

Clutch size and timing of breeding in the Arctic Tern in the Finnish archipelago

RISTO LEMMETYINEN

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The timing of breeding and the clutch size of the Arctic Tern *Sterna paradisaea* were studied in the middle and outer archipelago of southwestern Finland. They have been compared with the occurrence of the Three-spined Stickleback *Gasterosteus aculeatus*, which is the most important prey species of the Arctic Tern. The sticklebacks arrived to spawn in shore waters at the turn of May and June and disappeared, after breeding, in the middle of July.

The average clutch size of the Arctic Tern in the middle zone was 2.0 ± 0.02 . No significant annual differences in clutch size were found in 1965—1968, but significant seasonal variations were shown to occur, the clutch size decreasing towards the end of the laying period. In the outer zone, the clutches were highly significantly smaller (1.6 ± 0.05) than those in the middle zone.

Egg laying started in the latter half of May and the annual differences were small. There seemed to be a correlation between laying and air temperature. In the outer zone laying took place about 1—2 weeks later than in the middle zone. The smaller clutch size and the delayed start of laying in the outer zone were probably proximately caused by the poorer feeding conditions prevailing there in the laying period.

Owing to the departure of mature sticklebacks, feeding conditions deteriorated in the middle of July, after the majority of the tern chicks had fledged. This may be the reason, why the weight increase of chicks was slower and their mortality increased in late broods, hatched in July. By the end of the month, most of the Arctic Terns had disappeared from the area.

Introduction

Several factors affect the breeding time and the clutch size of birds (e.g. v. HAARTMAN 1954, 1971, KLOMP 1970, PERRINS 1970). LACK (1954) maintained that the breeding season of single-brooded species corresponds with the time at which it can raise its young most efficiently and that this has evolved through natural selection. Later studies have modified this idea by showing that the date of laying is determined, in some species at least, by the female's obtaining enough food to form eggs (SIIVONEN 1957, LACK 1966, PERRINS 1970).

In some species it is known that environmental conditions greatly modify clutch size (e.g. LACK 1954, 1966, 1968,

CODY 1966, HAUKIOJA 1970, KLOMP 1970). A number of scholars have studied the annual variation in clutch size of the Arctic Tern (HAWKSLEY 1957, NORDERHAUG 1964, BOECKER 1967, GROSSKOPF 1968, EVANS & McNICHOLL 1972). This variation appears to be attributable to climatic factors or to variations in food supply (HAWKSLEY 1957, NORDERHAUG 1964, BOECKER 1967, GULLESTAD & NORDERHAUG 1967, EVANS & McNICHOLL 1972).

In the present work I shall discuss the breeding time and clutch size of the Arctic Tern in different habitats in the archipelago of southwestern Finland. The breeding season and clutch size are compared with the occurrence of the

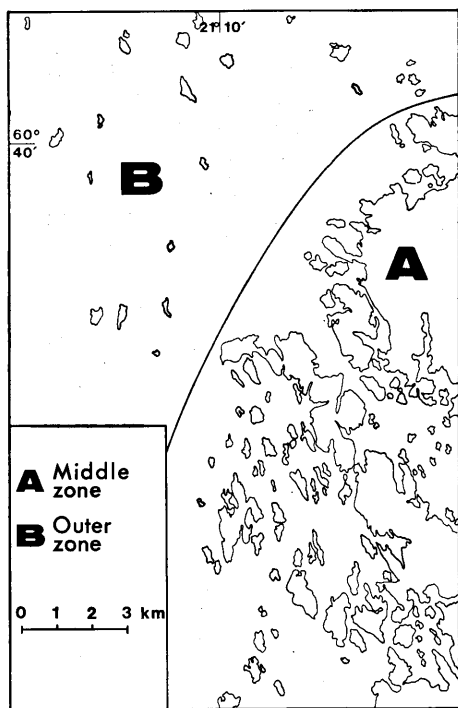


FIGURE 1. Study area at Kustavi, south-western archipelago of Finland.

Three-spined Stickleback *Gasterosteus aculeatus* in shore waters in the area. This fish comprises about 70–80 % of the food of the Arctic Tern (LEMMETYINEN 1973a).

Study area

The study area is situated in the archipelago of southwestern Finland (60°35'N, 21°10'E), and consists of two types of habitat. The first one falls within the middle zone of the archipelago with a great number of wooded islands and treeless skerries (zone A in Fig. 1). Rock and stone shores with dense growths of *Fucus vesiculosus* are dominant. Crustacean and fish fauna are abundant in the *Fucus*-vegetation. The second habitat consists of a number of treeless skerries near the open sea (zone B in Fig. 1). In this zone shallow shore waters are rare. The rocky shores are steep and exposed to waves and the washing effect of the sea. The fauna in shore waters are less abundant.

Material and methods

Most of the investigations were made in 1965–1968. The nests in the middle zone were marked by placing numbered markers in their vicinity, and were checked every 1–4 days throughout the incubation period. A clutch was regarded as complete if the number of eggs had remained unchanged for two or more days. This criterion relies on the fact that the eggs are laid every second day (HAWKSLEY 1957, v. HAARTMAN et al. 1967). Clutch size was checked on the outer islets on the following dates: June 10th, 1965, June 15th, 1966 and June 18th, 1966. In all 140 clutches were checked in nine colonies on outer skerries. Only nests with eggs or newly hatched chicks were taken into account.

The results that were based on one checking visit only may include some errors. Firstly, the average clutch sizes may appear too small if the first broods had hatched before the visit was made because early clutches are usually larger. On June 18th, 1966, hatching had only just commenced in two colonies, the oldest chicks being about 2–3 days old. Secondly, some clutches may be reduced by nest predators. As it is unlikely, however, that predation pressure is similar in different colonies, the average clutch sizes were determined for each colony separately.

In order to follow the growth and survival of the chicks, they were ringed immediately (usually 0–2 days) after hatching. The chicks were checked every 1–3 days before fledging. Chicks of known age were weighed at every visit with spring balances accurate to the nearest 0.5 g or 1.0 g.

Availability of food in shore waters

The Three-spined Sticklebacks were collected by hauling a seine net along the sea bottom straight towards the shore line (LEMMETYINEN 1973a). The hauls were made at intervals of 7–10 days at the same places in the middle zone of the study area from the end of April to the end of July in 1972. Some supplementary hauls were also made in the outer zone in 1971 and 1972.

The number of sticklebacks was small in samples obtained before the middle of May (Table 1). Towards the end of the month populations of sticklebacks close to the shore greatly increased. Most

TABLE 1. The numbers of the Three-spined Stickleback *Gasterosteus aculeatus* in the samples collected by hauling a seine net in 1972 at Kustavi.

Date	No. of pulls	No. of sticklebacks	No. of stickleback/pull
4—26	4	1	0.3
5—02	4	54	13.5
5—13	7	11	1.6
5—22	3	383	127.7
5—31	2	1554	777.0
6—05	2	989	494.5
6—12	2	287	143.5
6—22	2	1436	718.0
7—03	3	98	32.7
7—14	3	87	29.0
7—21	2	—	—

Clutch size

The average clutch size of the Arctic Tern in the middle archipelago was 2.0 ± 0.02 (Table 2). There were no significant annual differences (Brandt-Snedecor χ^2). Instead, seasonal variations were significant. The largest clutches were those laid during the first week, the clutch size decreasing towards the end of the laying period (Table 3). The differences between successive laying weeks were significant ($F=7.0$, $f_1=4$, $f_2=406$, $p<0.01$). Exceptionally, the clutches laid first were smaller in 1967 and 1968.

Average daily weather conditions ten days before the start of laying in 1965—1968 were as follows:

Year	Temperature °C	Precipitation mm	Average cloud cover 0—9
1965	4.9	7.8	4.67
1966	8.6	0.0	3.47
1967	6.2	14.7	6.17
1968	6.4	23.2	5.79

of the fish obtained in May were rather small, but larger individuals became dominant when sticklebacks began to spawn in shore waters at the beginning of June (LEMMETYINEN 1973a).

In early July, the number of sticklebacks decreased quickly. After the offspring had hatched, mature individuals disappeared from shore waters and only the newly hatched offspring were left behind (LEMMETYINEN 1973a).

Not much is known about the spawning of Three-spined Sticklebacks in the outer archipelago. On the July 15th, 1971, three hauls with the seine were made on a small outer skerry. The catches included 59 males which, judging from their appearance, were spawning and 210 grey individuals most of which were probably females. Three hauls made a day later in the middle zone included in all only 5 mature sticklebacks. Thus most of the mature individuals had already disappeared from the shore waters of the middle archipelago indicating earlier spawning. But the difference cannot be great because the fishing hauls made on the 30th May, 1972, included several dozens of mature sticklebacks in the outer archipelago.

(The figures indicating temperature, precipitation and cloud cover are derived from observations made three times a day at the airfield at Mariehamn, some 100 km southeast of the study area. The monthly weather reports 1965—1968 by the Finnish Meteorological Office and Meteorological Year book of Finland Vol. 65—68, parts 1a and 2).

Differences in cloud cover were fairly significant between the years ($F=6.3$, $f_1=3$, $f_2=119$, $p<0.05$). The small size of the clutches at the beginning of the laying seasons of 1967 and 1968 could not have been caused by temperature. On the other hand, rain and cloud cover showed clearly higher values in these years, perhaps rendering it more difficult for the terns to catch food. Especially in the case of the Arctic Tern it has been found that overcast weather has a negative effect on the growth of chicks (HAWKSLEY 1957, LEMMETYINEN 1972).

The average clutch size of the Arctic Tern in 1965—1966 in the outer archipelago was 1.6 ± 0.05 eggs ($n=140$) but

TABLE 2. Annual clutch sizes of the Arctic Tern in the middle archipelago of Kustavi 1965—1968.

Clutch size	1965	1966	1967	1968	Total
1	14 (10 %)	15 (11 %)	9 (10 %)	11 (6 %)	49 (9 %)
2	104 (79 %)	102 (76 %)	60 (71 %)	130 (80 %)	396 (77 %)
3	13 (9 %)	17 (12 %)	15 (17 %)	21 (13 %)	66 (12 %)
Total	131	134	84	162	511
Average size	1.99±0.04	2.01±0.04	2.07±0.06	2.06±0.03	2.03±0.02

in the middle archipelago 2.0 ± 0.03 ($n=265$). The difference is highly significant (Brandt-Snedecor $\chi^2=55.3$, $p<0.001$). Clutch sizes varied somewhat in different colonies: 1.7 ± 0.09 ($n=23$), 1.7 ± 0.17 ($n=21$), 1.3 ± 0.10 ($n=24$), 1.7 ± 0.33 ($n=20$), 1.5 ± 0.12 ($n=17$), 1.8 ± 0.14 ($n=19$), but were in all colonies considerably smaller than those in the middle archipelago in the same years.

That the clutch size of the Arctic Tern is smaller in the outer archipelago is also indicated by the fact that only 2.9 % of the nests included three eggs, whereas the figure in the middle zone was 11.3 %. The difference is significant (student's t -test, $p<0.01$). According to Jorma Tenovuori (pers. comm.), the proportion of clutches of three eggs in a group of outer islets, Isokari ($60^\circ 44'N$, $21^\circ 10'E$), was 5.7 % and the average clutch size 1.6 ± 0.08 ($n=56$) in 1966. His calculations were based on checking visits made at regular intervals.

Egg laying

Fig. 2 presents the dates of the laying of the first egg in different clutches where it could be determined sufficiently exactly. The determination was based (1) on clutches found during the laying period and (2) on the date of hatching, by considering the length of egg laying 2—3 days and incubation 22 days (v. HAARTMAN et al. 1967).

The annual differences in the beginning of egg laying were small varying between 17th and 22nd May. There appears to be a correlation between the dates of laying and air temperatures. The sums of daily mean temperatures from May 10th to 25th at the airfield at Mariehamn were about 95, 141, 122 and 81 in 1965, 1966, 1967 and 1968, respectively. The sum of temperatures was highest in 1966 when egg laying was earliest, but in 1965 and 1968 when the sums were lowest, laying also began later than in the other years.

TABLE 3. Seasonal variations in average clutch size of the Arctic Tern at Kustavi 1965—1968.

Laying week	1965	1966	1967	1968	Total
1st	2.3±0.12 (14)	2.3±0.10 (37)	2.0±0.11 (13)	1.7±0.33 (3)	2.2±0.07 67
2nd	2.1±0.06 (52)	2.0±0.09 (26)	2.2±0.07 (31)	2.2±0.07 (38)	2.1±0.03 147
3rd	1.8±0.08 (24)	1.8±0.22 (9)	2.0±0.11 (24)	2.1±0.05 (66)	2.0±0.04 123
4th	2.0±0.00 (5)	1.9±0.08 (21)	1.5±0.16 (11)	2.0±0.19 (11)	1.8±0.07 48
5th	1.7±0.33 (3)	1.7±0.18 (7)	2.0±0.00 (2)	1.9±0.14 (7)	1.8±0.10 19

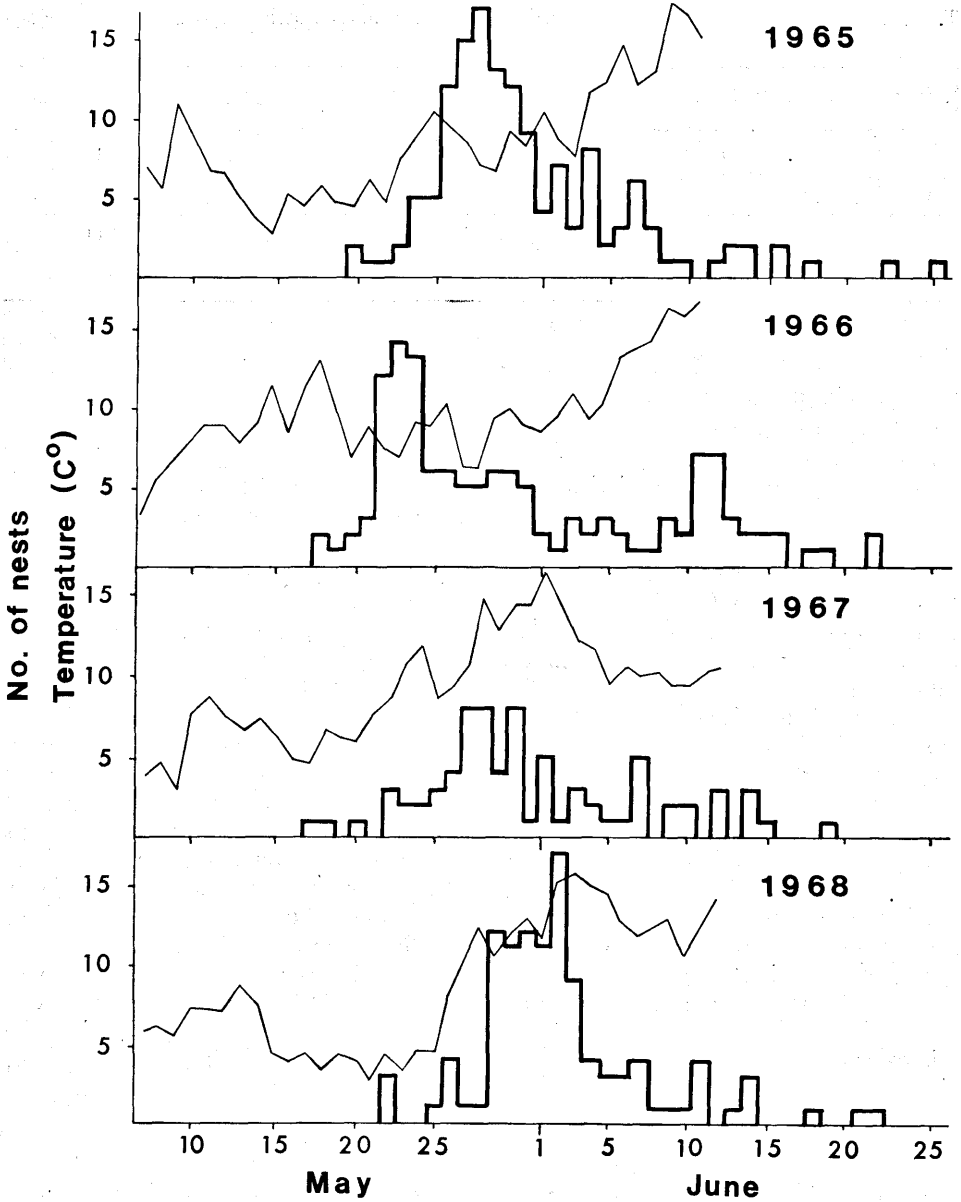


FIGURE 2. Mean daily temperatures and egg laying of the Arctic Tern at Kustavi in 1965—1968. Temperatures were measured at the airfield of Mariehamn, about 100 km southwest.

In all years, the temperatures increased clearly 3–7 days before the peak of laying (Fig. 2). The increase in temperature which began on the 17th May, 1966, was followed by the peak of egg laying on 23rd–25th May, in spite of a redecree of the temperature on 19th–20th. Also, a decrease in temperature on the 23rd May, 1967, did not prevent the start of laying.

The weather was deviating in the course of May in 1968. The temperature decreased clearly after the 13th May and was only about 2–4°C between the 15th and 24th May. This delayed laying. After the temperature had increasing again on May, 26th, laying reached a peak on May, 29th–June, 2nd.

A temperature increase occurring too early in the spring cannot release laying. For instance, temperatures increased markedly between the 7th and 12th May, 1966, and between the 10th and 11th May, 1967, without causing laying. In both years, the first Arctic Terns arrived in the study area on May, 8th.

The commencement of egg laying was not influenced by snow cover or ice conditions as in some northern areas (LACK 1933, BIRD & BIRD 1940, EVANS & McNICHOLL 1972). In the years when clutches were destroyed at an early stage of incubation, replacement clutches were usually laid (LEMMETYINEN 1973b). For this reason, a second peak of laying occurred between the 10th and 15th June, 1966, and, to a lesser degree, also in the first half of June, 1967.

In the outer archipelago, laying took place about 1–2 weeks later than in the middle zone. For instance, only very few nests contained eggs in the outer archipelago at the turn of May and June in 1965, 1967 and 1968, although several clutches in the middle zone had been incubated for a week. A more accurate estimation of the differences in laying time was made on the 10th and 11th June, 1972. The data concerning the incubation stages of the eggs of the Common Tern presented by HAYS & LeCROY (1971) were used. In all, 38 eggs both from the middle and outer archipelago were floated in water and ages of embryos were recorded (Table

TABLE 4. Age of embryos in the nests of the Arctic Tern on the 10th and 11th June, 1972 at Kustavi.

Age of embryo (in days)	No. of eggs	
	Outer archipelago	Middle archipelago
1–2	18	3
3–4	7	2
5–6	5	1
7–8	3	6
9–12	5	14
over 12	—	12
	38	38

4). Incubation was found to have started about 1–2 weeks earlier in the middle zone. The difference was highly significant (Mann-Whitney, $p < 0.001$).

Growth and mortality of chicks

The peak of hatching occurred at Kustavi in the middle of June and most of the chicks reached the fledging stage about July, 10th. As early as the end of July most of the Arctic Terns have migrated from the area and the species is very uncommon at the turn of July and August.

A more detailed description of growth rates and survival of the chicks is presented elsewhere (LEMMETYINEN 1973b). A comparison of growth rates of the chicks hatched late (in July) and early in the season is given in Fig. 3. Some of the late chicks grew just as well as the early ones, but in a number of chicks growth was clearly slower from the very beginning. Also mortality caused by starvation or disease was highly significantly heavier among late chicks less than one week old (Table 5). Both in early and late broods, the proportion of chicks known to have perished from starvation or disease was smallest in broods of two and largest in broods of three.

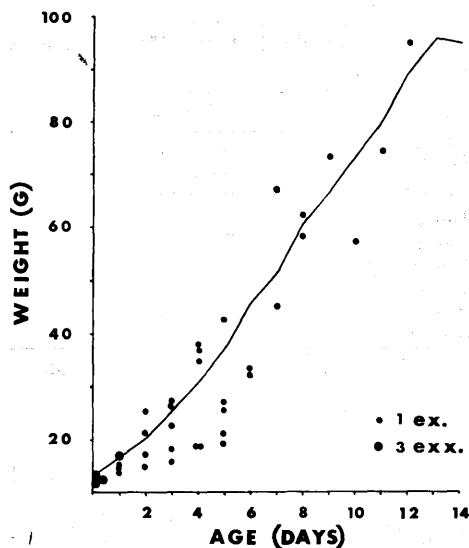


FIGURE 3. Weight development of chicks of the Arctic Tern in the first two weeks of life, at Kustavi. Solid line = weights of chicks hatched in June, circles = weights of late chicks hatched in July.

Discussion

According to CODY (1966, p. 174) "clutch size is a hereditary phenotypic characteristic which is affected by prevailing environmental conditions, and which exhibits the normal variability of such characteristics". How strongly the clutch size is determined by environmental conditions and what the importance of its genetic basis is has been a matter of much controversy.

The clutch size of terns has been proved to be modified by the availability of food, climatic conditions, the age of the birds, etc. (AUSTIN 1940, HAWKSLLEY 1957, NORDERHAUG 1964, EVANS & McNICHOLL 1972).

At Kustavi, the clutch sizes were considerably smaller on outer skerries. This may be caused by the smaller supply of food in the outer zone or food might be more difficult to obtain, making it impossible for the Arctic Terns to obtain the amount of nutrition necessary to produce large clutches. It is known that clutch size in some species may be directly controlled either by the amount or by the quality of food available for the laying female (LACK 1954, 1966, SIIVONEN 1957, BELOPOLSKII 1961, KLOMP 1970, PERRINS 1970, MOSS et al. 1971). It is possible that the Arctic Tern, after its long migration route from the Antarctic to Europe (SALOMONSEN 1967) has exhausted its energy resources on arrival in its nesting areas so that a vigorous accumulation of energy is necessary. After a rather short time (about two weeks in south Finland) the female will lay eggs whose total weight amounts to about 35–50 % of its own. At this time the male repeatedly feeds his mate and as the quantity of food that the male can carry at one time is limited, it is important that the food is of high nutritional value and contains a low proportion of indigestible material. Fish

TABLE 5. Number of chicks of the Arctic Tern perishing from starvation or disease when less than one week old at Kustavi in 1965–1969.

Brood size	Hatched before 26th June		Hatched in July	
	Perished	Survived	Perished	Survived
1	2 (9.5 %)	19 (90.5 %)	1 (33.3 %)	3 (67.7 %)
2	3 (2.5 %)	116 (97.5 %)	2 (25.0 %)	8 (75.0 %)
3	14 (15.7 %)	75 (84.3 %)	3 (100.0 %)	0 (0.0 %)
Total	19 (8.3 %)	210 (91.7 %)	6 (35.3 %)	11 (64.7 %)
χ^2	15.8 ⁺⁺⁺			

forms such a type of food.* BOECKER (1967) proved that in the years when *Clupeidae* are scarce, Arctic Terns switch to crustaceans as the main source of food. This causes, however, a decrease in the average clutch size and delayed the start of laying.

During the laying period, the Arctic Terns ate highly significantly more small crustaceans (*Idotea baltica*) in the outer archipelago than in the middle one (LEMMETYINEN 1973a). This was caused by scarcity of fish food in the outer archipelago at this time. This difference in the food composition of terns nesting in different zones and BOECKER's discoveries (1967) make it likely that the smaller clutch size and delayed start of laying in the outer zone was mainly caused by poorer feeding conditions.

The food of the Arctic Tern, especially in some arctic areas, includes mainly crustaceans and its average clutch size is there under two (LØVENSKIOLD 1964, NORDERHAUG 1964, BENGTON 1971, DE KORTE 1972, LEMMETYINEN 1972). Obviously, the clutch size of the Arctic Tern does not exceed two if fish is scarce during the pre-laying period. This is evident in the outer archipelago of Kustavi. The middle archipelago was only 5—10 km from the outer one, but here clutch size was large as a consequence of the fish diet of the Arctic Terns.

It is known that, in many bird species, clutch size decreases as the season progresses (among Laridae the Caspian Tern *Hydroprogne caspia*, BERGMAN 1953, SOIKKELI 1973, the Kittiwake *Rissa*

tridactyla, COULSON & WHITE 1958, the Herring Gull *Larus argentatus*, and Lesser Black-backed Gull *L. fuscus* BROWN 1967, Red-billed Gull *L. novae-hollandiae* MILLS 1973), and that individuals laying later in the season are to a large extent first-breeders or individuals laying replacement clutches. In both cases clutches are, in general, smaller in size (AUSTIN 1940, KLOMP 1970). But COULSON & WHITE (1961) emphasized that clutches of the Kittiwake laid later in the season were usually smaller than those laid at its beginning regardless of the experience of the female. The same is known of other species, too (KLOMP 1970).

The average clutch size of the Arctic Tern decreased in the middle zone of Kustavi in the course of the season. But simultaneously the number of Three-spined Sticklebacks, which were the main food supply of terns, clearly increased in shore waters. Thus it seems unlikely that food conditions in the first half of June would be the main reason for the decrease in clutch size.

But in the course of July, there is a marked decrease in the number of Three-spined Sticklebacks in shore waters. Thus food becomes less abundant after most of the chicks have fledged, which takes place at Kustavi before the middle of July. This deterioration in the supply of food might also cause the slower initial growth and the greater number of newly hatched chicks perishing from starvation or disease in July. LANGHAM (1972) proved that the first week of life is most critical for tern chicks. It is hard to decide to what extent a reduction of the clutch size is a sign of adaptation to the reduced supply of food available in the latter half of July. As far as I know, increased chick survival has not been verified in smaller as compared with larger late broods among the Laridae.

As shown in Fig. 2, the peak of laying occurred in every year about 3—7

* After leaving the paper to the press, I found an article written by I. C. T. NISBET on "Courtship-feeding, egg-size and breeding-success in Common Terns" in *Nature* 241, No. 5385 (1973):141—142 in which he expresses the correlation between the courtship-feeding performance of the male Common Tern and the total fresh weight of the clutch and also the fresh weight of the third egg.

days after a rise in temperature. The short term fluctuations of air temperature cannot to any greater extent affect the temperature of the sea water, which is very cold at this time, nor the availability of food. Therefore, the onset of egg laying is in part triggered by the direct effect of temperature on the bird. On warm days, courtship displays of terns are common. But the food required to form eggs is considerable and the female is not able to lay earlier than about 1—2 weeks after arrival at the nesting site, in spite of high temperatures. Moreover, the length of the pre-egg period is determined by food quality. If the female has to feed on a large amount of small crustaceans the start of laying may be delayed, as is the case in the outer archipelago.

The timing of the breeding season of the Arctic Tern coincides with a large supply of food, i.e. the occurrence of the Three-spined Stickleback in the shore waters of Kustavi. It is possible, that the disappearance of the sticklebacks from shore waters in July forces the Arctic Tern to lay as early as possible in order to raise more surviving young, and that is why the Arctic Tern is very uncommon in the area at the end of the month.

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Selostus: Lapintiiran pesyekoko ja pesinnän ajoittuminen Suomen rannikolla.

Kustavin ulko- ja välisaaristossa (kuva 1) verrattiin lapintiiran pesyekokoa ja pesinnän ajoittumista rantavesissä tarjolla olleiden kolmipiikkien lukumäärään. Kolmipiikki muodostaa n. 70—80 % lapintiiran ravinnosta ko. alueella.

Sukukypsät kolmipiikit saapuivat rantavesiin touko—kesäkuun vaihteessa ja katosivat jälleen heinäkuun alkupuolella (taulukko 1). Heinäkuun loppupuolelta lähtien tavattiin alueella ainoastaan samankesäisiä pieniä poikasia. Ulkosaaristossa kolmipiikin kutu on todennäköisesti jonkin verran myöhäisempi.

Lapintiiran pesyekoko oli välisaaristossa 2.0 ± 0.02 ja vuosittaiset erot olivat hyvin vähäiset (taulukko 2). Sen sijaan keskimääräinen pesyekoko pieneni merkitsevästi pesintäajan kuluessa (taulukko 3). Muninta alkoi vuosina 1965—1968 välisaaristossa toukokuun jälkimmäisellä puoliskolla ja vuosittaiset erot olivat vähäiset (kuva 2). Muninnan alkaminen korreloi 3—7 vrk aikaisemmin tapahtuneeseen lämpötilan nousuun.

Ulkosaaristossa lapintiiran pesyekoko (1.6 ± 0.05) oli erittäin merkitsevästi pienempi ja muninta alkoi noin 1—2 viikkoa myöhemmin kuin välisaaristossa (taulukko 4). Tämä johtui ainakin osittain siitä, että tiirat joutuivat ulkosaaristossa muninta-aikana saalistamaan ravintoarvoltaan vähäisempiä pikkuäyriäisiä (*Idotea baltica*) kalaravinnon kustannuksella.

Heinäkuun aikana välisaaristossa kuoriutuneista poikasista oli suurempi osa alipainoisia ja ne kuolivat runsaammassa määrin ravinnon puutteeseen tai sairauksiin kuin kesäkuussa kuoriutuneet poikaset (kuva 3, taulukko 5). Eräs tähän vaikuttavista tekijöistä oli kolmipiikkien lukumäärän väheneminen alueelta.

Sukukypsien kolmipiikkien katoaminen Kustavin rantavesistä sattuu yksiin lapintiiran poismuuton kanssa ja molemmat ovat alueella harvinaisia heinäkuun lopussa.

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