

A change in clutch size in the Arctic Tern *Sterna paradisaea* in the northern Baltic

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The modal clutch size in Arctic Terns breeding on the southern coast of Finland was observed to differ from that reported in previous studies. In 1989 and 1990, the frequency of 3-egg clutches was 60% and 45%, respectively in one study colony, and 61% and 54% in another colony. In 1990, the frequency of 3-egg clutches in a pooled sample of 65 nests was 54%. Spring was early in both years and breeding in terns was also early. It is possible that abundant food and early laying explain the switch in modal clutch size, but owing to a lack of data on fish abundance, a conclusive assessment cannot yet be made.

1. Introduction

The modal clutch size of terns (Sterninae) ranges from 1 to 3 eggs (Winkler & Walters 1983). In the Baltic, most Common Terns (*Sterna hirundo*) lay 3 eggs, while Arctic Terns (*S. paradisaea*) typically lay 2 eggs (Lemmetyinen 1973, Hario 1986). In both species, interpopulation differences exist (Winkler & Walters 1983).

At any colony, the average clutch size of Arctic Terns will vary between years (Bianki 1977, Lemmetyinen 1973), but such variation does not alter the modal clutch size. During 6 years of study in the White Sea, the frequency of three-egg clutches ranged from 1 to 23% of all nests (Bianki 1977), and in a 4-year study in the Northern Baltic, the frequency ranged from 9 to 13% (Lemmetyinen 1973).

Within a population, the clutch size in one year varies between pairs due to several factors, including the age of the female and timing of

breeding (Lemmetyinen 1973). In the Arctic Tern, the cost of a single egg is high (about 16% of female weight, see Nisbet 1977 for Common Terns). Winkler (1985) demonstrated a switch in modal clutch size (from 3 to 2) in a population of California Gulls (*Larus californicus*) due to food limitation. Such shifts seem to be rare. In this paper we will present a case of a shift in modal clutch size from 2 to 3 eggs in a population of Arctic Terns and discuss the possible reason for this observation.

2. Study area and methods

We gathered data on Arctic Terns at breeding colonies off the Hanko peninsula, SW Finland (60°N, 23°E). Breeding was monitored in a small colony (Långbodagrønna) in 1986–90, and in 4 colonies off Tvärminne (Vikarskär, Sjöbjörkskär, Pappasharun and Ören) in 1989–90. We marked

all nests, and checked them at 2–3-day intervals throughout the laying and incubation period. We know the exact number of eggs in every clutch (referred to here as a full clutch). We included all nests within the first synchronized laying peak, and omitted re-layings from the analysis.

3. Results

3.1. Clutch size at Långbodagryнна in 1986–90

In 1986–90, the mean size of the full clutch at Långbodagryнна (Table 1) ranged from 2.0 to 2.7, varying significantly between the years (Kruskall-Wallis test, $H = 15.1$, $df = 4$, $P < 0.01$). The frequency of 3-egg clutches varied between 0% and 60%.

3.2. Clutch size at Ören in 1989–90

In 1989 and 1990, the mean full clutch at Ören was 2.6 and 2.5, respectively (Table 1). The mean clutch sizes did not differ statistically between years (Mann-Whitney U-test, $z = -0.5$, ns.). The frequency of 3-egg clutches was 61% and 54%, respectively.

3.3. Clutch size in 1990

The clutch size for all Arctic Terns studied in 1990 averaged 2.5 (Table 1). The frequency of 3-egg clutches was 54%, and 3-egg clutches thus constituted the modal clutch. For comparative purposes, we divided the terns off Tvärminne into those breeding in the middle archipelago (Vikarskär, Sjöbjörkskär) and the outer archipelago (Pappasharun, Ören). The pairs in the inner zone laid a mean clutch of 2.6 ($SD = 0.6$, $n = 22$), those in the outer zone had a mean clutch of 2.4 ($SD = 0.6$, $n = 34$), with no difference between the zones (Mann-Whitney U-test, $z = -0.4$, ns.). We also checked for differences between the areas using only one late census around the time of hatching to facilitate comparisons with previous studies. The mean size of the clutch at hatching was smaller in the outer zone (2.2, $SD =$

0.7, $n = 34$) than in the middle archipelago (2.6, $SD = 0.6$, $n = 20$, Mann-Whitney U-test, $z = -2.0$, $P = 0.02$). The difference is due to a higher rate of egg predation by Turnstones (*Arenaria interpres*) in the outer colonies (J. D. Wuorinen, unpubl.).

3.4. Timing of laying

In both years, laying was early (see Discussion). The median dates at Ören were 21 May in 1989 ($n = 20$) and 23 May in 1990 ($n = 39$), while the median for all Arctic Terns studied in 1990 ($n = 64$) was 20 May.

4. Discussion

Published accounts of Arctic Tern clutch size in the Baltic almost all report a modal clutch of 2 eggs (see Table 2). A modal clutch of two seems to be the rule outside the Baltic as well. Winkler & Walters (1983) show the clutch size for nine populations of unreported origin, which had a mean of 2 or less. The mean clutch sizes that we have documented differ strikingly, and thus we need to be certain the figures are true, and not artefacts. For the Baltic studies, methodological differences may pose a problem. Lemmetyinen (1973) appears to have checked his colonies in the middle archipelago repeatedly, and these data should be comparable. His figures for the outer archipelago are based on single visits, and are

Table 1. Clutch size of Arctic Terns in the study area in 1986–90. The means, (SD, n) and the frequency of 3-egg clutches are given for all data sets.

Year	Colony	Mean (SD, n)	% 3-egg clutches
1986	Långbodagryнна	2.0 (0.0, 9)	0%
1987	Långbodagryнна	2.0 (0.5, 8)	12%
1988	Långbodagryнна	2.1 (0.3, 9)	11%
1989	Långbodagryнна	2.7 (0.5, 10)	60%
1990	Långbodagryнна	2.5 (0.5, 11)	45%
1989	Ören	2.6 (0.5, 23)	61%
1990	Ören	2.5 (0.6, 26)	54%
1990	All colonies	2.5 (0.6, 65)	54%

thus prone to errors due to predation. Even if we use only data based on a single visit at hatching time, our results show a larger mean clutch in the outer archipelago, and the difference in the middle archipelago still holds. Thus we are inclined to believe that the modal clutch size off Hanko is truly different, and a modal clutch of three has, as a phenomenon, persisted for two seasons at least. This calls for a biological explanation.

Terns are probably not true determinate layers, removal of newly laid eggs may induce them to lay additional eggs (like many *Larus* gulls), but this has not been tested (Winkler & Walters 1983). Arctic Terns are clearly capable of laying a third egg. If the potential clutch is larger than the realized clutch, then what proximate factor limits most Arctic Terns to two eggs?

Nisbet (1977) showed that female Common Terns with larger body reserves also lay larger clutches. The interpretation given to this has been that the laying of Common Terns is food-limited (the "pre-egg food limitation hypothesis" of Ankney & MacInnes 1978, see also Winkler 1985), and this may apply to the Arctic Tern as well. Safina & Burger (1988) write of Common Terns that "in two years, the terns laid earlier, more synchronously and had larger clutches in the year when food was plentiful during the egg-laying period".

The egg of the Arctic Tern weighs about 19 g (Cramp 1985), which is 16% of the weight of a

typical adult in the Baltic (Hario 1986). Thus a clutch of 2 weighs 32% of the female weight, and a clutch of 3 weighs 48%. One egg is therefore a significant cost for an Arctic Tern. These figures are very close to the figures presented for Common Terns (Nisbet 1977). Modal clutch size could thus be affected by a significant increase in food during the courtship feeding phase, which could alter the clutch size distribution of this species.

The model for single-brooded altricial species with a seasonal decline in clutch size proposed by Meijer et al. (1990) treats the clutch size as the result of a function between the time when rapid follicle growth starts and the time brooding behaviour starts. Endogenous reserves do not, however, play a causal role in determining the final clutch size. According to this model, a larger clutch will be laid early in the season, and a good feeding situation will affect the clutch size by advancing laying. This is an extension of Nisbet's (1977) specific hypothesis for terns. Thus the observed change in modal clutch size may have been due to (a) superabundance of food prior to laying per se (Nisbet 1977), or to (b) early laying caused by an abundance of food (Meijer et al. 1990).

The springs of 1989 and 1990 were very early. Terns arrived in the last days of April, and started laying on 8 May. Lemmetyinen (1973) observed arrival on 8 May, with the first laying on 17 May. Arctic Terns operate at short notice, with a very short pre-laying period in the colonies. This may imply that follicle growth is released immediately on the basis of the body reserves present in the arriving bird, since follicle growth will require a minimum of 10 days, and eggs are laid at one-day intervals (Grau 1984). Though the spring was in fact early in 1989 and 1990, we seriously doubt that the advancement of laying by 7–10 days would in itself allow for a 3-egg clutch. If so, Arctic Terns all over their range would in most years live within a time-frame too short for realization of the potential clutch of three.

The decision to lay a third egg may be made later than the decision to start laying, possibly a few days before laying of the second egg. In the Black-headed Gull (*Larus ridibundus*), the Herring Gull (*L. argentatus*) and the Lesser Black-

Table 2. Mean clutch sizes and frequencies of 3-egg clutches in previous studies in the Baltic. Data from von Haartman 1982 (Archipelago Sea, A), Hario et al. 1986 (Gulf of Finland, B) and Lemmetyinen 1973 (Archipelago Sea, C = middle archipelago, D = outer archipelago).

Year	Area	Mean clutch (n)	% 3-egg clutches
1979–81	A	2.07 (108)	18%
1985	B	2.19 (21)	
1986	B	2.11 (27)	
1965	C	1.99 (131)	9%
1966	C	2.01 (134)	12%
1967	C	2.07 (84)	17%
1968	C	2.03 (162)	13%
1965–66	D	1.60 (140)	3%
1966	D	1.60 (56)	6%

backed Gull (*L. fuscus*), resorption of additional follicles takes place about four days prior to laying of the c- (third) egg (Meijer et al. 1990). In several species resorption is affected by the feeding situation (Meijer et al. 1990). The early springs may have induced small littoral fish, such as three-spined sticklebacks (*Gasterosteus aculeatus*), to spawn early, and they would thus become available immediately after the arrival of the terns in early May. This may, in turn, have prompted the decision to produce a third egg, and not to resorb it.

Lemmetyinen's (1973) data suggest that three-spined sticklebacks do not become abundant in "normal" years until the end of May. Our data (unpublished) indicate that three-spined sticklebacks became abundant in shallow waters as early as in the first two weeks of May in both years. We do not have data on courtship feeding rates under different food regimes, or female body condition upon arrival, and therefore we do not know the exact mechanism which determines clutch size in Arctic terns. The complex relationship of the food situation, timing of laying and courtship feeding to the final clutch size and the resultant change in modal clutch size cannot thus yet be assessed.

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Sammanfattning: En förändring i kullstorlek hos silvertärnor i Norra Östersjön

Den dominerande kullstorleken hos silvertärnor i den finländska skärgården har varit 2 ägg, endast en liten del av paren (3–17.5%, Tabell 2) har lagt tre ägg. Under somrarna 1989–90 fann vi att andelen kullar med tre ägg i Hangö skärgård var betydligt högre. I två kolonier var andelen kullar med tre ägg 60% ($n = 33$) och 51% ($n = 37$) år 1989 och 1990, respektive. Av alla silvertärnebon som vi följde upp år 1990, innehöll 54% tre ägg ($n = 65$). Bägge åren var våren tidig och varm, och tärnornas häckning kom också

igång tidigt. Under bägge åren förekom också ett viktigt byte för tärnorna, storspiggen, rikligt i grunda vatten tidigare än normalt. Det är möjligt att tidig häckning kombinerat med riklig tillgång på spigg förklara den ovanligt stora andelen kullar med tre ägg. Eftersom tidigare kvantifiering av bytesförkomst och bytespreferenser hos silvertärnan inte finns, är det inte möjligt att bindande knyta tendensen att lägga tre ägg till dessa yttre faktorer.

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