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ECOLOGY OF A BREEDING POPULATION OF ARCTIC TERNS

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Introduction

Biologists today are much concerned with the ecological factors which control natural populations. Avian populations, particularly of colonial species, lend themselves well to investigations of the survival and mortality rates of offspring up to the age of attaining flight. Factors which control the success of the social unit or colony as a whole during the reproductive period may also be readily studied. The present study was made during the breeding seasons of 1947 and 1948 as a part of a study of the behavior and ecology of the Arctic Terns *(Sterna paradisaea)* of Machias Seal Island, Bay of Fundy, New Brunswick, Canada. Although a greater portion of time had to be allotted to behavior studies, sufficient data have been acquired to allow an analysis of egg and chick mortality of the Arctic Tern and to provide material for discussions of the factors affecting group success in this breeding colony. This is fortunate since Dr. Raymond A. Paynter made detailed studies of the egg and chick mortality of Herring Gulls *(Larus argentatus smithsonianus)* and other species on Kent Island, only fifteen miles away, during the summers of 1947 and 1948 (Paynter 1949). Thus, by coincidence, some comparison of data obtained in the same locality, during the same years and for a related species, is possible.

Due to the exceptionally wide distribution of the Arctic Tern, information on the species is scattered throughout the ornithological literature of many countries and of many years. In this paper, an attempt has been made to bring together much of the more important information dealing with the ecology of the species.

I wish to express my appreciation to Dr. Ralph S. Palmer for many helpful suggestions based on his experience with terns. Drs. Robert T. Clausen, Richard H. Backus and Charles L. Remington have assisted with identification of plant, fish and invertebrate specimens. My wife assisted constantly with field work which could hardly have been completed without her.

Spring Arrival

For many years, the lightkeeper and his wife, Mr. and Mrs. Ottawa Benson, kept records of the arrival dates of the Arctic Terns at Machias Seal Island. Arrival dates and comments from their log for five consecutive seasons are presented below.

In 1945, the terns arrived on May 17 and started laying on May 29. In 1946, they also arrived on May 17. In 1947, the terns arrived on May 12 but did not alight on the island until May 20. Terns were first seen on May 12 again in 1948 but did not alight until May 17. In 1949, the birds were heard on May 11 and first seen on May 12. They landed briefly on May 14, but the presence of a Duck Hawk *(Falco peregrinus) anatum)* kept them off for a couple of days. After the hawk was killed by the keeper, the terns returned and eggs were found by May 29.

Although the terns arrived on May 12, 1948, there were only a few eggs laid when I arrived on June 3. We received the impression that the number of birds on the island increased for several days after that, but saw no arriving flocks. According to the Bensons, the terns arrive at Machias Seal Island in large, high-flying flocks. The first time they appear, they circle high above the island, then leave. After that they fly over the island each morning in social flight but do not alight until they have done this for several days. Palmer (1941: 40) has described this last type of behavior similarly for the Common Tern *(Sterna h. hirundo)*.

THE ENVIRONMENT

FOOD AND FOOD-GETTING

The rich waters surrounding Machias Seal Island provide an abundant food supply for that ternery. Arctic Terns, like other species of terns, probably colonize areas close to good food supplies. This does not necessarily mean that the ternery must be located close to the sea. Colonies are known to exist even in the interior of the Scandinavian countries (Kullenberg 1946: 12) where the birds fish in lakes and rivers. In Baffin Land, Dalgety (1936) noted that Arctic Terns "appeared to prefer fishing in fresh water."

In contrasting terns with gulls, Tinbergen (1932: 11-12) remarks (trans.):

> In many ways the gulls appear remarkably adaptable, much more so than the terns. The gulls look for food in many ways, changing with the circumstances. The terns, on the other hand, show a strange psychic unadaptability. Their behavior, especially on their search for food, is very stiff. We could call them, briefly, over-specialized plungers.

Although this concept is fundamentally correct, one must not think of the Arctic Tern as a wholly unadaptable species. It is principally a deep-water feeder, yet it quickly adapts to the use of shallow-water food organisms or of insects at times when these are especially abundant.

In a colony five miles from the sea, Wright (1909) observed that the young were being fed not with fish, but with large crane-flies and may-flies. These terns were caught for banding on hook and line baited with crane-flies and "greendrake." Palmer (1941: 17) did not see pellets from Common or Roseate Terns *(Sterna dougalli)*, but I frequently noticed pellets, containing insect parts, on the rocks in the roosting areas on Machias Seal Island.

The food habits of the Arctic Tern have been little studied. A compilation of specific food organisms which the species is known to utilize the world over would be of little value in this study and might even give an incorrect impression. Specific names will be used only in referring to food used in the study area.

A survey of the literature indicates that the three most important food groups include fish, crustaceans and insects. Fish from the families Gasterosteidae, Ammodytidae, Stromateidae, Scorpaenidae, Cyclopteridae, Blenniidae, and Gadidae are much used. Crustacean groups much used include branchiopods, copepods, mysids, amphipods, euphausids, and decapods. Insect orders represented are Ephemeroptera, Odonata, Lepidoptera, Coleoptera, Hymenoptera and Diptera. A few pelagic molluscs such as *Clio*, *Limacina* and *Loligo* are eaten, as well as marine worms.

Availability is obviously a very important factor in what food is used. In Labrador, O. L. Austin, Jr. (1932: 128) did not see Arctic Terns eat anything but the lance *Ammodytes americana*, but these shallow water fish were not used at all at Machias Seal Island. Captain Fielden (1877) made the interesting observation in polar regions, where continual ice prevents fish from coming to the surface, that the amphipod *Anonyx nugax* works its way up through tidal ice cracks and is eaten in numbers by the Arctic Tern.

The fishes most used for food by the terns at Machias Seal Island were hake *(Urophysis* sp., probably *U. chuss)*, the lumpfish *(Cyclopterus lumpus)* and the dollar fish *(Poronotus triacanthus)*. However, the supply of skeleton shrimps *(Meganyctiphanes norvegica)* and of lumpfish appeared to be most constant. These were used extensively during intervals when hake and dollar fish seemed to be less plentiful and were used to some extent throughout the entire season.

There were noticeable seasonal "runs" of most of the food organisms. Notable among these were the "runs" of cicadas *(Okanagana canadensis)* an annelid *(Nereis pelagica)*, small squids *(Loligo pealei)* and dollar fish. The cicadas were used during the second week of July in both 1947 and 1948. In 1947, *Nereis* was used from July 8 to July 11, squids came into use from July 10 to July 17, and dollar fish were used in large numbers from July 24 until we left the island in early August.

Other fish, in the order of the frequency with which they were brought to the colony, were four-bearded rockling *(Enchelyopus cimbrius)*, *Clupea* sp., haddock *(Melanogrammus aegelifinus)*, rock eel *(Pholis gunnellus)*, three-spined stickleback *(Gasterosteus aculeatus)*, rosefish *(Sebastos marinus)*, and barrelfish *(Palinurichthys pereiformis)*. The nine-spined stickleback *(Pungitius pungitius)* was commonly used at colonies near Churchill, Manitoba, during studies made there in 1949.

Unidentifiable moths and a dragonfly *(Tetragoneuria spinigera)* were found in nests with young.

EFFECTS OF WEATHER AND LIGHT

The importance of weather to Arctic Terns is indicated in many parts of this paper. Weather conditions have a direct effect upon the ability of adults to seek food. Later it will be shown to what extent weather affects the survival of the young. Roosting or brooding adults may become so wet in rain or dense fog that they are unable to fly out of tall

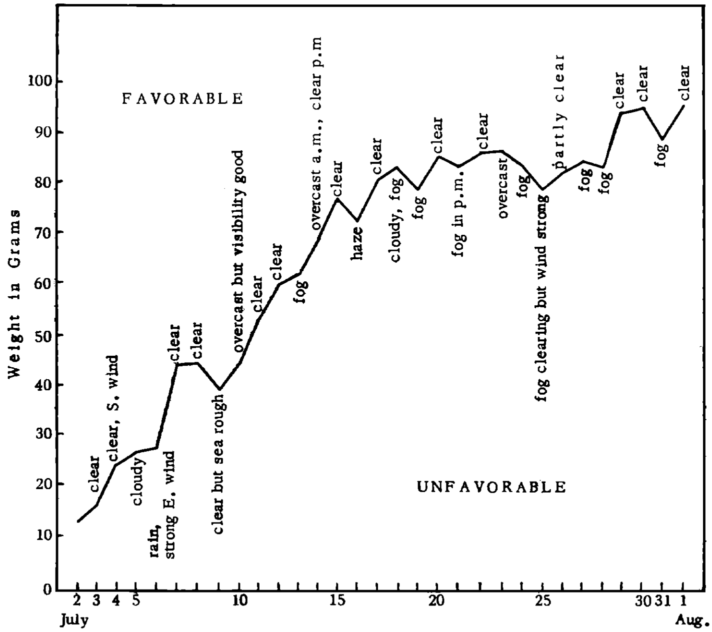

Fig. 1. Growth of chicks as related to weather.

vegetation and may be easily caught. Weather and light influence the amount of social flying to some degree.

Weather, especially that which affects visibility, and the need for brooding young, has a very decided effect upon the ability of Arctic Terns to provide food for their young. Weights of chicks from July 2 to August 1, 1948, showed a definite correlation between certain weather conditions and the average weight of the group of chicks. Figure 1 is a graph showing the average daily gains and losses in weight and the visibility factors which seemed to control them. It is interesting to note that a single day of fog or unfavorable weather may not result in weight losses, but that several days of unfavorable weather cause a definite weight loss. It becomes understandable that a continuation of adverse weather of this sort might greatly decrease the survival of young. Kullenberg (1946) is probably correct in thinking that the absence of the Arctic Tern as a breeding bird on the eastern Asiatic coast south of the Tchuktch Peninsula and at the Sea of Okhotsk is to some extent due to the great frequency of fog there.

The Arctic Tern is generally credited with seeing more daylight during a year than any other species, but detailed investigations of its daily rhythm as correlated with light in the Arctic regions, and histological studies to search for special adaptations in the retina of the eye, have still to be attempted. Palmgren (1935) found that birds in Lapland were most inactive between 6 and 11 p.m. This period of rest followed the hottest and dryest part of the day. Several authors have mentioned feeding throughout the night by Arctic Terns in high latitudes and at Machias Seal Island the terns fly around to some extent even during the hours of darkness when they cannot see to feed. A. J. Marshall (1938) mentions periods of quiescence for some species, including the Arctic Tern, even during the perpetual light of the Arctic, but also mentions that these are affected by weather conditions.

The observer who spends an extended period of time in a ternery cannot help but be aware of the spectacular type of social flight which is often performed by terns during the sunrise or sunset hours.

This type of flight is closely allied to the morning and evening flights performed over the ternery before it is occupied. It may be considered as a temporary reversion to flocking behavior which probably serves partly to maintain the social organization of the colony so necessary for communal defense. It is not entirely clear, however, what serves as the releaser for these mass flights. In 1947, I received the impression that social flights reached a peak of intensity at times of special stress and excitement. Some of the most intense social flying occurred just on the "eve" of the hatching of most of the young in the colony, and again at the time when many of the young had begun to fly. However, weather and light intensity seem also to be involved and in order to check this possibility, I kept daily records of evening social flights and weather in 1948 from June 21 to August 2. From June 21 until July 13 the amount of evening social flying recorded each evening checked closely with the weather for that evening. Social flights were large on clear evenings, less intense on partly overcast evenings and did not occur or were hardly noticeable on evenings when there was rain or fog. The only exception occurred on the evening of July 2 when no social flights were seen although the sky was clear. However, at that time, the adults were especially busy feeding newly hatched chicks right up until darkness descended and this drive may have been stronger than that of flocking.

From July 14 until August 2 there was a frequent lack of evening social flying even in good weather, but it should be kept in mind that the young required increasingly greater amounts of food during this period and that frequent periods of bad weather made fishing more difficult for the adults.

Light appears to also have a definite connection with morning social flights, and with the incubation drive. The following incident accompanied a change in the amount of light at 10:15 a.m., July 1, 1948, on Machias Seal Island. The sky grew dark and fog came in on a sudden breeze. Within a few moments the light reading on a Weston meter dropped from 400 to 25. All eggs and chicks in the area were immediately covered by adults. Five minutes later the fog had passed and the sky became bright again. With this, a series of outflights occurred much as they would have during social flight at sunrise.

Evening social flights occur at various times and show little close correlation to the time of sunset. If the sky suddenly darkens in late afternoon, then brightens again, the flights may occur early. On clear days with normal sunsets, flights occur about the time that the sun appears brightest on the horizon. Morning social flights always occur close to the time of sunrise and are less often prevented by dull skies than are evening social flights. This I believe to be due to the extreme change from darkness to daylight which occurs in spite of weather. It is quite possible that not only a sudden increase of light, but suddenly increased light preceded by relative darkness, stimulates social flying.

These obesrvations agree rather well with Armstrong's statements (1954) that the general activity levels of birds may be affected by changes in light-intensity and elevation of the sun and that bird activity "seems to be more closely geared to the light-intensities in the morning than in the evening." Brackbill (1952) has made observations which suggest a correlation between departure times of water fowl and light intensities.

GROUND AND VEGETATION

The Arctic Tern prefers nesting sites with less vegetation than do other northern nesting tern species. Gravel bars, sandy beaches and outer islands with little or low vegetation are typical breeding places. The use of outer sea islands by the Arctic Tern contrasts sharply with the more frequent use by the Common Tern of islands in mouths of rivers and in bays.

Suomalainen (1939) believes that the intense reflection of light from the sea on gravel beaches where it nests is important to the Arctic Tern. However, O. L. Austin, Jr. (1929) pointed out what is perhaps the most important factor in the relationship between terns and the vegetation in their nesting colonies, that is, the wing and tarsus lengths of the species in question. He found that Roseate Terns, which have relatively short wings and long tarsi, are well adapted to comparatively dense growths of grass and shrubbery. Common Terns have medium length wings and tarsi and are fairly well adapted to either open spaces or rather densely covered areas. The Arctic Tern, with its long wings and short tarsi, is least well adapted to high vegetation, but prefers to nest in open places where it can fly to its nest or at least to the immediate vicinity of its nest. An Arctic Tern colony at Hopkins Island, Massachusetts, ceased to flourish when the island became overgrown with bushes (Austin, Sr. 1940).

In view of these relationships, it is interesting to note that Arctic Terns rather than Common Terns occupy the most densely vegetated part of the nesting area on Machias Seal Island. This situation occurs because the jumbled rocky area most used by Common Terns on the island is irregular enough to be undesirable for use by Arctic Terns, which accordingly have preempted the open turf locations more desirable for them. However, as the season advances, these open turf areas produce some of the tallest vegetation on the island.

If Arctic Terns are surprised while on the ground in high vegetation, they often may be caught by hand. Nest sites are chosen so early in the season that there is no indication of high vegetation at the time the site is selected. Individuals which become thus hampered by vegetation hold their wings above them in readiness for flight more than do birds nesting on open ground.

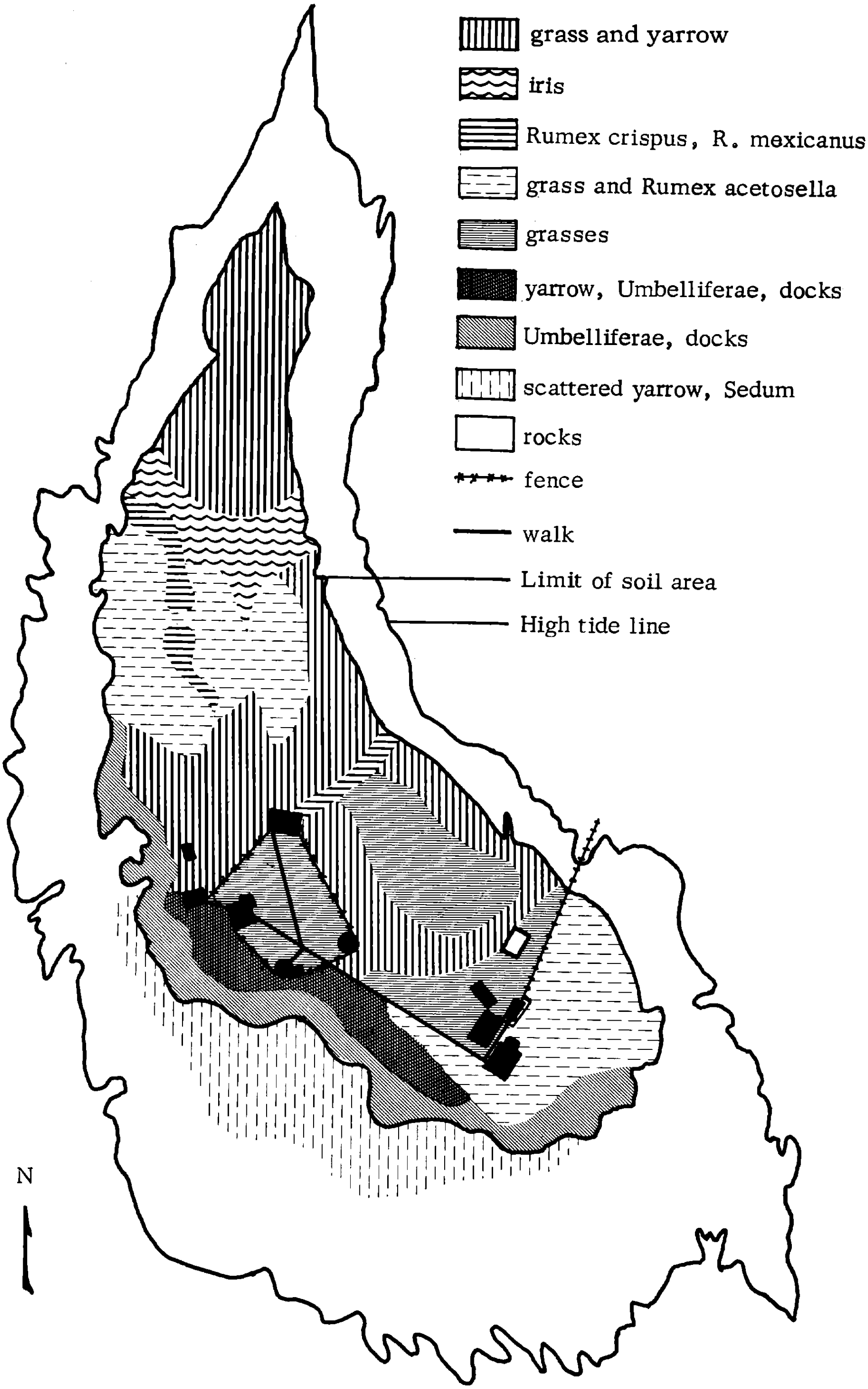

Fig. 2. Distribution of cover plants on Machias Seal Island, New Brunswick, during summers of 1947 and 1948.

Machias Seal Island is granitic with a thin layer of peaty topsoil on the central portion where most of the vegetation grows. An attempt was made to collect all the species of vascular plants occurring on the island. No woody plants occur on the 15-acre island. In two years, 41 species of plants from 18 families were collected and preserved. Fourteen species were European introductions. These European forms probably came to the island in hay brought there for domestic animals. Only one of these, *Rumex acetosella*, furnishes extensive ground cover in tern nesting areas. The yarrow *(Achillea lanulosa)* is the most important plant on the island from the standpoint of controlling habitat. *Rumex acetosella* is next in importance and *Iris versicolor* controls a reasonably large area. Figure 2 indicates the distribution of the important cover plants and groups of plants on the island. Terns nested on nearly all the vegetation-covered areas except those closest to buildings, and nest areas extended out a short distance onto rocky areas with sparse vegetation.

Near-by Gull Rock has only two vascular plants. They are *Agrostis stolonifera* (dwarfed) and *Plantago maritima.* Both grow in cracks in the rocks.

The islets occupied by breeding Arctic Terns at Churchill, Manitoba, were usually located in lakes or ponds. The most common plant community on these islets was a *Cladonium*-Ericaceae community in which *Ledum decumbens* was very abundant (Shelford and Twomey, 1941). One such island which has supported an Arctic Tern population of about 20-30 pairs for many years measured only 16 by 50 yards and lay but 24 yards from the nearest point on the shore of the lake.

WATER

The Arctic Tern is probably less dependent upon water for food than is the Common Tern. Even though the Sugarloaf Islands (Maine) "were teeming with grasshoppers" in July, 1938, Palmer (1941: 24) did not see the Common Terns there catch any. He believes that Common Terns usually take insects only from the surface of the water and not from the air or on land. The Arctic Tern seems to be more adaptable. There are numerous accounts of Arctic Terns hawking insects. One such account is given by Roberts (1934: 256) who observed Arctic Terns in Iceland taking numbers of moths in this manner. The moths were captured at heights of about 10 to 20 feet in the air. One stomach contained 56 moths and as many as 60 per cent of the terns present were feeding on moths. Roberts also reports a spider *(Lycosa tarsalis)* from one stomach and small amounts of grass *(Agrostis palustris)* from two stomachs. He believed that the birds had picked up the grass while hunting for insects on the ground.

On numerous occasions I saw both adults and pre-flying juvenals drink from fresh-water pools on Machias Seal Island. These same pools were used for bathing by a few juvenals but the adults regularly resorted to salt water to bathe. Adult Arctic Terns at Churchill, Manitoba, bathe in fresh-water ponds near the terneries. Both fresh and salt water appear to be suitable for this purpose.

During migration at sea, or during pelagic wanderings, the birds must either drink sea water or obtain sufficient water from their food. Studies on this subject have not been made.

Arctic Terns alight on floating objects at sea in preference to alighting on the water but are buoyant and swim well when in the water. The length of time they can remain on the water without becoming waterlogged has not been determined.

ASSOCIATES

A variety of other species has been reported as nesting in close association with Arctic Terns. These associates include birds from other families as well as numerous species of Laridae.

In Alaska, the Glaucous-winged Gull *(Larus glaucescens)*, the Short-billed Gull *(Larus canus brachyrhynchus)*, the Pacific Kittiwake *(Rissa tridactyla policaris)*, Sabine's Gull *(Xema Sabini)* and the Aleutian Tern *(Sterna aleutica)*, comprise the Laridae most often found nesting in company with Arctic Terns.

An Alaskan colony of 23 pairs of Arctic Terns was unmolested by a pair of Short-billed Gulls nesting near them according to R. B. Williams (1947). Bailey (1927) reports that Arctic Terns in Alaska continually harrassed the Short-billed Gulls. In a colony of 60 to 75 pairs of Aleutian Terns with a few pairs of Arctic Terns among them, Friedmann (1933) thought that the Aleutian Terns seemed more selective in preferring to nest by themselves. Howell (1948), on the other hand, reports no segregation in a mixed colony of Aleutian Terns and Arctic Terns in which Pacific Kittiwakes also nested.

On the eastern coast of North America, the Common Tern, Roseate Tern, and Least Tern *(Sterna albifrons)*, nest with the Arctic Tern as far north as their breeding ranges extend. In 1948, two pairs of Laughing Gulls *(Larus atricilla)* nested among the terns on Machias Seal Island (O. and J. Hawksley 1949). These gulls were unmercifully harrassed by the terns each time they attempted to alight near their nests, but once on the ground they were not disturbed. One pair raised two young, the other pair deserted. A single pair of Herring Gulls nested on Gull Rock, adjacent to Machias Seal Island, in 1948 and 1949, but neither Herring Gulls nor Great Black-backed gulls *(Larus marinus)*, were tolerated on Machias Seal Island proper except below the tide line on the north end of the island. This was the part of the island closest to Gull Rock, where the gulls regularly roosted and sunned. In 1948, about 20 pairs of Arctic Terns attempted to nest on Gull Rock but failed. This may have been due to marauding by the gulls but no evidence of such destruction was found.

Ross's Gull *(Rhodostethia rosea)*, nests with Arctic Terns in Siberia (Buturlin 1906). The first nest of this gull discovered in Greenland was in the midst of a colony of Arctic Terns (Dalgleish 1886).

The Marples (1934) studied tern colonies in which not only Common Terns and Roseate Terns nested with Arctic Terns but also Sandwich Terns *(Thalasseus s. sandvicensis)*, and Least Terns.

A most interesting ecological relationship exists between Sandwich Terns and the gulls with which they associate. This has been reported on by Salomonsen (1947). The terns nest in the center of the colony and are surrounded by Black-headed Gulls *(Larus ridibundus ridibundus)*. Common Gulls *(Larus canus canus)*, are in turn scattered at the edge of the Black-headed Gulls, and Herring Gulls *(L. a. argentatus)*, are permitted only among the more scattered nests of the Common Gull. The terns nest late and force themselves into the center of the Black-headed Gull concentration by destroying eggs and driving out gulls. Nevertheless, the Black-headed Gulls are aggressive and may give some protection to other species in the colony.

This brings forth the question of commensalism in nesting colonies of Laridae and relationships of Arctic Terns to species outside the Laridae.

Small birds such as sandpipers are usually ignored by terns. Spotted Sandpipers *(Actitis macularia)* often wandered among the nests of terns on Machias Seal Island. They were chased by the terns only at the time when tern eggs were close to hatching and incubating birds were exceptionally nervous.

Important associates of the terns on Machias Seal Island by sheer weight of numbers, were approximately 400 pairs of Common Puffins *(Fratercula au arctica)* and 2,000 pairs of Leach's Petrels *(Oceanodroma leucorhoa leucorhoa)*. However, there seems to be no direct relationship between these species and the terns in that colony. Williamson (1948) reported that Arctic Terns in the Faeroe Islands gleaned the fish dropped by puffins, but that they did not molest the incoming puffins and seemed to be eating most of the food on the spot rather than carrying it to their young. I never saw terns scavenging in this manner on Machias Seal Island.

Red Phalaropes *(Phalaropus fulicarius)* occupied an island (about 100 x 50 yards in size) in Spitzbergen on which Arctic Terns also nested (Padget-Wilkes 1922). Sutton (1932: 192) reported Mandt's Guillemots *(Cepphus grylle mandti)*, Common Eiders *(Somateria mollisima borealis)*, and Old-squaws *(Clangula hyemalis)*, nesting with Arctic Terns on a small island near Southampton Island.

The status of species of Anatidae which nest in gull and tern colonies has been much discussed. The Tufted Duck *(Aythya fuligula)* is most noted for this habit in northern Europe and the Old-squaw is commonly found nesting with Arctic Terns in North America. Fabricius (1938) and Haartman (1938) both felt that Tufted Ducks preferred to nest with Laridae because of the protection thus afforded them from predation of Hooded Crows *(Corvus c. cornix)* upon their eggs. The most important fact pointing to commensalism is the open situation of the nests of these ducks in gull and tern colonies as opposed to concealed situations when they nest away from gulls and terns. I have observed this same phenomenon with Old-squaws nesting in the Churchill, Manitoba, region. On the basis of observations in Finland, Bergman (1941) believes these associations are based on social instinct rather than on protection. Durango's important paper (1949), however, does not bear this out.

He mentions that Tufted Ducks and Ruddy Turnstones *(Arenaria i. interpres)* change their breeding grounds to follow changes made by Common Terns and Arctic Terns. He feels that the colony of terns is a releaser for the Turnstone and thinks that both hereditary and learning elements guide the birds to their choice of a nesting site. He further points out that in England, where they breed rather late and on ponds and lakes with dense vegetation, Tufted Ducks do not nest with Laridae. Thus the probability of pure sociability seems doubtful and it is more likely that the Tufted Ducks which nest on islets with scant vegetation in Sweden and Finland, do so because they are less disturbed by enemies there. There is a hint of mutualism in Sutton's (1932: 192) statement that he found at least six Arctic Tern nests on one island "which appeared to have been made in old nests of the Old-squaw."

The occurrence of Arctic Tern eggs in the nests of other birds is interesting but probably of little significance in most cases. Sugden (1947) found exotic eggs in nests of California Gulls *(Larus californicus)* and felt that the gulls carried them to the nest to eat, but were overcome by brooding impulses instead. The gulls supposedly carry the eggs in their bills. Bailey (1925) found a Glaucous Gull's *(Larus hyperboreus)* nest which contained one egg of its own, one of an Arctic Tern and one of an Old-squaw. The gull may have acquired these two eggs in the way Sugden suggested. The Arctic Tern egg which Bailey (1926) found in a Black-bellied Plover's *(Squatarola squatarola)* nest was undoubtedly laid there by a tern. It is common to find clutches containing eggs of both Common Terns and Arctic Terns in mixed colonies. On Machias Seal Island, an Arctic Tern egg somehow came to rest in a burrow with an egg of Leach's Petrel (J. Hawksley 1950).

Mammalian associates which cannot be classed as predators are not numerous. In the outer Hebrides, Gray Seals *(Halichoerus grypus)* frequent some of the rocks used by Arctic Terns but probably do not enter the nesting area. At Churchill, I found that both the Muskeg Meadow Mouse *(Microtus pennsylvanicus drummondii)* and the Varying Lemming *(Dicrostonyx groenlandicus richardsoni)* lived on the islets in tundra ponds where Arctic Terns nested, but saw no evidence to indicate that either harmed eggs or young terns.

PREDATORS

Relatively few animals are able to catch and kill adult Arctic Terns. The great majority of species which may be considered predators of the Arctic Tern prey upon the eggs and nestlings or upon juvenal birds which are less adept at escaping on the wing. The line of distinction between parasitic and predatory species is rather fine, especially where such birds as jaegers are involved. Jaegers might be classed as social parasites, but they are definitely predators at times.

Except at the southern limit of its range, snakes are not important predators of the Arctic Tern. Over-abundant snakes *(Thamnophis ordinatus)* were credited by Floyd (1932) with consuming eggs and young of terns on Penikese Island, but snakes are seldom found on the outer islands where Arctic Terns nest farther north.

Avian predators are probably the most important. These consist chiefly of three types: jaegers, hawks, and other Laridae.

Although Eifrig (1905) mentions finding bones and feathers in the stomachs of Parasitic Jaegers *(Stercorarius parasiticus)* these were probably of small birds for it is doubtful that jaegers could seriously injure terns or gulls. The weakness of the Parasitic Jaeger's bill and feet has been pointed out by McCabe and Racey (1944). They show that its ability to terrify its victim with psychological warfare which "*smothers the flight*" of the victim is the important feature. The killing of an Arctic Tern by Parasitic Jaegers is reported by Roberts (1934), but death was the result of the crashing together of four jaegers as they converged on a single tern which had a fish.

Jaegers are more effective against terns when several gang up on one tern, but two or three terns may easily drive off a jaeger. It was felt by Trevor-Battye (1897) that neither a Parasitic Jaeger nor a Long-tailed Jaeger *(Stercorarius longicauda)* had a chance when opposed by a pair of Arctic Terns.

Jaegers also follow migrating Arctic Terns. Long-tailed Jaegers were noted traveling in company with them by Willett (1918) in Alaska.

Falcons are among the few birds which are actually able to catch and kill adult Arctic Terns. Duck Hawks were the most important predators on adult terns at Machias Seal Island. These falcons presumably came from the island of Grand Manan and made the trip rather frequently. In spite of the mass defense which was made by the whole colony, the Duck Hawks did succeed in taking terns. I found remains of an adult tern, which had undoubtedly been eaten by a falcon, on Gull Rock in 1948. Mr. Benson, the lighthouse keeper, usually shot at Duck Hawks which came near the island and once shot a tern from the talons of one. Duck Hawks were blamed by Norton (1907) for the abandonment of Libby Island, Maine, by terns, but damage by Duck Hawks at Machias Seal Island seems relatively slight and the falcons should not be molested.

At Churchill, I saw a Pigeon Hawk *(Falco columbarius columbarius)* mobbed by Arctic Terns. Rawcliffe (1949) reports the taking of a young Arctic Tern by a Kestrel *(Falco tinnunculus tinnunculus)*. Dr. Arthur A. Allen informs me that Gyrfalcons *(Falco rusticolus)* in Alaska take Arctic Terns and Sabine's Gulls.

The Laridae which prey upon Arctic Terns include most of the large species of gulls which breed in the same range. Sabine's Gull, like the jaegers, tends to be more a parasite than a predator. It is so dependent upon the Arctic Tern in Greenland that it fails to nest when conditions are unsuitable for the terns (Bird and Bird 1940). It is also frequently seen migrating in company with Arctic Terns and jaegers.

Although larger species of gulls such as the Glaucous, Iceland, Glaucous-winged, Great Black-backed and Herring Gulls are generally conceded to prey upon terns to some extent, little quantitative work has been attempted to determine the extent of their depredations. The general effect of larger gulls upon the dynamics of a tern population will be discussed later.

Owls and crows may sometimes prey upon Arctic Terns but are probably not serious predators since there is little to indicate so in the literature. Eastern Crows *(Corvus b. brachyrhynchos)* were mobbed and driven off by the terns at Machias Seal Island. Kirkman (1908) cites Howard Saunders on an incident in which Arctic Terns mobbed and drowned a Hooded Crow.

Unusual and serious avian predators on Machias Seal Island were a few semi-domesticated Mallards *(Anas platyrhynchos)*. Mr. Benson first discovered that the ducks were eating eggs and newly hatched young of Arctic Terns. A few days later, while in a blind, I saw two ducks in action. They were gobbling nearly-hatched eggs as quickly as they could find them in spite of vicious attacks by the terns. They must have eaten at least a dozen before I could get out of the blind to chase them. After that, the ducks were fed more liberally in an attempt to prevent further damage to the terns.

Although the slaughter of terns for the feather trade no longer continues, man is still a serious predator upon terns. Fortunately, the birds are small enough not to be very attractive as food under most conditions. However, tern eggs are usually very well liked by humans living within the range of the Arctic Tern. Where people impose some regulation of egging upon themselves, as they often do in the Bay of Fundy, the actual harm done may be small or no harm at all may result. Under primitive conditions, people such as Eskimos and Indians are less inclined to regulate their egging. They do not object to eating eggs in advanced stages of incubation and thus take the eggs whenever they can find them. Such a situation is cited by Salomonsen (1955) for the Grønne Islands in Greenland where at least 100,000 Arctic Tern eggs were collected each season, causing a decrease in the species. O. L. Austin, Jr. (1932) cites a case in which one Eskimo girl took 800 eggs at one time from a ternery in Labrador.

In his extensive paper on the subject of egging, Cott (1953-1954) lists the Arctic Tern as being among the group of birds second most heavily exploited for eggs. He further lists the Arctic Tern as "showing decline, or egged-out locally," but feels that the effect of egging on bird populations in the Arctic areas of the Old World is not clear.

The people of the Grand Manan region consider tern eggs to be a delicacy and collect them whenever possible. More important to them, of course, is the collecting of gull eggs. This was a rather well-regulated process in the past. Owners of islands often rented them by the day to parties of eggers. The natives claim that Herring Gulls lay up to nine eggs if eggs are taken as soon as they are laid. They claim to have always left the last few for the birds.

Egging has been conducted on Machias Seal Island for years in spite of the fact that it is a sanctuary. This has been done mainly by the keepers or their guests. The local "rule" is that eggs may be collected until clutches of two are found. This simple rule is enforced by the condition of the eggs after that, so that egging only lasts for about a week in the first part of June.

I doubt that any harm comes from this early egging. If anything, it might tend to make the time of hatching come a bit later and thus young chicks would be less likely to die in storms which seem to be frequent in late June and early July. At least, the Machias Seal Island colony has flourished in spite of egging. Cott (1953-1954) lists a number of birds which are probably similarly benefited by egging. Among them is the Lapwing *(Vanellus vanellus)* in Holland.

Tern eggs were used for food during the first World War in Great Britain and research has been carried on in Britain recently to determine the palatability of the eggs of birds with a view to possible future consumption. Egg tasters at the Research Station, Cambridge, have given eggs of the Arctic Tern a rating of 6.5 which is in the "relatively palatable" group. A rating of 10.0 is ideal and 2.0 is inedible. The Domestic Fowl has a top rating of 8.6, the Common Tern rates 7.3 and the Herring Gull 7.9, all three being in the "highly palatable" group (Cott 1949).

Some of the damage done by humans in terneries, such as those along the coasts of Maine and Canada, is not true predation, but a form of vandalism. Picnickers and sight-seers who visit terneries inadvertently step on eggs and chicks. They pick up and misplace chicks which are later killed by adults for trespassing on adjoining territories. If they bring dogs to a ternery, untold damage may result.

The dog kept by the family at Machias Seal Island was trained to stay away from the tern nesting areas, but former keepers had dogs not so well trained. Sheep and cows kept in terneries step on many eggs and young. A cow on Machias Seal Island picked up and badly mauled juvenal terns.

There were no wild mammals living on Machias Seal Island except bats *(Myotis)*. Farther south, however, Norway Rats *(Rattus norvegicus)* are serious predators in tern colonies. O. L. Austin, Sr. (1948a) has reported extensively on this predator in the Cape Cod colonies. A report by Forbush (1921) stated that a small colony of Arctic Terns at Chatham, Massachusetts, was wiped out by high tides and later by raids of "cats and skunks, which destroyed both eggs and young and drove the parent birds away."

In the Arctic, foxes may be serious predators upon terns. In 1949, Mrs. T. C. Stanwell-Fletcher and Miss Hazel Ellis found no less than five dens of the Arctic Fox *(Alopex lagopus)* on the Fox Islands near Churchill. There were perhaps a thousand pairs of terns nesting there and it appeared that eggs, at least, were being taken by the foxes. The fox pups were extremely curious and followed the humans about. When attacked by the terns, the pups jumped into the air in attempts to strike back.

In Northeast Greenland, Ermines *(Mustela erminea)* prevented the breeding of Arctic Terns on Ternholme Island in 1938 according to Bird and Bird (1941).

The Arctic Tern's habit of frequently nesting singly on the mainland in arctic regions may be effective in reducing predation, especially from mammalian predators such as the Arctic Fox.

INVERTEBRATE PARASITES

Relatively few invertebrate parasites are known from the Arctic Tern. In searching for Mallophaga on adults and chicks I was not always able to find any on the birds. Only a few individuals on Machias Seal Island were found with heavy infestations of lice. No macroscopic endoparasites were noticed.

Slater and Carter (1886) found young Arctic Terns in Iceland dying in the downy stage soon after hatching due to either "the cold summer or to the presence of huge tapeworms" with which they were infested. A heterophyid trematode *(Cryptocotyle lingua)* is known to infect gulls, terns and other piscivores (Willey and Stunkard 1942). Another trematode *(Aporchis rugosus)* is definitely a parasite of the Arctic Tern (Linton 1928).

The most interesting host-parasite relationships are those between the terns and their Mallophaga. During the summer of 1947, I collected all the Mallophaga I found on Arctic Terns. They were eventually sent to England for identification. These lice proved to be of two new species, *Quadraceps houri* Hopkins, (Hopkins, 1949) and *Saemundssonia lockleyi* Clay (Clay, 1949a). Fourteen of the Machias Seal Island specimens became paratypes of the new *Quadraceps.*

The Common Tern has the same two genera of lice, but two different species. They are *Quadraceps sellatus* and *Saemundssonia sternae.* This is interesting in view of the fact that all three species of terns of the genus *Chlidonias* have the same species of Mallophaga, *Saemundssonia lobaticeps* (Clay 1949b). Even more important is the fact that *Saemundssonia lockleyi* is found not only on the Arctic Tern but also on the Antarctic Tern *(Sterna vittata).* Miss Clay (1948) believes that this suggests a close relationship between the two hosts and supports Kullenberg's supposition (1946: 78) that the Antarctic Tern is a relatively recent derivation from populations of the Arctic Tern which remained in the antarctic and sub-antarctic waters during the northern summer.

Gross (1937) reports a species of *Philopterus* taken from an Arctic Tern. There are a few other references in ornithological literature to Mallophaga from Arctic Terns, but the identifications would bear checking now that two new species have been described for that host.

One mite was taken from an Arctic Tern at Machias Seal Island and proved to be *Euhaemogamasus oudemansi.*

EGG AND CHICK MORTALITY

A knowledge of mortality prior to fledging is essential to an understanding of the reproductive capacity and management of a species or of population problems in general. Machias Seal Island is especially well suited for a study of natural mortality because it is relatively free from disturbing outside influences. The environment has been only slightly altered by the presence of man and no unnatural predators have been introduced except a few domestic animals which are fairly well controlled.

The term "fledging" has been variously used and might lead to confusion if not defined. In this paper, the term is used to refer to the age of attaining flight.

Large-scale banding of young was carried out in the summers of 1947, 1948, and 1949. A continuation of this banding and additional trapping of adults in the summer of 1950 was done by Glen Woolfenden.

The method of study was essentially the same in both 1947 and 1948. Four areas were used, two in each year. Owing to the pressure of other work, those used in 1948 contained fewer nests but were carefully chosen so as to be representative of typical breeding areas on the island.

One area in 1947 included 100 nests which were marked with numbered wooden stakes on June 14. The 100 nests represented all the nests containing one or more eggs which could be found in that area on the day of marking. This assured a random assortment of clutch sizes. The area was located at the northern end of the island and included part of a beach of smooth pebbles. The remainder, and greater part of the area, was on peaty ground made irregular by tussocks of vegetation and by burrows of Leach's Petrel. The predominant vegetation was a yarrow *(Achillea lanulosa)*.

The second area used in 1947 contained 50 nests marked on June 23. This area was located on higher ground, nearer to the center of the island. It was covered by short grasses and *Rumex acetosella* except on its outer (seaward) edge where there was some yarrow. It included a few somewhat later nests than the first area because again all nests with eggs in the area were used.

In 1948, one area with 50 nests and one with 25 nests were marked. The 50-nest area, which was marked on June 7, was located on the west side of the island between the dwellings and the sea. The inner section of the area had some grasses, but most of the area was rocky with only small amounts of yarrow and *Sedum roseum* growing where there were patches of soil. The 25-nest area was located nearer the southern end of the island, west of the "whistle house." The presence of a blind in this area made more detailed observations of the occupants of the area possible. Another difference in this study area was the fact that nests were marked as they were established. The laying process and marking began on June 4 and was not completed until June 13. All nests were in adjacent territories.

The nests in each area were checked daily. When the young hatched, they were banded with color bands until old enough to hold regular aluminum bird bands. In addition, notes were taken on the colors of the soft parts and on the down of chicks. When chicks became older and began to wander, nests were checked in both morning and evening. In this way few chicks were lost to the study. It is reasonable to assume that those which did disappear died, because the island was thoroughly covered during banding operations and had any of these chicks survived they would probably have been identified immediately.

CLUTCH-SIZE

Lack (1947) gives the usual clutch size for the Arctic Tern as two for both England and Norway. The number varies from one to three. In a later part of the same paper, Lack (1948) gives the average clutch as 2¼ eggs in mid-Europe. Bickerton (1909) studied the clutch size of the Arctic Tern in the British Isles and reported 355 eggs in 209 nests. This gives an average of 1.7 eggs per nest. The difference between these figures and those of Lack may well be connected with the fact that Lack's are "based on general statements" and that some of his authorities were oölogists. I have noted a tendency among oölogists to assume that the normal clutch for this species is two and to avoid collecting the one egg clutches which they suspect of being incomplete.

Data on clutch size tend to be more accurate if taken from studies such as Pettingill's (1939), and my own study on egg and chick mortality, for then the history of the clutch is known. Pettingill's 100 nests on Machias Seal Island contained 144 eggs, or an average of approximately 1.4 per nest. In 225 nests studied on the same island, I found 308 eggs, or an average again of approximately 1.4.

Eklund (1944) checked 279 nests in Greenland which averaged 1.7 eggs per nest and R. B. Williams (1947) reports an Alaskan colony of 45 nests in which all of the clutches were of 2 eggs. It would appear that the average clutch, at least in North America, is smaller than indicated by Lack. Clutches of four, five, or more eggs have been reported by many authors. Call (1891) discussed some sets of four to six but noted that most showed clearly that they had been laid by two birds.

The 50-nest plot of 1947, which included later nests, showed no statistically significant difference in clutch size when compared to the earlier 100-nest plot. The average clutch size for the 50-nest plot was $1.16 \pm .05$ and that for the 100-nest plot was $1.20 \pm .04$. The 50-nest plot of 1948 had an average clutch size of $1.76 \pm .07$ compared to $1.68 \pm .11$ for the 25-nest plot. This again is an insignificant difference, showing that the average clutch size was approximately the same regardless of the fact that one group was picked at random after one or more eggs were laid and the other group was picked as the first egg was laid in each nest.

In a study of Herring Gull and Lesser Black-backed Gull *(Larus fuscus graellsi)* colonies, Darling (1938: 62) found that the average clutches in 1936 were 2.1 for Herring Gulls and 2.2 for the Lesser Black-backed Gulls. In the same colonies the following year, the number of birds present doubled and the average clutch size was 2.9 for both species. Darling concluded that these figures pointed to "an improvement in the environmental complex in 1937."

The difference on Machias Seal Island, between an average clutch size of 1.19 in 1947 and of 1.73 in 1948 may have a similar significance but clearcut reasons are not evident. There were three known changes in the Machias Seal Island colony in 1948 from the conditions in 1947. In 1948 the weather was generally less severe, the height of the vegetation was lower and the breeding population had increased to some extent. However, the collective effect of these changes, early in the season when eggs were laid, could not have been great. Darling worked with relatively small populations in which changes in numbers would be very noticeable, whereas the population increase at Machias Seal Island was relatively slight compared to the total population.

The theory, that some birds in the southern part of their range lay fewer eggs than those in the north and that the increased length of day in the north allows the parents to collect more food to feed more young, has

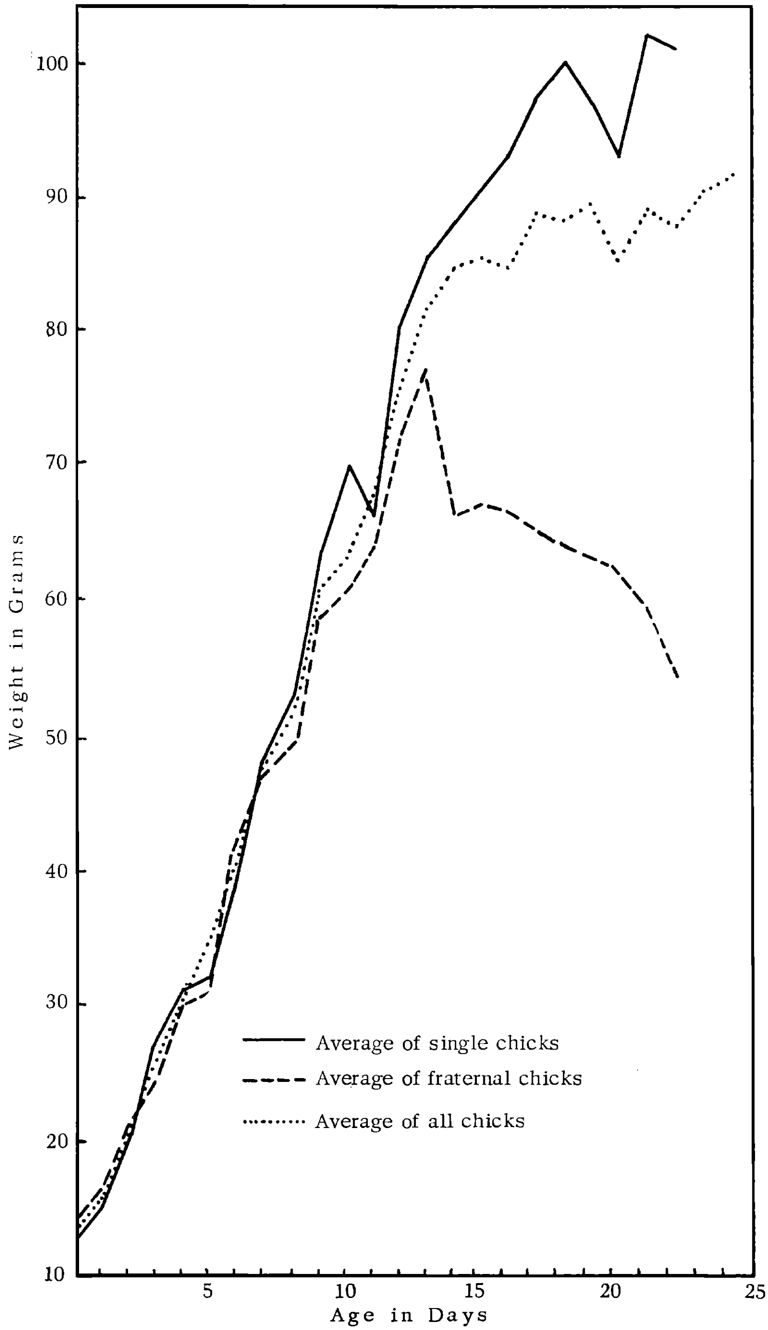

Fig. 3. Chick growth as related to brood-size.

been revived by Lack (1947). Lack did not present any data indicating that this was true for the Laridae. Paynter (1949) states that "it is probable that it does not exist in this group since . . . the survival rate of the young seems to be independent of the number of chicks in the nest and greater food-gathering time would not increase the chances for survival."

Although Paynter's data for the Kent Island Herring Gulls support his statement, my own data from the main study (see Tables V and VI) and from a supplementary study of Machias Seal Island Arctic Terns, do not agree with this general statement for the Laridae. Unfortunately the number of nests with which I was able to work in the supplementary study was small, but I believe that the data show a definite trend which might be even more clear with more data, and therefore include this study.

In 1948, while taking routine weights of chicks, I was able to check to see what difference there was between the development of single chicks and chicks which competed for food with another chick in the same nest. Accordingly, the routine weighing of chicks was expanded into a supplementary study to provide comparative survival data. Weight gains and losses of chicks were correlated with weather conditions as already shown in figure 1.

Twelve nests were selected for this study but only eight of them produced chicks. Five of the nests produced two chicks each and three produced single chicks. Figure 3 shows the results. Weights of single chicks, weights of fraternal chicks, and the average weight for all chicks are plotted for comparison from hatching to an age of 22 days.

The fraternal chicks' weights represent only those still competing at the same nest on any given day. From the fourteenth day on, only one nest still had two chicks alive. The younger chick in that nest died at an age of 22 days, at which time it weighed only 46.2 grams. The other chick in the nest was then down to 63.6 grams but eventually recovered and lived.

The average weight curve for fraternal chicks which survived would come close to the average for all chicks, and is therefore not shown in the graph, to prevent confusion.

Since the number of nests studied is small, these results are not conclusive but they indicate that the survival rate of the young may very well be affected by the number of chicks in the nest, at least in some of the Laridae. No studies of the survival of young Arctic Terns appear to have been made in any latitude higher than that of Machias Seal Island, but there is some indication that the clutch size may average larger. Table I summarizes the accurate average clutch sizes obtainable for points enough farther north than Machias Seal Island to have considerably more summer sunlight. However, these colonies are represented only by data from single years or even single days. Also, as is pointed out in Paynter's (1954: 139) paper on Tree Swallows *(Iridoprocne bicolor)*, the really significant difference in length of day is based more on the time of nesting than on latitude. Birds nesting further north do so nearer to the summer solstice than those farther south.

TABLE I. *Average clutches for Arctic Tern at latitudes higher than Machias Seal Island.*

Locality	No. Nests	Av. Clutch	Source
British Isles	209	1.7	Bickerton (1909)
Bear Is., Barents Sea	49	2.0	Duffey and Sergeant (1950)
Greenland, lat. 62°	279	1.7	Eklund (1944)
Southampton Is.	127	1.8	Sutton (1932)
S. E. Alaska	45	2.0	R. B. Williams (1947)

DURATION OF INCUBATION

In a paper on a "biological distinction" between Common and Arctic Terns, Van Oordt (1934) stated that the Arctic Tern does not begin incubation until the clutch is complete while the Common Tern begins when the first egg is laid. I have found no such clear-cut distinction. Arctic Terns hatch at intervals of a day or more just as Common Terns do. Only occasionally do two chicks in the same nest hatch on the same day.

Table II shows the histories of laying and hatching at nine nests. All nests in the 25-nest study area which had two eggs, and in which both eggs hatched, are included. Birds in this area were observed daily from a blind so that the actions of most of the adults were known. The figure for the second egg in each nest represents incubation time for that egg. As indicated, the first egg may or may not have been incubated for the number of days it was in the nest.

TABLE II. *Intervals between hatching and laying of individual marked eggs of the Arctic Tern.*

Nest No.	Days in Nest Egg 1	Days in Nest Egg 2	Interval in Days Laying 1 & 2	Interval in Days Hatching 1 & 2	Remarks on Incubation
3	24	21	4	1	Began with 2
6	22	22	1	1	" " 1
8	23	20	4	1	" " 2
13	23	21	2	0	" " 2
15	23	22	2	1	" " 2
16	21	22	1	2	" " 1*
18	24	23	2	1	" " 2
19	22	22	2	2	" " 1
X	26	26	2	2	" " 1†

* Chick wandered.

† Late nester; birds very nervous.

It may be readily seen, even in this small sample, that not all birds delay incubation until the clutch is complete. Those which do, tend to cover the nest at irregular intervals until the clutch is complete. This accounts for the fact that the first egg usually gets about one day ahead of the second in these cases. In the table, egg 2 in nest 16 was incubated longer than egg 1 because the wandering of the first chick had kept the brooding bird off the nest for much of the last two days.

Nest X represented a late nesting. The "nervousness" of the birds resulted in rather intermittent incubation. Excluding this nest, the average period of incubation for second eggs in the other 8 nests was about 22 days. Pleske (1928: 224) arrived at this same figure by calculations based on the time that Common Tern eggs required in an incubator (Evans 1891). The period is given by Witherby et al (1941) as 21-22 days.

Beside the lengthening of the incubation period due to the irregularity and "nervousness" of the birds, some variations may be caused by the nesting habitat itself. Some Arctic Terns nest in bare rocky areas. The rocks retain the sun's heat and act as a natural incubator when the eggs are not covered. Other individuals nest in shaded areas where the sun's heat is much less.

HATCHING SUCCESS

Of the 308 eggs in the four main studies, 111 failed to hatch. This gives a hatching success of slightly less than 64 per cent.

Nests which had complete or partial hatching success are analyzed in Table III. Those nests which contained only one egg had a hatching success of 59.3 per cent while those containing two eggs had a hatching success of 68.9 per cent. Application of the Chi-square test for the significance of these frequencies shows that they might occur by chance alone and therefore cannot be considered significant. The figures for nests with three eggs represent too few data to be significant but are included in the table for completeness.

TABLE III. *Clutch-size related to failure to hatch.*

No. Eggs in Nest	Total No. of Eggs	Hatched	
		No.	Per Cent
1	144	85	59.3
2	158	109	68.9
3	6	3	50.0
Totals	308	197	64.0

A summary of causes for the failure of eggs to hatch is given in Table IV. There is little in the literature on the fertility of Arctic Tern eggs. Montague (1926) examined between forty and fifty clutches. "Of the clutches which contained two eggs, just under fifty per cent contained one infertile egg. Of the single clutches, a small proportion were infertile." Pettingill (1939) found 5.5 per cent of 144 eggs "sterile." Since the eggs are not examined until the end of the incubation period in mortality studies such as Pettingill's, it is nearly impossible to distinguish infertile eggs from eggs which become addled early in development. Accordingly, I have designated eggs incubated for a long period but failing to hatch as "infertile or addled early" unless an identifiable embryo was present. Embryo deaths include those chicks which died in hatching. Punctured eggs appeared to be punctured by the terns them-

TABLE IV. *Summary of nesting success of Machias Seal Island Arctic Terns.*

Year	1947				1948					
	100-nest		50-nest		50-nest		25-nest		Totals	
Plot	No.	%	No.	%	No.	%	No.	%	No.	%
Total eggs in nests	120	100.0	58	100.0	88	100.0	42	100.0	308	100.0
In 1-egg clutches	80	66.7	42	72.4	13	14.8	9	21.4	144	46.7
In 2-egg clutches	40	33.3	16	27.4	72	81.8	30	71.4	158	51.3
In 3-egg clutches	0		0		3	3.4	3	7.1	6	1.9
Egg failures:										
Infertile or addled early	21	17.5	9	15.5	0		1	2.4	31	10.1
Death of embryos	20	16.7	1	1.7	2	2.3	0		23	7.5
Abandoned	0		0		1	1.1	2	4.8	3	1.0
Disappeared	4	3.3	0		10	11.4	6	14.3	20	6.5
Punctured	0		0		8	9.1	2	4.8	10	3.2
Rolled from nest	2	1.7	0		2	2.3	0		4	1.3
Dest. by man or dom. animals	2	1.7	0		17	19.3	1	2.4	20	6.5
Total egg failures	49	40.8	10	17.2	40	45.5	12	28.6	111	36.0
Total eggs to hatch	71	59.2	48	82.8	48	54.5	30	71.4	197	64.0
Chick mortality due to:										
Starvation	15	12.5	7	12.1	5	5.7	6	14.3	33	10.7
Disappeared	6	5.0	8	13.8	8	0.1	1	2.4	23	7.5
Killed by domestic animals	0		1	1.7	4	4.5	0		5	1.6
Killed by adult terns	3	2.5	1	1.7	0		0		4	1.3
Adverse weather conditions	5	2.5	0		1	1.1	3	7.1	7	2.3
Unknown factors	5	4.2	3	5.2	3	3.4	2	4.8	13	4.2
Drowning	0		0		3	3.4	1	2.4	4	1.3
Premature	1	.8	0		0		0		1	.3
Total chick mortality	33	27.5	20	34.5	24	27.3	13	30.8	90	29.2
Total chicks fledged	38	31.7	28	48.1	24	27.3	17	40.5	107	34.7
Pairs fledging a chick		38.0		56.0		48.0		68.0		47.6

selves. Some punctures were of a size that could have been made by the birds' bills, but some were small and may have been made by the toes of the birds when they flew off suddenly. Most of the eggs indicated as having been "destroyed by man or domestic animals" were stepped on by four sheep which frequented the 50-nest plot in 1948.

FLEDGING SUCCESS

Of the 308 eggs in the four plots, 197, or 64 per cent, hatched. A daily search was made for each chick and its history was recorded until it died or was fledged. Seldom was a chick which was missing for over five days found alive. Young chicks missing for that long a period could rather safely be assumed to be dead.

The average age at fledging varied in the four areas from about 24 days to about 30 days. Robust chicks which were well feathered and ready for flight were considered fledged when they disappeared at ages close to 30 days. Many of the young birds were actually observed in their first flights and many were caught after they had flown. The first primaries of a few birds, caught just after a first flight, were measured to determine the length (flattened). The primaries of birds nearly able to fly were then measured and the measurements recorded with their histories. This provided an additional check on whether or not a bird of fledging age had actually flown when it disappeared. Birds having primaries over 100 mm. long were considered able to fly if light enough and strong enough.

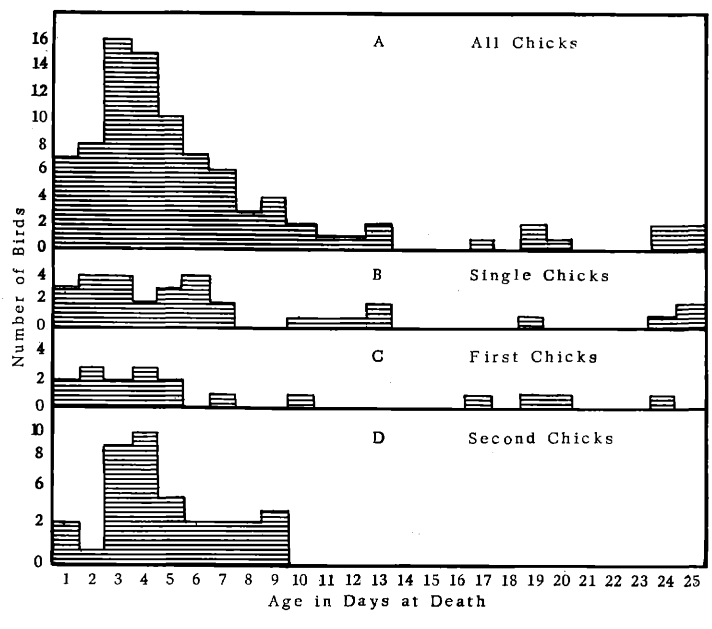

Fig. 4. Brood-size as related to survival.

A histogram (figure 4-A) shows the ages at which chicks died. It can be seen that over 76 per cent of the deaths occurred during the first week of life. The heavy mortality shown for the third and fourth days represents deaths of second chicks (see figure 4-D), in nests with two chicks. First chicks in nests of two, and single chicks also show high mortality during the first week (figure 4-B and C) but not as heavy as that of second chicks. The higher mortality of second chicks is due to increased competition as the older chicks in the nests become disproportionately larger and stronger due to their head start. Another factor is that the presence of two young chicks in a nest often means that the parents must both spend a great deal of their time fishing and consequently, two chick nests are seldom guarded by an adult (as single chick nests are) while the second adult is off fishing.

Since a test has been made to determine whether clutch-size affects hatching success, it will also be of interest to test for the effects of clutch-size and brood-size on post-hatching mortality. This may be done by comparing the number of young fledged from one-egg nests and one-chick nests with the number fledged from two-egg and two-chick nests. The basic data are shown in Tables V and VI. Fledging of one chick per nest is considered to constitute successful fledging.

TABLE V. *Clutch-size as related to fledging success.*

No. Eggs in Nest	Total No. Eggs	No. Young Fledged	Young Fledged Per Nest
1	144	54	.38
2	158	52	.66
All nests	308	107	.48

A Chi-square analysis of these data shows that the frequencies are significant. There is less than one chance in 100 that the variation in

TABLE VI. *Brood-size as related to fledging success.*

No. Young in Nest	Total No. Young	No. Young Fledged	Percent of Young Fledged
1	106	75	70.8
2	88	31	35.2
All nests	197	107	54.3

fledging success could have arisen by chance. It may be concluded that although clutch size has no significant effect on hatching success, both clutch-size and brood-size show an ultimate effect in the success of fledging. One-chick nests have better hatching success, but two-egg nests give better fledging results than one-egg nests. This seeming incongruity is partly explained by some reduction of two-egg clutches to one before hatching. Parental age, as related to clutch-size and to successful breeding, may give other explanations when such a factor is studied in Arctic Terns.

These results differ notably from those obtained with the Herring Gull (Paynter, 1949) in which three-egg nests had the best hatching success and in which "surival of the young, at least until the thirtieth day, is independent of the brood-size." This indicates that it would be difficult to make general statements on the significance of clutch-size in the Laridae from data on one or two species only. It may also point to a basic difference between gulls and terns, between a species much subject to early predation and one little subject to such predation, or to a difference between species laying clutches averaging less than two and those species laying larger clutches on a whole. This cannot be determined until more species within the family have been investigated.

The causes of chick death are summarized in Table IV, but need some elaboration here.

A large proportion of the 33 deaths by starvation occurred in two-chick nests. The younger chick was usually the victim due to its inability to compete.

Twenty-three chicks disappeared. There was little doubt that these died. Pettingill (1939) had 29 chicks disappear in his study of Arctic Tern mortality on Machias Seal Island. This is a rather high figure for only 100 nests, and raises a question as to the amount of disturbance which occurred in the study area. He attributed the loss of these chicks to "kidnapping or wanderlust."

One chick was stepped on by a cow, and four were stepped on by sheep. One cow was on the island in 1947, and four sheep replaced it in 1948.

Seven died due to exposure in periods of cold rain. Those which drowned fell into pools surrounded by steep rock sides which prevented their climbing out.

The one chick designated as "premature" still had a large yolk sac when completely hatched, even though it hatched on the twenty-second day of incubation.

In all, 107 chicks fledged. This gives a success of only 34.7 per cent if figured on the total number of eggs but represents 47.6 per cent success in terms of pairs which succeeded in fledging a chick. The latter is a more reasonable type of figure for a species which seems to be capable of raising only one chick per breeding pair per season. The figure of 34.7 per cent may be used, however, to compare with Pettingill's very low figure (1939) of 15.9 per cent success from 144 eggs in 100 nests.

Pettingill gives three reasons for this low figure (27.3 per cent was the lowest figure for any one area in my studies): 1) marauding by adult terns, 2) failure of nesting drive, especially in young breeders, and 3) competition for food. The first reason is logical enough and well supported. In evaluating the second, however, it must be pointed out that Pettingill's study did not begin until July 2, when he "selected . . . one hundred nests with eggs still unhatched." At this late date in the season, many of the nesting birds which still had eggs may not only have included young adults in which the nesting drive was "incomplete," but would also have included second nesting attempts in which the birds had passed the peak of the nesting drive. Thus, the nests selected were hardly typical of the entire season in that colony. Further, the stated span of his stay on the island is less than incubation plus the period for attaining flight in the Arctic Tern. Competition of adults (as implied) for food seems unlikely because the surrounding waters are rich and the terns adapt themselves quickly to changes of supply. When one food supply fails, the birds turn to one or several of the other abundant food sources. O. L. Austin, Sr. (1946) states that all writers, including himself, "have failed to append credible, substantiating data" when reporting food shortages affecting chick mortality in tern colonies.

The summer of 1948 was comparatively free of storms and fog, but the summer of 1947 produced a bad rainstorm with cold northerly winds on July 4 and 5. In addition to this, the summer of 1947 was extremely foggy. One period of fog in July lasted for 400 hours. The generally better weather conditions of the 1948 season may account partially for the better nesting success of that year.

Paynter (1949) found that 36.8 per cent of the eggs in his study of Kent Island Herring Gulls produced fledged young. In the same year, 1947, I found that 37.1 per cent of the eggs in the study of Machias Seal Island Arctic Terns produced fledged young. Similarity of weather conditions may well have been involved in the likeness of these figures and the general success of fledging because weather undoubtedly has indirect effects as well as the direct effect of killing young.

POPULATION VARIATION AND MANAGEMENT

NON-BREEDING AND DESERTION

Many authors, including O. L. Austin, Sr. (1934), have suggested that tern populations are cyclic in numbers, but little information has been presented by anyone but Austin on this matter.

One of the most interesting phenomena bearing on this subject is that of non-breeding. Many cases have been reported in which Arctic Terns were present at arctic breeding grounds during the breeding season but were prevented from nesting or made no attempt to nest. The following are examples.

In 1855 Evans and Sturge (1859) found the Arctic Tern to be common in Western Spitzbergen but its eggs were not found that year. Manniche (1910) reported that terns and some other species did not nest in northeast Greenland in 1907. Bird and Bird (1935) reported the species as present on Jan Mayen Island in 1934, but the birds "made no attempt to breed." The Birds (1941) mention non-breeding of the Arctic Tern in northeast Greenland in 1938 but believed that predation by Ermines prevented the species from breeding. Late arrival, and as a consequence, the possibility that the birds had passed the peak of breeding condition was probably the cause of the very reduced breeding reported by Seligman and Willcox (1940) for Jan Mayen Island in 1938. J. G. Williams (1941) reported that all the breeding colonies on the Varanger Peninsula, East Finmark, were deserted in the late, cold summer of 1939.

A consideration of the factors involved led Lack (1933) to the conclusion that periodic non-breeding of the type exhibited by the Arctic Tern is due to "late seasons" in which suitable nesting sites are covered with snow and ice until the gonads have regressed to the point where the birds are no longer capable of breeding that season. This conclusion is borne out by more recent observations such as those of the Birds (1940) and A. J. Marshall (1952). This non-breeding cannot be considered then, as a truly cyclic phenomenon.

Desertion has been known to occur in tern colonies due to excessive egg robbing or due to the continued presence of certain predators. Where terns nest in large colonies, they have little success if they are hampered by numerous predators and often desert.

Another type of desertion, however, has been described by N. Marshall (1942) who observed it in Common Tern colonies on Lake Erie. The desertion took place in the form of extended evening social flights in which nearly the entire population took part and from which they did not return to their nests until the following morning. Marshall was completely puzzled by this performance which he saw take place several times in the years 1939, 1940 and 1941. The colony he studied at Starve Island was unsuccessful all three seasons. In 1939, the 1,052 nests of May 25 produced only a single chick. The population dropped off to 513 pairs in 1940 and to 109 pairs in 1941 with only a few young raised each year. Chilling of the eggs during the periods of night desertion may have been responsible for the lack of success.

Marshall was apparently unaware that evening social flights in which the birds return, are normal, almost daily, occurrences in terneries. If, as he seemed reasonably sure, neither human disturbance nor predators were causes, only one explanation seems plausible in the light of our present knowledge of tern behavior. That is, that for some reason, the intensity of the social flight increased to such a point that social behavior dominated individual behavior so that the terns went off in a flock instead of returning to incubation. If the breeders were predominantly young, their incubating drive may have been more readily overcome by a flocking drive (see O. L. Austin, Sr., 1945).

On June 27, 1948, I witnessed a peculiar social flight of Arctic Terns at Machias Seal Island which had some of the characteristics of the desertion flights described by Marshall, but the birds finally returned to their nests. Out-flights began on the north end of the island at 12:50 p.m. These soon spread to most of the island and took on the form of the morning social flight. The day was clear and bright and upon searching the sky for a predator which could have caused the alarm we saw nothing. At 1:05 p.m., a group of about 100 terns alighted in a raft on the water about one-half mile off-shore. They did not bathe, but a few moments later arose *en masse* and flew back to the island. It was not until 1:30 p.m. that the ternery quieted down to continue its normal activities. Since this phenomenal flight occurred just prior to the time of the hatching of most of the young, it may be that it was a result of pent-up tension in the incubating birds. I have no definite evidence for this idea, however, and it would not explain similarly puzzling flights which occurred at other times. These flights are much like those which the Marples (1934: 169) called "panics." Although in neither this case nor in Marshall's observation, any predator was seen, this does not exclude the possible presence of one, since outflights are typically set off by visual or auditory alarm stimuli.

ECOLOGICAL SUCCESSION AND OTHER HABITAT CHANGES

Plant succession and other vegetational changes have a definite effect on tern populations, either directly, or indirectly through consequent changes in populations of other species of birds inhabiting the area. Many environmental changes have occurred during the past 50 years in areas that have been used by breeding terns. Most of these changes have been due to changes in land use rather than to true succession. Since they have often been abrupt and drastic changes, their effect on tern populations has been more disastrous than the normal ecological succession would have been, for, in many cases, the outer islands on which Arctic Terns nested had rather stabilized ecological conditions until man interfered.

In 1932, thousands of young or eggs of Common Terns and Roseate Terns were destroyed or mysteriously disappeared from Penikese Island, Massachusetts. Floyd (1932) thought that the disappearance of eelgrass *(Zostera marina)* from the surrounding waters at that time may have caused a failure of food for the terns, but there was no conclusive evidence for this.

Vegetational changes on islands in the Cape Cod region have had a very clear connection with population changes. I have already cited the instance (Austin, Sr. 1940) in which the overgrowth of Hopkins Island by bushes forced out a flourishing colony of Arctic Terns. Reclamation (by humans) for terns of some of these areas has been accomplished by destroying the high vegetation.

The Marples (1934) refer to the encroachment upon tern nesting territory by Black-headed Gulls and the resulting moves made by the terns. The terns either move to an entirely new area, or if there is sufficient room, they move to another part of the same area, apart from the gulls.

The increase in numbers of Herring Gulls and Great Black-backed Gulls and the decrease or shifting of tern populations along our eastern seaboard has been a matter of concern to many students of birds in recent years.

In stating that the Common Tern "must have an inherent ability to make readjustments to the necessities of altered environment," O. L. Austin, Sr. (1942) must have referred mainly to situations in which the terns were not in direct competition with gulls. Crowell and Crowell (1946) have shown that on relatively small islands, such as those in the Weepecket group (Mass.), where terns must compete with gulls, the terns are forced out as the gulls increase.

The succession of nesting species on Muskeget Island, Massachusetts, has furnished an outstanding example of population change. Early in the nineteenth century, Muskeget was primarily a tern colony and probably the largest such colony on the New England coast. Later, the Laughing Gull appeared there and by 1850 became an abundant breeder. Its numbers fluctuated, due to egging and the feather trade, but in 1945, 16,000-22,000 pairs were estimated to be present. Since that time, Herring Gulls, which began nesting on the island in 1922, have become so numerous that there was a reduction of Laughing Gulls to about 2,500 pairs in 1947. The terns then nesting on Muskeget numbered only about 1,000 and were limited to one area (Gross 1948).

The Laughing Gull is often found nesting with terns, but usually this association occurs on islands with high growing herbs and thus they are islands more used by Common Terns and Roseate Terns than by Arctic Terns. The Laughing Gull is more tern-like in its movements than the larger gulls and due to its manoeuverability it is more readily able to colonize in terneries. Once it becomes established, however, the way is opened for intrusion by the larger species of gulls.

The nesting of two pairs of Laughing Gulls on Machias Seal Island in 1948 might not have occurred if the island had not had so much high vegetation. Some of the changes which have taken place on Machias Seal Island have a direct bearing on populations there and will now be discussed.

The estimates of Arctic Tern populations on Machias Seal Island have largely been guesses which appear to have been influenced by the guesses of former visitors to the island. Estimates of about 2,000 pairs have been given from 1911 (Brown) until 1937 (Pettingill 1939) but it seems unlikely that the population would have been that constant. It is apparent from details given to me by the keeper that it has varied greatly in recent years. When Mr. Benson became keeper in 1944, there were about 40 sheep on the island. These belonged to the former keeper and since they could not be taken off until August or September, the terns failed to raise any young that year. Needless to say, the vegetation on the island was close-cropped and much of it was destroyed completely. In 1945, the birds returned and nested successfully and by 1946 they were present in larger numbers than Benson had ever seen them, although he had worked as assistant keeper or had visited the island during a period of many years. In 1946, the vegetation was still low, but by 1947 it reached a height of about 40 inches, which caused the permanent residents to talk about the island being the "weediest" they had seen it. This was probably due to the lack of grazing animals (except for one cow), and to the fertilizer contributed by the 40 sheep which were taken off in 1944.

In 1948, a decline in the island vegetation began (with the aid of four sheep) and the yarrow was four to six inches shorter at blooming time than in 1947. Four sheep were still present in 1949 and the yarrow was only a few inches high when we arrived on July 6. It then had only about two more weeks to reach maximum height which probably was much lower than in 1948. In addition, much yarrow had been supplanted by *Rumex acetosella* and grasses.

Several methods of making a census of the breeding Arctic Terns on Machias Seal Island in 1947 and 1948 were considered but only one method seemed practical. This was an indirect method which used data obtained from the mortality studies and "saturation" banding of young. The majority of birds banded were banded close to fledging age when mortality was slight. Banding was done systematically by moving up and down marked lines which extended from the center of the island to the edge of the nesting area. When a complete circuit of the island had been made in this manner, a second circuit was made and so on. With each succeeding circuit of the island, fewer young were banded until the bandings per unit of effort approached almost zero and it was estimated that practically all young on the island had been banded. During the process of banding, bands were removed from the few dead chicks found and placed on live chicks. The total breeding adult population was then figured by using the number of chicks fledged by the total pairs nesting in the survival study areas as an index.

In 1947, the number of juvenals banded was 1,281 which were all that could be found. From this and the fact that 150 pairs in the study areas fledged 66 young, it was calculated that the breeding adult population was approximately 2,900 pairs.

A total of 1,592 juvenals were banded in 1948 but we could have banded about 300 more if we had had more bands. Since 75 pairs fledged 41 young, this indicated that the total breeding adult population was around 3,450 pairs.

The limitations of statistical reliability of such figures are obvious but they do allow some means, better than guessing, for comparing the populations of the two years.

Our party banded 1,384 juvenals in early July, 1949, and Dr. and Mrs. Southgate Hoyt banded 308 more in the latter part of the month. Since our three-day banding effort by no means included all birds bandable at that time, and since some birds fledged before the Hoyts arrived, I am reasonably sure that the colony was as large or larger in 1949 than it was in 1948. The weather in 1949 was much like that of 1948 and success in rearing young seemed to be good.

During the fall and winter following a banding season, Allison Benson, son of the keeper, searched for bands on skeletons or on crippled young left on the island. He found 22 bands after the 1947 season and 27 after the 1948 season. Most of these bands were taken from juvenals which had broken wings. They had probably received these injuries in flying, so this would not alter the population estimates.

The steady increase in the size of the breeding population from 1945 through 1949 might have been prevented if the high vegetation of 1947 had continued to persist or if the Laughing Gulls which nested on the island in 1948 had renested and increased the following year. The vegetational change from 1947 to 1948 showed up in the great increase of nesting material in nests of 1948. The material was mostly stems of dead yarrow left from the year before. It was also noticed that some 1948 nests were formed of rings of dried bits of sheep dung.

Common Terns showed some increase during the three years. In 1947 a total of 42 young were banded. Common Terns were not banded after the band supply ran low in 1948, but 40 had been banded up until that time. A total of 110 young Common Terns were banded on the island in 1949. The Common Tern has pressed back and replaced the Arctic Tern in several localities in Great Britain (Robinson, 1920, 1921a, 1921b) but it is unlikely that this will occur on Machias Seal Island unless the vegetation increases for a period of several years.

"INTERNAL FACTORS"

Thus far, mainly "external factors," or factors of the outside environment, have been considered as affecting tern populations. "Internal factors," or factors within the behavior of the species itself, are also important.

The certain threshold of numbers necessary for successful breeding in many species of Laridae (Darling 1938) is a factor of this sort. Palmer (1941: 101) has already mentioned that Arctic Terns which nest singly on the tundra near Churchill, Manitoba, gather together for social flights which probably result in necessary sensory stimulation.

Darling's idea that the larger the colony, the earlier and more successful the breeding, was borne out by the attempted breeding of Arctic Terns on Gull Rock in 1948. These birds nested later (still laying on June 20) than the birds on Machias Seal Island and did not reach numbers exceeding 20 pairs. By July 16 all eggs had disappeared from Gull Rock and no young were found. These birds were close enough to take part in social flights with birds from the main island so their failure may have been due partly to small numbers and partly to the presence of a pair of nesting Herring Gulls and other roosting gulls on the smaller island.

Townsend (1923) tells of a population of 1,000 pairs of terns on this rock, equal to the number breeding on the main island at that time. These were either driven off by gulls or otherwise found conditions better on the main island for no terns have nested on Gull Rock for some time. Pettingill (1936) found that six pairs of Herring Gulls (presumably in 1935) had replaced the terns on this rock and thought that they would have a bad effect on terns on the main island if not checked.

The inability of terns to compete with gulls is thought by Tinbergen (1932) to be due to the unadaptability of terns under changing conditions. There are other "internal factors" which affect population, such as infertility, breakage of eggs and maltreatment of chicks, but these are of small importance individually as compared with the basic psychic make-up of the birds as mentioned by Tinbergen.

One other "internal factor" which is important is the age composition of the breeding population. Austin, Sr. (1945) has shown for the Common Tern that the behavior pattern and success of the whole colony depends to some degree upon the influence of older breeders which have nested in the same locality over a period of time.

MANAGEMENT

The probability of the management of sea birds to obtain their eggs as food for human consumption is not entirely remote, but most management that takes place in the near future more likely will be for aesthetic reasons. Management of this type has already been carried out with success by the Austin Ornithological Research Station on Cape

Cod. Tern breeding areas which had become overgrown were at first reclaimed by removing the vegetation by hand, although plowing, harrowing and raking were recognized as a better answer. Later, tractors were employed in this work, much of which took place on Tern Island which is sandy. The terns responded by decreasing nest concentration, thus decreasing mortality due to internal strife and allowing more area for nesting in general.

In addition, debris, wreckage and shacks which harbored rats were eliminated and red squill was planted generously. (Austin, Sr. 1934, 1940, 1946; Floyd 1938).

Hundreds of terns, including 10 pairs of Arctic Terns, nested on a new area created by dredging at Cape Cod in 1947 (Austin Sr., 1948b).

Management of the Machias Seal Island ternery is unnecessary except for the possible fencing-in of domestic animals which show signs of doing damage to the terns. The central part of the island (see figure 2) has much grass which could be used by grazing animals. This area is not used by terns, sheep or cows because of the presence of humans in the central area, but enclosed animals would be forced to use it.

Management at Matinicus Rock, Maine, would be beneficial. U. S. Coast Guard personnel allowed cats to run free there during the second World War. These cats became feral and were credited with the destruction of the large tern colony which formerly existed there. It is said that rats also inhabit the island. Extermination of these predators should eventually bring back the terns, but to my knowledge such a program has not been undertaken.

SUMMARY

Arctic Terns are principally deep water feeders but adapt readily to changes in food supply. Insects become important in the diet when abundant.

Weather and light affect food procuring and social activity. The Arctic Tern depends less on water for food than the Common Tern, but most of its food is taken from the sea. Water is also important for bathing.

Nesting sites with little vegetation are most desirable. A change to high vegetation in a breeding area will often prevent Arctic Terns from breeding in that spot, either directly for mechanical reasons, or indirectly by favoring species better adapted to higher vegetation.

Associates include a great variety of other charadriiform and anseriform birds. There is evidence of commensalism in which Old-squaws and Tufted Ducks, especially, are benefited by nesting in Arctic Tern colonies.

Important predators include gulls, hawks, jaegers and some mammals. Jaegers and Sabine's Gull tend toward being parasitic on the Arctic Tern.

The Mallophaga of the Arctic Tern indicate that it is more closely related to the Antarctic Tern than to the Common Tern.

Arctic Terns lay smaller clutches in the Bay of Fundy area than they do in arctic or sub-arctic regions. Clutch-size for the species averages under two eggs. This is significant, for the species seems incapable of

raising more than one chick per pair of adults, at least at the Machias Seal Island colony. The incubation period for individual marked eggs of the Arctic Tern at Machias Seal Island is 22 days. Not all of the birds delay incubation until the clutch is complete. Clutch-size does not affect hatching success but two-egg clutches and one-chick broods contain the optimum number for fledging success. The fledging success (Table IV) for the combined years 1947 and 1948 was 34.7 per cent figured on the total number of eggs. However, 47.6 per cent of the breeding pairs succeeded in fledging a chick.

Non-breeding in the Arctic caused by late summers, ecological changes in the ternery, "internal" factors and predation, reduce populations. Egging probably has a serious effect on populations only in primitive areas.

Estimates based on average fledging success and banding of essentially all young ready to fledge placed populations for the Machias Seal Island colony at approximately 2,900 pairs for 1947 and 3,450 pairs for 1948. The population appeared to be as large or larger in 1949.

Suggestions for management include control of vegetation and predators, including domestic animals.

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A SEROLOGICAL SURVEY OF ORNITHOSIS IN BIRD BANDERS*

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INTRODUCTION

Ornithosis is a chlamydial (somewhat virus-like) disease occurring at times among birds of many species including pheasants, chickens, pigeons, turkeys, ducks, certain wading birds and even fulmars. It is related to, and may be identical with, psittacosis which occurs in psittacine birds. All avian species tested to date have been found to be susceptible to infection by experimental inoculation. There have been well-marked epidemics associated with commercial enterprises such as breeding aviaries, transport agencies, poultry and pheasant farms and poultry-processing plants. It has occurred also among bird hunters in Louisiana. Infection of human beings by the causative agent may be followed by mild or severe illness or may not be attended by clinical symptoms.

Little is known of the occurrence of ornithosis in the native wild avifauna of the United States. Only the Herring Gull, Snowy Egret, Willet, Magpie, Painted Bunting and Goldfinch have thus far been found naturally infected. If the disease exists among the hundreds of other native species to any appreciable extent, especially among other

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