

Variations in the Reproductive Activities of Arctic Terns at Churchill, Manitoba

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ABSTRACT. Nest locations and contents were observed in 16 colonies over a 3-year period. Laying times correlated with spring temperatures, but not with colony size. Clutch size increased with time between ice breakup and laying onset. Egg losses were insufficient to account for differences in clutch size. The results are taken to indicate that under arctic conditions, variations in clutch size, timing of the nesting cycle, and associated events in the Arctic Tern are closely related to variations in the physical environment.

RÉSUMÉ. *Variations dans les activités de reproduction chez les Sternes arctiques à Churchill, Manitoba.* On a observé la localisation et le contenu des nids de 16 colonies, pendant une période de trois ans. Le moment de la ponte est lié aux températures printanières mais non à la taille de la colonie. La taille des couvées augmente entre la débâcle et le début de la ponte. Les pertes d'œufs sont insuffisantes à expliquer les différences dans la taille des couvées. Ces résultats indiquent que dans les conditions arctiques, les variations dans la taille des couvées, le rythme du cycle de nidification et les autres événements vitaux du Sterne arctique sont intimement liés aux variations du milieu physique.

РЕЗЮМЕ. *Вариации воспроизводительной активности арктических крачек в окрестностях Черчилля (Манитоба).* В течение трехлетнего периода проводились наблюдения расположения и содержимого гнезд в 16 колониях полярных крачек. Обнаружено, что время кладки яиц коррелирует с весенними температурами, а не размерами колонии. Величина кладки увеличивается со временем между ледоломом и началом откладки яиц, и потери яиц, как оказалось, недостаточны для объяснения разницы в величине кладок. Полученные результаты показывают, что в условиях Арктики изменение размеров и расписания кладок, а также другие жизненные события у полярных крачек тесно соотносятся с вариацией в окружающих физических условиях.

INTRODUCTION

Although the arctic tern (*Sterna paradisaea*) is widely distributed throughout the arctic regions of the world, studies of the reproductive biology of the species have been conducted mainly where it nests on oceanic islands in temperate regions (Marples and Marples 1934; Pettingill 1939; Bullough 1942; Hawksley 1957; Cullen 1956, 1960). Belopol'skii (1957) has provided further information for populations breeding on subarctic islands in the Barents Sea, and Drury (1960) has described observations of arctic terns breeding on Bylot Island, in the Northwest Territories of Canada. Considerable information about clutch size, habitat, and dispersion under arctic conditions is also available (e.g. Longstaff 1924; Bailey 1925; Lack 1933; Taverner and Sutton 1934; Lovenskiold 1954; Gudmundsson

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1956; Burton and Thurston 1959; Parmelee and MacDonald 1960; Nero 1961), but detailed studies of these and related aspects of the reproductive biology of this species during the breeding season on mainland North America appear to be lacking. The present study is an attempt to fill the need for further information. The breeding population of arctic terns located along the west coast of Hudson Bay, at Churchill, Manitoba, was selected for study, as it was the nearest and most accessible population breeding on the mainland under essentially arctic conditions (Shelford and Twomey 1941).

STUDY AREA AND GENERAL METHODS

The study was conducted during the summers of 1967, 1968, and 1969 over an area of approximately 6,500 hectares. Most observations were restricted to a narrow band of habitat, about 2 to 3 km. wide extending along the west coast of Hudson Bay for a distance of approximately 20 km. immediately east of the townsite of Churchill. An area extending inland for about 7 km. near Farnworth (Landing) Lake, and a lake containing a single colony (Colony N) lying about 7 km. inland near the eastern edge of the study area (Fig. 1) were also examined. The area included in the study ranged from bare or lichen-encrusted rock along the coast, to groves of Black Spruce (*Picea mariana*) inland, with *Sphagnum* and lichen climax tundra, dotted with many lakes and small ponds, lying between. Seral stages and the various types of sub-climax vegetation of the region have

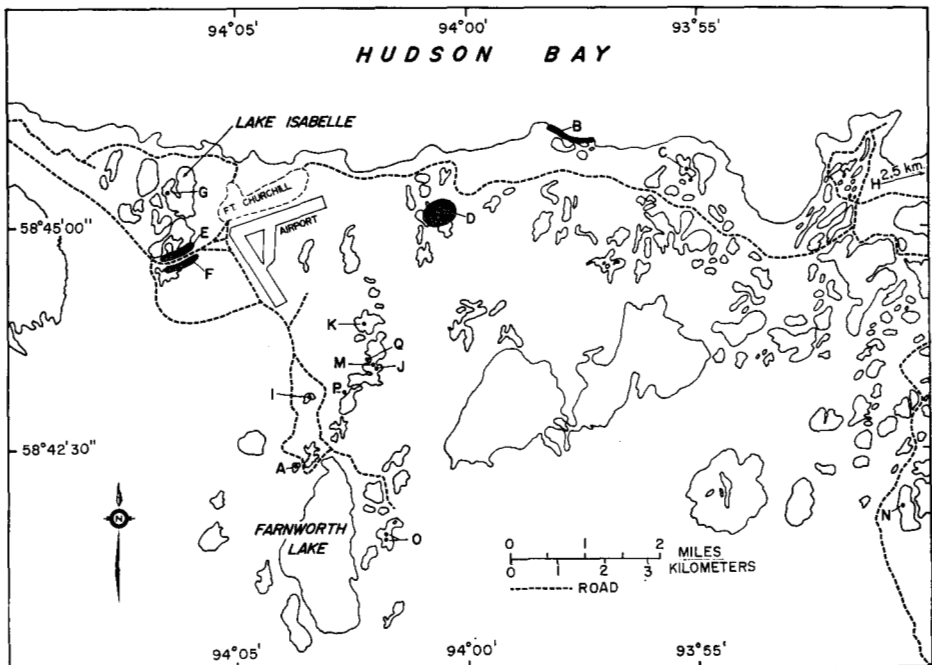


FIG. 1. Map of the Churchill, Manitoba, region, indicating the locations and letter designations of arctic tern colonies included in this study. Colony H was located approximately 2.5 km. east of the area covered by this map. See Table 1 for additional descriptions of colonies.

been described in detail by Shelford and Twomey (1941). Lake Isabelle, which contained the largest island colony of arctic terns studied (Colony G, Fig. 1), was also described by those authors (1941, pp. 58-59). General descriptions of the birds breeding on the tundra at Churchill are included in Taverner and Sutton (1934), and Jehl and Smith (1970). Additional information about the fauna at Churchill is contained in the studies by Farley (1939, 1940), Grinnell and Palmer (1941), Shelford and Twomey (1941), Allen (1945), Breckenridge *et al.* (1954), Jehl and Hussell (1966), and several other papers. Specific references to arctic terns at Churchill have been made by Hawksley (1957) and Palmer (1941). Observations of nesting associations between arctic terns and oldsquaw (*Clangula hyemalis*) at Churchill are treated in a separate report (Evans 1970).

To obtain relatively rapid access to various parts of the study area, extensive use was made of the limited number of roads (Fig. 1). When located, all nests were marked for future study by placing numbered nest markers nearby, and noting them on maps of the area. Distances from Hudson Bay were estimated from maps (1 cm.: 250 m.) except that a direct estimate of distance to high tide mark was made for the one colony found along the beach. In 1967 and 1968, eggs were examined periodically, to determine the dates of hatching and to obtain information on egg loss during the incubation period. Such losses were slight (see below), and bore no apparent relation to the frequency of human visitation. Observations were terminated on 13 July in 1967, and on 14 July in 1968. In 1969, the major colonies were inspected briefly, between 28 and 30 June.

TABLE 1. Size, location, and habitat type of arctic tern colonies found at Churchill in 1967 and 1968.

Colony designation	Maximum nest count		Distance from coast (approx.) metres	Habitat Type*
	1967	1968		
A	1	—	6,300	III
B	12	14	25	I
C	7	12	650	III
D	18	12	1,575	II, III
E	9	3	2,200	II
F	10	—	2,450	II
G	36	32	975	III
H	2	2	1,750	III
I	1	—	4,975	III
J	—	15	4,275	III
K	9	10	3,375	III
M	—	4	4,000	III
N	—	8	6,450	III
O	—	22	7,000	III
P	—	2	4,500	II
Q	—	5	4,200	II
Total nests	105	141		
No. colonies	10	13		
Colony size:				
mean	10.5	10.8		
median	9	10		
range	1 - 36	2 - 32		

*I: mainland beach; II: mainland tundra; III: islands in freshwater ponds.

NUMBERS, SIZES AND LOCATIONS OF COLONIES

A total of 16 arctic tern colonies were found (Fig. 1). Of these, 10 colonies were found in 1967. In 1968, 7 of the colonies found the previous year were still active, and 6 more were found, providing a total of 13 colonies under surveillance in that year (Table 1).

Colony size was highly variable, ranging from 1 to 36 nests in 1967, and from 2 to 32 in 1968. Median and mean colony sizes were 9 and 10.5 nests respectively in 1967; both values increased slightly in 1968 (Table 1).

Like colony size, the physical locations and habitats of the colonies were variable. For purposes of analysis, it was found useful to group nest locations into 3 broad habitat types. As indicated in Table 1, almost 70 per cent of the colonies at Churchill were entirely or in part on islands in small freshwater ponds (habitat type III). Less than half this proportion were on mainland tundra or marsh habitats (type II), and only a single colony was found on the mainland beach (type I).

Comparison of colonies between habitat types revealed that colonies with nests on mainland tundra or marsh tended to be smaller, averaging only 8.8 nests, compared to 11.2 nests per colony for those on islands in freshwater ponds, and 12 nests for the colony on the mainland beach (basis 1967 data where available). For colonies censused in both 1967 and 1968, 3 that were located on mainland tundra or marsh declined an average of 7.33 nests per colony in the second year, compared to an average decline of only 0.86 nests between the same 2 years for 11 colonies on islands in freshwater ponds. The single colony on the mainland beach increased by 2 nests in 1968.

Colony distance from Hudson Bay ranged from a minimum of approximately 25 m. for nests on the mainland beach habitat to a maximum of approximately 7 km. for those located inland (Table 1, Fig. 1). No apparent relationship between colony size and distance from the bay was present.

CLUTCH SIZE AND HATCHING TIMES

Clutch size and hatching times were found to vary between years and between different colonies within years; these variations are considered below together with possible effects of egg predators.

Differences between years

In 1967, 64 per cent of 105 nests examined contained 2 eggs. Clutches with 1 egg were less common (Table 2), and only 12 nests (11 per cent) contained 3 eggs. This distribution of clutch sizes differed markedly in 1968, when well over half of the nests contained only 1 egg, and none contained 3 eggs (Table 2). This

TABLE 2. Clutch size of arctic tern nests in 1967 and 1968.

Year	Number and percentage of clutches			Total	Total eggs	Mean clutch size
	1 egg	2 eggs	3 eggs			
1967	26 (25%)	67 (64%)	12 (11%)	105	196	1.87
1968	87 (62%)	54 (38%)	0 (0%)	141	195	1.38

shift towards smaller clutch sizes in 1968 was reflected in the mean clutch size, which decreased from 1.87 to 1.38 eggs per nest. Comparison by 2 x 2 Chi-square analysis between years indicated a highly significant reduction ($P < .001$) in the proportion of multiple-egg clutches in 1968.

Hatching, which was first noted in Colony G in both 1967 and 1968, was similar in onset between these two years, the first eggs hatched on 6 July in 1967, and 7 July in 1968. Once initiated, however, hatching continued at a much slower rate in 1968. By the end of 14 July 1968, hatching had not yet begun in 71.9 per cent of the 114 nests under observation; on 13 July 1967 43.4 per cent of the nests had remained unhatched after an equivalent time lapse (Table 3). The proportions of nests in which hatching had begun by the end of the 1967 median date of 13 July differed significantly between the two years ($P < .001$).

Although the onset of hatching was not directly observed in 1969, evidence based on the presence or absence of eggs laid, and on the extent of incubation in eggs examined in 5 colonies in late June, indicated a significant delay in the onset of breeding activities that year. As in previous years, Colony G appeared to be the most advanced, but even this colony contained mainly fresh eggs on 30 June, as indicated by an increase of from 3 to 9 in 2-egg clutches and from 9 to 19 in total clutches present between 28 June and 30 June. By 30 June, the most advanced egg examined, taken from one of the 2-egg clutches known to be present on 28 June, contained early stages of blood vessels which, compared with standard developmental stages of the domestic fowl, indicated that incubation had probably not progressed beyond about 3 days. Other colonies, in which no eggs were laid or in which examined eggs were either fresh or contained an embryo at an early blastodisc stage, were even later than Colony G. Assuming an incubation period for the arctic tern of approximately 21 to 22 days (Cullen 1956, p. 73), then it is evident that the onset of hatching in 1969 was on about 18 July, some 11 to 12 days later than in the preceding two years.

TABLE 3. Frequency distribution of date of hatch onset in arctic tern nests at Churchill, in 1967 and 1968.

		<i>Date of hatch onset</i>										
<i>1967, July:</i>		6	7	8	9	10	11	12	13	>13	Total	
Frequency		1	4	4	6	5	6	7	10	33	76	
Per cent		1.3	5.3	5.3	7.9	6.6	7.9	9.2	13.1	43.4	100	
<i>1968, July:</i>		6	7	8	9	10	11	12	13	14	>14	Total
Frequency		0	2	2	7	2	4	1	11	3	82	114
Per cent		0	1.8	1.8	6.1	1.8	3.5	0.9	9.6	2.6	71.9	100

Relationship to spring weather

The climate at Churchill is typically severe compared with more inland regions at comparable latitudes in western North America. Throughout the month of May, which precedes the onset of laying by arctic terns, mean daily temperatures below freezing are typical, and few days are without frost. Freezing temperatures

and snow flurries are still common in June, but mean daily temperatures are above freezing at that time (Table 4).

The data summarized in Table 4 indicate that the mean daily temperature for the month of June was essentially normal in 1968, when it deviated from the long-term average by only 0.1 degree F. Using 1968 as a standard of comparison, the weather was warmer, on the average, in June of 1967, and appreciably colder in June of 1969. For the month of June, the cooling trend from 1967 to 1968, and again from 1968 to 1969, is indicated in each case by lower average maximum, minimum, and daily temperatures in successive years, by lower monthly maximum and minimum temperatures in successive years, and by an increase in the number of days with freezing temperatures from 9 in 1967, to 16 in 1968, and to 19 in 1969. The colder weather in 1969 is further suggested by a greater snowfall in both May and June of that year compared with either of the preceding years (Table 4).

TABLE 4. Summary of temperature and snowfall at Churchill*, Manitoba, in May and June, 1967-1969.

	1967	May 1968	1969	1967	June 1968	1969
Temperature (°F):						
<i>Mean maximum</i>	34.3	36.0	30.2	54.2	51.2	44.5
<i>Mean minimum</i>	20.4	22.1	17.2	36.4	34.0	31.9
<i>Mean daily</i>	27.4	29.1	23.7	45.3	42.6	38.2
<i>Difference from normal</i>	-0.4	1.3	-4.1	2.8	0.1	-4.3
<i>Maximum (date)</i>	79 (31)	74 (25)	50 (25)	87 (26)	81 (27)	65 (2)
<i>Minimum (date)</i>	-7 (1)	5 (4)	7 (18)	29 (3)	28 (1)	25 (10)
Days with frost	29	28	31	9	16	19
Snowfall, total (inches)	5.4	0.8	15.1	4.5	3.8	5.6
Days with snow	10	3	13	3	3	6
Snow at month end	Tr	Tr	5	0	Tr	0

*Data for Churchill taken from Monthly Record of Meteorological Observations in Canada, published by the Department of Transport, Meteorological Branch, Toronto. Tr=trace

Observations of ice conditions at Churchill in each of the three years of the study indicated that colder spring temperatures were associated with corresponding delays in the melting of the ice. For example, in 1967, when we arrived at Churchill on 22 June, ice was absent from the inland lakes and Hudson Bay was clear of ice except for occasional periods when ice drifted inshore as a result of strong north winds. In 1968, when mean temperatures were lower, drift ice was prevalent in Hudson Bay until after 22 June, and there were still small bits of floating ice on the larger inland lakes such as Lake Isabelle on which Colony G was located. In 1969, there was little open water to be seen on Hudson Bay as late as 28 June, and the major portion of Lake Isabelle was still frozen when first visited on the same day. These observations, although incomplete, indicate clearly that June temperatures were associated closely with the melting and break-up of the ice, both on the bay and on the freshwater lakes.

Comparison of the weather data presented in Table 4 with the year to year variations in clutch size and hatching times described in the previous section (See Tables 2, 3), indicates that colder temperatures, particularly just prior to and during egg laying in June, were closely associated with reduced clutch sizes and retarded laying dates.

Relationship to habitat type and nest dispersion

Where nests were dispersed, either along the beach (habitat type I) or farther inland on tundra or marsh (habitat type II) mean clutch sizes were strikingly similar to each other in both years in which these data were obtained (Table 5). In 1967, mean clutch size differed by only 0.01 eggs per nest between these habitats, whereas in 1968 they differed by an average of only 0.02 eggs per clutch. Differences between years were also small on habitat types I and II (Table 5). In contrast, nests on islands in freshwater ponds (habitat type III) fluctuated widely between years, as indicated by a significant change in the proportion of single to multiple-egg clutches ($P < .001$). In 1967, the proportion of multiple-egg clutches in habitat type III was significantly greater than in the other 2 habitats combined ($P < .02$). In 1968, as a result of the smaller clutch sizes in habitat type III, the proportion of multiple-egg clutches in that habitat was actually smaller, although not significantly so ($P > .30$), than for nests located in the other habitats. This reversal in rank between habitat type III and the other 2 habitats suggests that the largest clutch sizes were not necessarily always produced in any single habitat type.

The time of hatching did not differ significantly between the two inland habitats (II and III) in either 1967 or 1968 ($P > .05$), as indicated by the proportion of nests in which the onset of hatching had begun by the end of the 1967 median date of 13 July (Table 5). The small number of eggs hatched in nests located along the beach in habitat type I (Table 5) suggests that hatching was delayed there compared to the more inland habitats. This difference, although suggested in both years, reached statistical significance only in 1967 ($P < .05$).

TABLE 5. Relationship between arctic tern clutch size, hatching times, and habitat types at Churchill in 1967 and 1968.

Year	Habitat type*	No. of colonies	Total eggs	Total nests	Mean clutch size	Nests with hatching by July 13 (%)
1967	I	1	21	12	1.67	1 (8.3)
	II	3	62	37	1.68	13 (35.1)
	III	6	113	56	2.02	30 (53.6)
1968	I	1	20	14	1.43	1 (7.1)
	II	4	32	22	1.45	2 (9.1)
	III	8	143	105	1.36	26 (24.8)

*Colony D, in which nests were widely scattered (See Fig. 1) over both mainland tundra and adjacent small islets, is included in the mainland tundra habitat, type II. See Table 1 and text for descriptions of habitat types.

Variations independent of colony size

The results described above have suggested that non-social environmental variables may be associated with variations in clutch size and hatching dates. Relationships with social influences due to colony size (Darling 1938) were less evident.

In 1967, clutch size was largest (2.17) in the colony (G) that had the greatest number of nests. However, this trend was not consistent for all colonies, either in that year (Rank correlation: $r = .37$, $P > .05$), or in 1968 ($r = .25$, $P > .05$). The relationship between colony size and hatching times was even less consistent in that trends, while not significant in either year, were in the opposite direction between years; a positive relationship between colony size and onset of hatching occurred in 1967 ($r = .60$), and a negative relationship between these variables occurred in 1968 ($r = -.43$).

Egg losses during incubation

In the preceding sections, many of the values for clutch size, particularly those for 1967, are based on census data obtained towards the end of the incubation period. This raised the possibility that differences in clutch size may have been due to differential egg losses rather than to differences in the numbers of eggs laid. The possibility that differences in clutch size reflected differential egg loss due to predation or other causes was assessed in 1968 by comparing rates of egg loss during the incubation period. A total of 195 eggs from 141 nests were observed over an average period of 13 days each.

Egg losses were small in 1968, only 16 (8.2 per cent) having been lost over the entire period of observation. The small proportion lost, due to predators or other causes, suggests that it was not sufficient to account for the clutches being smaller in 1968 than in 1967.

Egg losses in 1968 were further analysed according to colony size and habitat type. Using median colony size as a basis for comparison, egg loss for colonies containing up to 14 nests was 10 (10 per cent) compared to 6 (6.3 per cent) for those containing 15 or more nests. There was thus no evidence that clutches in colonies of different sizes were influenced by differential egg loss. Differences in egg losses due to habitat type appeared more likely, in that all but one of the 16 eggs known to have been lost were in nests on small islands in freshwater ponds. Total egg losses were small, however, and differences between habitats did not reach statistical significance even when losses from all dispersed nests (mainland beach and tundra) were compared to losses on islands in freshwater ponds ($.1 < P < .2$).

DISCUSSION

The main generalizations that emerged from the present study may be summarized as follows: 1) nest dispersion, clutch sizes, and timing of reproductive activities of the arctic terns at Churchill were highly variable, both between and within years; 2) biological variability appeared to be closely associated with corresponding variation in the local environment. The possibility that these variations in physical conditions influenced reproductive activities is examined below.

Nest dispersion and egg losses

Several authors have described the tendency of certain species of Laridae, including the arctic tern, to disperse widely over the available habitat when breeding on the ground in the Arctic (Twomey 1934; Williams 1947; Mowat and Lawrie 1955; Sutton and Parmelee 1956; Drury 1960; Macpherson 1961; Smith 1966; Brown *et al.* 1967). This tendency has been interpreted as an adaptive response that spreads the breeding population out over a wide area when this contains only sparse food resources (Lack 1954). The arctic tern colonies at Churchill (Fig. 1) appear to be dispersed over the habitat in a manner consistent with this hypothesis.

Of perhaps equal significance to the pattern of dispersion of colonies throughout the Churchill area were differences in the degree of nest dispersion within the various colonies. Distances ranged from less than 1 m. between nests for many of the island colonies to occasional instances in which nests were over 100 m. apart, as in the beach colony, D. Since dispersion within the colonies showed no obvious correlation to colony distance from the coast or to particular sources of food, it does not seem realistic to attribute differences in the nest dispersion within colonies to differences in the local abundance of food. The more likely explanation, as suggested by Tinbergen (1956) and Kruuk (1964) for gulls would appear to be that on accessible mainland colonies, dispersion of nests constitutes an important adaptation against predators (cf. Cullen 1960; Nero 1961). This view is consistent with our finding that few eggs were lost from dispersed nests on mainland beach or tundra, all but one loss being from less dispersed nests on islands in freshwater ponds.

Hatching time and clutch size

Many investigators have commented on the tendency for cold weather and ice conditions to delay or stop breeding activities in arctic birds, including arctic terns (Lack 1933; Bertram *et al.* 1934; Bird and Bird 1940; Gudmundsson 1956; Hawksley 1957). It is therefore significant that one of the most striking relationships noted at Churchill was for the breeding cycle to be retarded when spring temperatures were lower. Whether delays in breeding when spring temperatures were lower was due to a shortage of food while the females were forming eggs (see Perrins 1970), or to a delay in the availability of nesting habitat, as found for arctic terns in Greenland by Bird and Bird (1940) and on Bear Island in the Barents Sea by Lack (1933), could not be determined with certainty from our observations. Observations of this species at Churchill reported by Jehl and Smith (1970), however, indicated that the time at which the nesting habitat became available was not critical in determining the timing of the breeding cycle of arctic terns in this region.

From our direct observations (see section on weather at Churchill) it was evident that in 1968 compared to 1967, and in 1969 compared to both of the preceding years, colder spring temperatures were associated with a corresponding delay in the melting and breakup of the ice, both on Hudson Bay and on the freshwater lakes near which arctic terns nested. The obvious importance of open water for feeding arctic terns (Pettingill 1939; Hawksley 1957; Drury 1960; Jehl

and Smith 1970) suggests that a delay in the appearance of spring food when the ice breakup is delayed provides the most likely explanation for the relationship between delayed breeding and cold spring weather.

The possibility that food supplies may also have had a proximate influence on the number of eggs laid (Lack 1968) was suggested by variations that occurred between years. In 1968, despite the colder spring temperatures (Table 4) and corresponding delay in the breakup of the ice compared to 1967, the onset of hatching was delayed by only one day. For the early layers, at least, the time during which food for egg production was available on the breeding grounds was therefore less in 1968 than in 1967. The decrease in clutch size between 1967 and 1968 is thus consistent with the view that the amount of food available during or immediately before laying was an important proximate factor influencing clutch size in this population.

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