 days as a criterion of survival as older chicks were very difficult to find. In addition, most chick mortality usually occurs before this age (HAWKSLEY 1957, SZULC-OLECHOWA 1964, own observations). As the search for chicks was carried out as carefully as possible and each chick was identified individually there is reason to believe that the results concerning the survival of chicks should be quite useful.

As shown in Table 2 the percentage of eggs escaping predation was nearly equal in the case of both solitary pairs and pairs nesting in colonies. On the other hand, the survival of chicks was about 30 per cent greater among solitary pairs but the difference was not, however, significant ($\chi^2 = 1.33$) because of the very small number of the chicks of solitary terns.

For this reason I laid out a total of 255 hens' eggs as follows: 113 eggs in six colonies, 13 to 15 in each, and 75 eggs in six territories of solitary pairs, 10 to 15 in each. In order to check whether nest predators visited the area I placed 47 eggs on six islets without nesting terns, with 5—10 eggs on each. The islets were situated in the immediate vicinity of the experimental area. All the eggs were put in places where they were as visible as possible. In addition, each of the eggs was

TABLE 2. Survival of eggs and chicks of terns nesting solitarily and in colonies at Kustavi in 1965—68.

	Eggs			Chicks		
	No. laid	No. escaping pred.	%	No. hatched	No. surviving	%
Solitary terns	65	48	73.8	21	18	85.7
Colonies of terns	1103	838	76.0	396	219	55.3

marked with a number for easy checking. I visited the experiment areas for inspection at intervals of 2—6 days and noted the numbers of the eggs found.

The eggs were best protected from predators (often during the whole of the experiment time) in the territories of pairs of terns nesting solitarily (Fig. 3). The only exception was a territory of the Arctic Tern where all the eggs disappeared within two days. This pair was very inactive in defending its nest during the experiments concerning attacking behaviour, too.

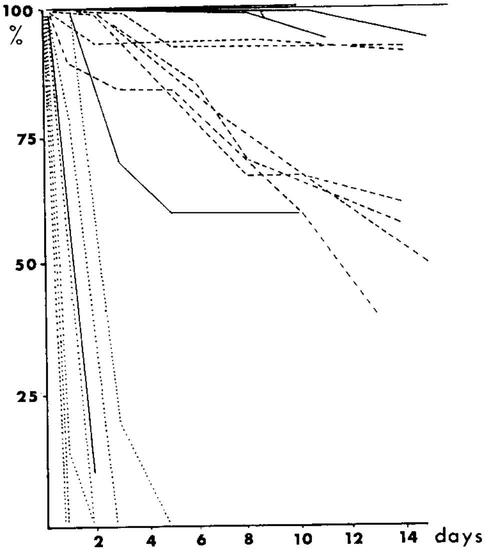

FIGURE 3. Decrease in numbers of hens' eggs in territories of solitary pairs (solid lines), in colonies (broken lines) and on islets unoccupied by terns (dotted lines) at Kustavi in 1968.

It is possible that the curves marking colonies in Fig. 3 decline a little too steeply as it was sometimes impossible to decide whether an egg was destroyed by a nest predator or by some quite harmless bird, e.g. the Common Gull *Larus canus* and Turnstone *Arenaria interpres,* which might have had the opportunity only in this experimental situation. The eggs destroyed by these species are not, however, numerous. The hens' eggs on control islets disappeared very quickly. Judging by the egg remains on the rocks the predator had been the Hooded Crow, at least in most cases.

The cause for heavier losses in the colonies is that the nest predators specialized in egg food — especially the Hooded Crow at Kustavi — seek colonies, where such food is most abundant (BERGMAN 1946, TENOVUO 1963a).

TABLE 3. Decrease in numbers of hens' eggs, experimentally offered to Hooded Crows, in relation to the distance from the nearest trees (distances are approximate values). Numbers show eggs still left at daily control visits. Material comprises a total of six experiments at Kustavi in 1969.

	Distance from trees (m)			
Day	3	5	7	9
0	30	30	30	30
0+1	24	26	30	30
0+2	18	21	26	30
0+3	16	18	24	28
0+4	11	15	19	23

Trees, often only one or two, and shrubs growing on the nesting islets provide effective shelter for predators. To clarify the importance of shelter I performed experiments on islets with a few trees or shrubs where terns were nesting in colonies by placing hens' eggs in four rows running in the same direction away from the trees. Five eggs were placed in each row. The first row was situated 3—5 metres from the trees and the distance between the rows was about 1.5—2 m. The fields were checked daily and the number of eggs that had disappeared from the rows was noted. The eggs disappeared first from the rows situated nearest the trees and only later from the rows farther away (Table 3).

Discussion

Many different factors affect the behaviour of birds towards their nest predators. Birds react in different ways towards different species of prey. This attitude is dependent on the bird's own physiological condition (illness, need for food, etc.), previous experience of the predator, especially such showing the readiness to plunder, etc. (MARKGREN 1960, KRUUK 1964). The experimental method I used was very simple and terns did not get any information concerning the behaviour of a predator. Despite this the stuffed gull was an effective stimulus when placed in the immediate vicinity of the nests or chicks of terns. Indeed, the stimulus was so effective that I was often able to move in the colony without being mobbed even after the attacks on dummy had begun. There is, therefore, reason to suppose that the methods used are valid comparing the ability to defend the nest.

According to HINDE (1954) the response of Chaffinches *Fringilla coelebs* to an object is influenced by those characteristics of the object which characterize a predator model. If the model used as a stimulus was only a rather poor imitation of a predator or the object was strange and did not obviously resemble a predator, then the response to such objects waned relatively quickly. On the other hand, HINDE claims that if there is an effective stimulus, the intensity of response does not reach a maximum immediately the predator has come within sight of Chaffinches but only after a few minutes. This time of increasing response intensity is called by HINDE "a warming-up period".

The releasing effect of the gull dummy was very weak before laying and therefore the reactions of terns to it were slight and rapidly waned. On the other hand, the stimulus of the same dummy during the fledging period was more effective and, in consequence, the number of attacks increased during the first four minutes ("warming-up period") and the total intensity of mobbing was very high throughout the experiment. The same object, therefore, had a different releasing effect depending on the phase of the nesting cycle.

The primary purpose of nest defence aggression is the protection of eggs or chicks from predators. Releasing of the behaviour does not, however, necessarily presuppose the existence of eggs or chicks. This is shown by experiments in which the terns attacked the dummy in their territory long before egg laying. After egg laying the attack-frequency increased very quickly and it continued throughout the incubation period and more or less clearly even during the fledging period.

Attacking is not the only behaviour pattern aimed at protecting broods from predators. Camouflage of the brood and habitat-selection also contribute to this. The effectiveness of protection is determined by the combined effect of these several features (TINBERGEN 1967).

In discussing the protection to broods given by the attacking behaviour of terns two different points must be considered.

Firstly, how many alternatives are available to predators at the same time? E.g. in the lake habitats of the Finnish mainland colonies of Black-headed Gulls are often very effectively protected from Hooded Crows because these birds find enough food and more easily elsewhere, very often from the refuse dumps of human settlements (T. Raitis, pers. comm.).

On the other hand, the safety of a colony increases, if there is no shelter afforded predators by shrub and tree vegetation. The more open the terrain of a colony is, the more effectively the predators are driven off. I have seen many times that e.g. Hooded Crows flew as fast as possible into the branches of trees or shrubs to escape attacking terns. In the shelter of trees they waited for an opportunity to plunder eggs in colonies (cf. TENOVUO 1959). This is also proved by my experiments concerning the importance of trees in the disappearance of hens' eggs.

Partly contradictory opinions have been presented concerning the importance of "protection theory" in the evolution of colonies (KOSKIMIES 1957). A considerable number of opinions concerning the problem has been presented in trying to explain the problems concerning bird species found to nest in colonies of larids. Very intensive criticism of the theory has been made especially by Finnish authors (e.g. BERGMAN 1941, 1946, v. HAARTMAN 1945, 1948, RAITASUO 1953). This theory has been accepted elsewhere, however, more readily (DURANGO 1945, 1954, CULLEN 1960, KRUUK 1964, TINBERGEN 1967, LACK 1968).

The difference of opinion may be affected by the fact that e.g. on the coasts of the North Sea terns commonly nest in large colonies. When studying the nest losses in colonies it has been observed that the predators were able to destroy nests more easily on the fringes of colonies than at their centres (KRUUK 1964). Therefore it is advantageous for a species to nest in large colonies. The terneries in Finland are, however, quite small in general, the largest colonies generally comprising only about 30—40 pairs. Colonies of 100—400 pairs are very exceptional (v. HAARTMAN *et al.* 1967). As a result the advantage of nesting in the centre of a colony has not been evident.

The other cause of different opinions is perhaps the differences in nesting habitats. On the coasts of the North Sea and partly of South Sweden, too, terns usually nest on dunes or rock coasts which are flat, treeless and mainly grass-grown only, whereas the habitats of the Finnish archipelago are much more varied. Trees and shrubs — usually juniper or alder — are usually to be found on islets with colonies of terns and, according to my observations they give very effective shelter to predators. The importance of trees and shrubs is not so great to old and experienced birds, which can also prey effectively on entirely treeless terneries, but especially young crows, which are still unspecialized take considerable advantage of these preying habitats. Taking advantage of shelter from trees and shrubs these young crows obtain experience and therefore their feeding habits gradually become fixed.

On 10 July, 1967, I observed Hooded Crows with four fledglings leaving a small colony of Arctic Terns where they had been protected from the attacking terns by an alder shrub. At the first attempt only four crows succeeded in flying out, two being forced to return very quickly to the branches of the alder. Only after many unsuccessful attempts did another fledgling succeed in escaping from the colony but the last crow had to stay in the branches until I came to the colony.

On the other hand, I have observed a few times experienced crows alighting on nest islets without any trees or shrubs. In spite of violently attacking terns they succeeded in plundering eggs from nests.

Because of the absence of shelter offered by tree and shrub vegetation it is understandable that Carrion Crows are quite rare and ineffective predators in many tern and Black-headed Gull colonies on the coasts of the North Sea and Hooded Crows on Gotland, too (DURANGO 1945, RITTINGHAUS 1951, KUMERLOEVE 1963, 1964, KRUUK 1964, GROSSKOPF 1968). TENOVUO (1963a) has proved that, in their feeding behaviour, Hooded Crows nesting in the Finnish outer archipelago are fully dependent on the eggs or chicks of other birds, because alternative foods are not available. Therefore, predation pressure by crows is directed especially to colonies, where food is most abundant.

The denser and larger the colony the greater the danger from large predatory mammals (TINBERGEN 1953, KRUUK 1964). In order to avoid this danger terns very often nest on islands off the mainland. The fox *Vulpes vulpes,* which is a very effective predator in some colonies of gulls and terns (KRUUK 1964), is insignificant at Kustavi, where the mink *Mustela vison* is the most effective predatory mammal in terneries. I have observed in the field that minks are quite helpless in open terrain in the face of attacks by terns and gulls. Observations of this kind have also been made by KRUUK (1964) with the stoat *Mustela erminea* in colonies of Black-headed Gulls. The mink causes, however, considerable damage on islets with colonies of terns and where there is juniper and other shrub vegetation by moving under cover of the bushes. E.g. in 1967 on an island colonized by one hundred pairs of Arctic and Common Terns mink caused mass mortality of chicks. Losses were, according to my calculation, about 70—80 %. In addition, the mink is a species which is able to move easily from one island to an other, and therefore its spread in Finnish archipelagos represents an ever increasing threat to bird colonies (TENOVUO 1963b).

For the reasons discussed above the nesting habitats on most of the Finnish coasts are less advantageous to terns in the avoidance of predators. The results of predation are clear in the mortality of tern broods for about 75 % of all egg losses and a very large proportion of chick losses are attributable to predators at Kustavi (unpubl.). This is notably greater than in other areas where brood damage has been examined (PETTINGILL 1939, HAWKSLEY 1957, NORDERHAUG 1964, GROSSKOPF 1968).

The attacking behaviour of terns does not completely prevent predators from robbing broods in open nest terrains. According to TINBERGEN (1967) the nests of Black-headed Gulls are spaced out to make it more difficult for a predator to find the camouflaged eggs and young, especially when the attacking birds distract it from searching as carefully as it could otherwise do. This explanation is accepted for Arctic and Common Terns, too (CULLEN 1960). The advantage has been lost when the predator is able to find shelter from attacks in the branches of trees and shrubs and there to watch for nests.

On the other hand, the increased spacing of nests makes mass attacks less affective since there are fewer individuals to take part. As the distances between nests are quite large in colonies of Arctic and Common Terns compared with colonies of the Black-headed Gull, the differences of attack-frequencies of terns nesting solitarily and in colonies are less evident.

Acknowledgements

I wish to thank Prof. Rauno Tenovuo for valuable advice and support he has given me at every stage of this work. My thanks are also due to Miss Anna Unhola for allowing me to use comparative material concerning experiments at Puulavesi lake. I am very grateful to Dr. E. Haukioja and Dr. M. Soikkeli for many helpful discussions and positive criticism of the manuscript. Mr. Pekka Savontaus, M.A., and Mr. Christopher Grapes, B.A. have checked my English both of whom I wish to thank.

This paper is a part of a larger study supported financially by the Leo and Regina Weinstein Foundation and the National Research Council for Sciences.

Selostus: Kala- ja lapintiiran pesien puolustaminen ja sen vaikutus pesimistulokseen.

Pesintäkierron eri vaiheissa verrattiin keskenään kala- ja lapintiiran hyökkäyskäyttäytymistä, joka kohdistui pesän tai poikasten lähelle sijoitettuun, täytettyyn merilokkiin. Lisäksi verrattiin toisiinsa yksin ja yhdyskunnissa pesineiden tiirojen hyökkäysfrekvenssejä. Hyökkäyskäyttäytymisen vaikutusta pesimistulokseen testattiin seuraamalla sekä tiiran munien säilymistä ja poikasten selviytymistä lentokykyisiksi että tiiraparien reviireihin sijoitettujen kananmunien säilymistä pedoilta.

Kokeet suoritettiin laskemalla tiirojen attrappiin kohdistamien syöksyjen lukumäärät minuutissa 16 ensimmäisen minuutin aikana siitä alkaen, jolloin tiirat suorittivat ensimmäisen syöksyn. Suoritettujen kokeiden lukumäärät kummankin lajin osalta ja pesimiskierron eri vaiheissa on esitetty taulukossa 1.

Kuvassa 1 on esitetty syöksyfrekvenssit kokeen kuluessa ennen munintaa, haudonnan aikana ja poikaskauden kuluessa. Ennen munintaa suoritetuissa kokeissa frekvenssi alkoi laskea heti ensimmäisen koeminuutin jälkeen. Sen sijaan haudontakauden lopulla ja varsinkin poikaskaudella hyökkäysfrekvenssi kasvoi kokeen ensimmäisten minuuttien kuluessa.

Tiirojen pesän puolustamisen aktiviteetti lisääntyi pesintäkierron edistyessä ja saavutti maksimin poikaskaudella (kuva 2). Tällöin myös kiinni-iskeneiden syöksyjen määrä oli suurimmillaan. Kala- ja lapintiiran välillä ei todettu eroja attrappiin kohdistuneiden syöksyjen määrässä. Sen sijaan pesäkarilla liikkuvaan ihmiseen kalatiira reagoi selvästi laimeammin.

Yksin pesineet tiirat kykenivät suuremman syöksymisaktiviteettinsa johdosta puolustamaan pesyeitään yhtä tehokkaasti kuin yhdyskunnissa pesineet tiirat (kuva 2). Koska lintuyhdyskuntien verottamiseen spesialisoituneet pedot, tutkimusalueella ennen kaikkea varikset ja minkit, hyvin usein hakeutuvat yhdyskuntiin, muodostuvat pesyetappiot siellä keskimäärin suuremmiksi kuin yksinäisten tiirojen reviireissä (taulukko 2). Tämä osoitettiin myös kananmunakokeilla (kuva 3).

Petojen aikaansaamat huomattavat tappiot tiirayhdyskunnissa johtuvat ennen kaikkea siitä, että rannikkojemme yhdyskuntakareilla kasvaa hyvin yleisesti muutama puu tai pensas, joka tarjoaa tehokkaan suojan tiirojen hyökkäyksiä vastaan. Vastaava suoja puuttuu esim. Pohjanmeren rannikon dyynirannoilta. Puiden ja pensaiden suojaa hyväksi käyttäen nuoret pedot vähitellen spesialisoituvat saalistamaan tiirayhdyskunnissa. Kokeneet spesialistit kykenevät tunkeutumaan täysin avoimillekin pesäkareille.

References

BERGMAN, G. 1939. Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. Acta Zool. Fenn. 23:1—134.

— 1941. Om simfåglars och vadares häckning i måsfågelkolonier. Dansk Ornith. Foren. Tidsskr. 35:120—123.

— 1946. Der Steinwältzer, Arenaria i. interpres (L.) in seiner Beziehung zur Umwelt. Acta Zool. Fenn. 47:1—151.

BOECKER, M. 1967. Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flusseeschwalbe (Sterna hirundo L.) und der Küstenseeschwable (Sterna paradisaea Pont.). Bonn. Zool. Beitr. 18:15—126.

CULLEN, J. M. 1960. Some adaptations in the nesting behaviour of terns. XII Intern. Ornith. Congr. Helsinki 1958:153—157.

DARLING, F. F. 1938. Bird flocks and the breeding cycle. Cambridge.

DURANGO, S. 1945. Om silvertärnans, Sterna macrura Naum., häckningssamhällen och sociabiliteten mellan denna art och andra fåglar. Svensk Faun. Revy 7:91—103.

— 1954. Viggens häckning i laridsamhällen. Ornis Fenn. 31:1—18.

GROSSKOPF, G. 1968. Die Vögel der Insel Wangerooge. Jever (Oldb).

v. HAARTMAN, L. 1945. Zur Biologie der Wasser- und Ufervögel im Schärenmeer Südwest-Finnlands. Acta Zool. Fenn. 44: 1—120.

— 1948. Utskärens fågelvärld. Skärgårdsboken, 442—459.

v. HAARTMAN, L., O. HILDEN, P. LINKOLA, P. SUOMALAINEN & R. TENOVUO 1967. Pohjolan linnut värikuvin, vihko 7. Otava, Helsinki.

Hawksley, O. 1957. Ecology of a breeding population of Arctic Terns. Bird Banding 28:57—92.

Hinde, R. A. 1954. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the Chaffinch (Fringilla coelebs), I. The nature of the response, and an examination of its course. Proc. Royal Soc. London, Ser. B, 142:306—331.

— 1966. Animal behaviour, a synthesis of ethology and comparative psychology. London.

Koskimies, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. Ornis Fenn. 34:1—6.

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (Larus ridibundus L.). Behaviour, suppl. 11:1—129.

Kumerloeve, H. 1963. Die Brutvogelwelt der Nordfriesischen Inseln Amrum und Föhr. Abh. und Verh. des Naturw. Ver. in Hamburg Bd. 7:79—123.

— 1964. Über Strukturänderungen einer Inselornis (Amrum). Zool. Abh. Ber. Mus. Tierk. Dresden 26, 25:323—330.

Lack, D. 1968. Ecological adaptations for breeding in birds. Bristol.

Lind, H. 1963. Nogle sociale reaktioner hos terner. Dansk Ornith. Foren. Tidskr. 57: 155—175.

Lorenz, K. 1968. Niin sanottu paha (Das sogenante Böse). Helsinki.

Markgren, M. 1960. Fugitive reactions in avian behaviour. Acta Vert. 2:1—160.

Norderhaug, M. 1964. Studier av rødnebbternas (Sterna macrura's) biologi på Vestspitsbergen. Fauna 17:137—154.

Patterson, I. J. 1965. Timing and spacing of broods in the Black-headed Gull Larus ridibundus. Ibis 107:433—459.

Pettingill, O. S. 1939. History of one hundred nests of Arctic Tern. Auk 56: 420—428.

Raitasuo, K. 1953. Die Beziehungen zwischen Reiherenten und Möwenvögeln in gemischten Kolonien. Ornis Fenn. 30:1—16.

Rittinghaus, H. 1951. Über das Verhalten koloniebrütender Seevögel gegenüber Raubvögeln und anderen Vogelarten, die nicht zur Brutsiedlung gehören. Vogelwelt 72:149—152.

Suomalainen, H. 1939. Über die Brutbiologie der Küstenseeschwalbe, Sterna macrura Naum., in ihrem Verhältnis zu derjenigen der Flussseeschwalbe, Sternah. hirundo L., in den Schären des Finnischen Meerbusens. Ann. Zool. Soc. 'Vanamo' Tom. 6, 6:16—21.

Szulc-Olechowa, Bogumila 1964. Studies on the postembrional development of Larus ridibundus L. and Sterna hirundo L. Acta Ornith. 8:415—444.

Taverner, J. H. 1965. Observations on breeding Sandwich and Common Terns. Brit. Birds 58:5—9.

Tenovuo, R. 1959. Saariston pesärosvolinnuista ja niiden aiheuttamien vahinkojen torjumisesta. Suomen Riista 13:52—65.

— 1963a. Zur Brutzeitlichen Biologie der Nebelkrähe (Corvus corone cornix L.) im äusseren Schärenhof Südwest-finnlands. Ann. Zool. Soc. 'Vanamo' Tom. 25, 5: 1—147.

— 1963b. Minkki saaristoalueilla. Suomen Riista 16:92—99.

Tinbergen, N. 1953. The Herring Gull's world. London.

— 1967. Adaptive features of the Black-headed Gull Larus ridibundus L. Proc. XIV Intern. Ornith. Congr. Oxford 1966: 43—59.