TRANSACTIONS
OF THE
LINNAEAN SOCIETY
OF
NEW YORK

Volume IX

Colonial Waterbird Group

2nd Annual Meeting

October 20-23, 1978

Invited Papers

New York

December 1980

THE LINNAEAN SOCIETY OF NEW YORK

The Linnaean Society of New York, organized in 1878, is the second oldest of existing American ornithological societies. Regular meetings of the Society are held on the second and fourth Tuesdays of each month from September to May (fourth Tuesday only in March), inclusive. Informal meetings are held at least once a month during June, July, and August. All meetings are open to the public and are held at the American Museum of Natural History.

Persons interested in natural history are eligible for election to membership in the Society.

The Society conducts field trips and maintains a circulating library for its members. It distributes free to all members a monthly *News-Letter,* and every few years an issue of *Proceedings* containing longer articles and notes of ornithological interest. At irregular intervals the Society publishes longer papers and monographs called *Transactions,* which members receive free or at a substantial discount.

Communications should be addressed to:

Secretary, Linnaean Society of New York
15 West 77th Street
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The following publications may be ordered from the Secretary of the Society:

The Species of Middle American Birds, by Eugene Eisenmann. Trans. Linnaean Soc. N.Y., vol. VII, 128 pp. 1955. A list of all species known to occur from Mexico to Panama inclusive, with scientific and English names, outline of distribution, and annotated regional bibliography.

Development of Behavior in Precocial Birds, by Margaret Morse Nice. Trans. Linnaean Soc. N.Y., vol. VIII, 211 pp., including 19 illustrations, bibliography, two indices. 1962.

Other publications of the Linnaean Society of New York are available from the Secretary.

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Contents

A paper by Rudolph Drent was delivered at the symposium but was not submitted for publication.

FOREWORD

The Linnaean Society of New York was founded in 1878 for the study and enjoyment of natural history in general, and of birds in particular. When the Society's centennial year approached, it was decided to mark its hundredth anniversary by serving as host to the Colonial Waterbird Group's second annual meeting.

The papers published here were invited by the organizers of that meeting. Other papers, volunteered for presentation at the symposium, have been published separately by the Colonial Waterbird Group.

The preceding volume of the Transactions of the Linnaean Society of New York was *Development of Behavior in Precocial Birds* by Margaret Morse Nice (1962), the eighth in a series that began in 1882 with an article on the vertebrates of the Adirondacks by C. Hart Merriam, a study of the winter range of the Fish Crow by William Dutcher, and a review by Eugene P. Bicknell of the summer birds of an area of the Catskills from which he described, in the same year, Bicknell's Thrush. The series has continued with works by Niko Tinbergen and Eugene Eisenmann, as well as Nice's classic *Studies in the Life History of the Song Sparrow* (1937, 1943).

This ninth volume of Transactions testifies to the Linnaean Society's continuing commitment to the support of research in ornithology.

Robert O. Paxton
President

ACKNOWLEDGMENTS

The Centennial Committee of the Linnaean Society of New York takes this opportunity to thank those who participated in the symposium and contributed the papers that appear in this volume. The Linnaean Society of New York was pleased to host the second annual meeting of the Colonial Waterbird Group and to sponsor the symposium as the final event of its Centennial Year. We were pleased to be able to meet at the American Museum of Natural History and to enjoy the excellent facilities provided by the Museum.

As Chairman of the Centennial Committee, I would like to thank the Committee members as well as all those members of the Linnaean Society of New York who helped make the Centennial Year a success. We are fortunate to have marked a moment in the Society's history, and wish it well as it embarks on its second century of dedication to and enthusiasm for birds.

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We thank the individuals and organizations listed below for their support of the Linnaean Society Centennial year. A National Science Foundation Grant was awarded to the Linnaean Society to sponsor the symposium on Colonial Species of Waterbirds, which began the second annual meeting of the Colonial Waterbird Group, the final event of the Centennial year. The papers given at the symposium appear in this volume, and we thank the Scherman Foundation, Inc. for support for this publication.

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Editor's Note

The members of the Editorial Committee who participated in the preparation for publication of this volume of the *Transactions* were Eugene Eisenmann, John Farrand, Jr., and Susan Wernert. I am grateful to them, and to Helen Hays for her helpful comments and suggestions.

I would also like to express my appreciation to those who assisted in the publication of these transactions—Catherine Pessino, my predecessor as Editor, Berry Baker, Mary LeCroy, and Elinor Conklin, who transcribed the Comments at the symposium.

MARC WEINBERGER

THE HABITATS, DISTRIBUTION, AND NUMBERS OF NORTHERN SEABIRDS

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It is a pleasure to be asked to address one of the more original as well as lively of the groups formed to study waterbirds around the world. This is especially the case when the meeting commemorates the centenary of the Linnaean Society of a great city, which has chosen to promote the study of seabirds, and when it takes place in the magnificent and enlightened museum which has done so much to assist the ornithologists of other countries as well as its own. It was, moreover, one of its many distinguished staff, Robert Cushman Murphy, who has made the greatest single contribution to the study of seabirds, notably in his classic book "The Oceanic Birds of South America," published by the museum in 1936. I am making use of this opportunity to enlarge upon details of the phenomena he expounded, originally discussed at the conference on "Seabirds of the North Atlantic" at Aberdeen in March 1977 (Bourne, 1978).

General Considerations

The general character of seabird communities and their ecology is now well-known. The families form an adaptive radiation of predators feeding upon the marine food chains. The species tend to show a largely complementary zonal type of distribution, both outward from the coast (Wynne-Edwards, 1935) and in different latitudes (Murphy, 1936). The largest concentrations of birds are found along shallow, irregular coastlines with large tidal fluctuations in sea level on the one hand, and where water welling up from the ocean depths brings nutrient salts to the surface to support an increased biological activity out at sea on the other, as expounded by Hutchinson (1950) in another remarkable publication from this museum. This upwelling is particularly marked where the prevailing wind blows the surface water offshore along the lee side of land masses (Fig. 1) including in low latitudes the western coasts of the Americas, Africa, and Australia, and also those affected by the monsoons around the Arabian Sea, and in higher ones off the east coasts of the Americas, Asia, Australia, and also Scotland. It seems to have escaped much comment that an equally rich coastal avifauna is also found in these areas because the tide also tends to bring the enriched water inshore.

The whole situation in the great areas of upwelling is infinitely complex and variable

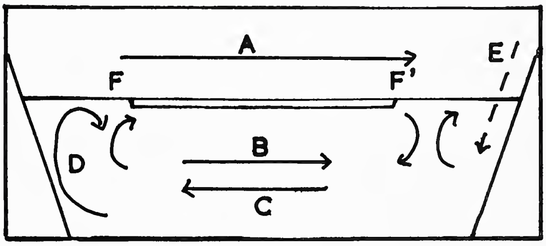

Figure 1: Circulation of water in the oceans A: prevailing wind. B: associated drift of surface water. C: compensating current in the ocean depths. D: cold upwelling current on upwind coast; it is dense, and soon sinks again, to be replaced by further upwelling. E: rainwater running off wet downwind coast; in summer it is warm and light and spreads on top of salt water. F-F′ Stratified water with thermocline and boundary front in center of ocean in summer, mixed by gales in winter in high latitudes. (The situation is complicated by the horizontal circulation.) The largest seabird concentrations are found in the areas of water mixing offshore.

(Bailey, 1971; Brown, 1979), and I cannot make much further contribution to its study here; it deserves much more attention, of the type which it is currently receiving in South Africa in particular. The problem which came to exercise me is why, if it is popularly supposed that most seabirds occur in the great areas of upwelling, there are an equal number along the European coasts washed by comparatively unproductive water from the tropics which has crossed the North Atlantic on the surface. It might be partly explained by its enrichment by water carrying nutrients from the land (Fig. 1), or the development of the type of annual cycle characteristic of high latitudes where fertility accumulates in water mixed by storms during the long dark winter to give rise to a burst of growth in the summer (though it is completed during the spring in Britain), but this was an incomplete explanation. This paper represents one stage in the formulation of a fuller one, while it also seems useful to make more easily available some estimates by Uspenski (1959) of the size of U.S.S.R. seabird populations and add comparable figures where they are available for the rest of the northern regions (see the Appendix).

In general, according to familiar geographical principles the rotation of the earth leads to a regular circulation of its air and water, to the west in both low and high latitudes and to the east in middle ones and near the equator. In the larger enclosed oceans an anticyclone tends to develop in the center of the part lying in each hemisphere, and the air and water circulate around it, clockwise in the northern hemisphere and counterclockwise in the south, owing to the operation of the Coriolis force due to the rotation of the earth, which causes currents to diverge to the right in the northern hemisphere and left in the southern. This is generally accepted on a large scale, and yet one sees little discussion of its local consequences, which are that a coastal current is likely to enter an inlet on the righthand side, looking in, in the northern hemisphere and on the left in the southern, and to leave on the opposite side. This has important implications for both the coastal topography and ecology of the area, expressed diagrammatically in Fig. 2.

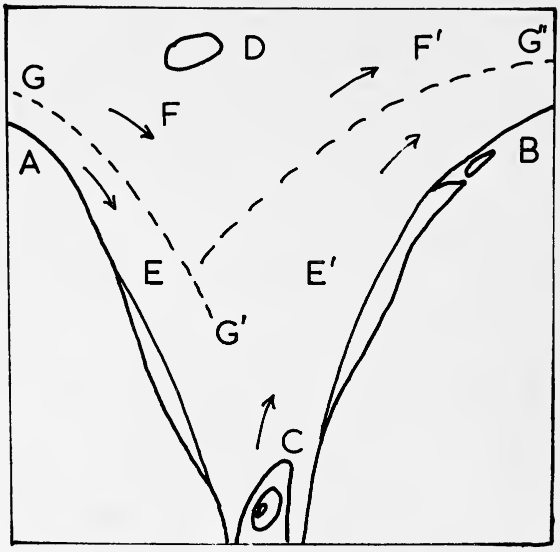

Figure 2: Circulation of water in a coastal inlet in the northern hemisphere. A: eroding coast with cliff-formation and oceanic water close to shore. Pelagic birds feed at sea and breed on the cliffs. B: accreting coast with mudflats and a spit leading to a barrier beach enclosing a lagoon where it is exposed to wave action. Coastal birds feed on the shore and in the turbid water and breed on the shore and round the lagoon. C: river mouth with delta containing lagoon. Estuarine species feed around the channel and breed on the marshes and especially islets in the lagoon. D: offshore islet, another breeding site for both coastal and pelagic birds, which feed in surrounding area of turbulence in offshore current. E-E′: coastal current, composed of sea-water mixed with fresh water from land in centre of inlet. F-F′: stratified oceanic water of open ocean, also moving along coast. G-G′: front marking boundary between stratified water offshore and mixed coastal water, where thermocline reaches surface, with local mixing; high plankton productivity, many fish and seabirds.

If we now consider the water of the sea, it varies considerably in its density due to variations in its temperature and salinity, and tends to become divided into distinct, comparatively uniform water masses of different origins which meet each other at sharp boundaries. These tend to be regions of high marine productivity comparable to the coast, though different in nature, because a redistribution of the salts and gases essential for life occurs there. Basically, water cooled and diluted by melting ice and mixed by storms sinks in the polar regions and flows through the ocean depths, accumulating nutrient salts to reappear in the subtropical areas of upwelling, where at first it supports a high level of biological activity. Then the nutrients are exhausted and the water concentrated by evaporation as it flows around the subtropical anticyclones, and some sinks again in the center, while the rest returns to high latitudes on the surface. The uppermost layer shows an extreme form of this trend, and comes to be separated from the cooler, more fertile underlying water at a sharp horizontal boundary, the thermocline, where apparently much of the biological activity of the open sea takes place.

The regularity of this circulation may be disturbed by many factors, which generally tend to lead to more mixing and biological activity. The first water to reach the surface in an area of upwelling may be too cold and dense to remain there, so it may sink again, leading to further compensatory upwelling and turbulence downstream. Distinct vertical fronts may form out at sea where different water masses are brought into contact by ocean currents, or where eddies pass along these currents or form in the lee of islands, or where the stratified oceanic water meets that mixed by coastal currents offshore and a front develops where the thermocline reaches the surface. There is likely to be an increased vertical circulation of the water in such regions, sinking predominating and floating matter (including oil pollution) accumulating where currents converge, and upwelling with increased productivity where they diverge. Turbulence in currents leading to increased productivity may also occur where currents flow past islands or irregularities of the coastline or ocean floor, though the consequences may not become evident until the marine food chains have had time to develop downstream. Thus, for example, possibly many of the benefits of water mixing off the west and north coasts of Britain are felt only when the water is passing down the east coast into the North Sea, with its rich fisheries and seabird community.

The action of the sea has a characteristic effect on the shore which has also received little attention from ornithologists (Fig. 2). Exposed coasts tend to have a small tidal fluctuation but to be severely eroded by wave action, which results in the formation of cliffs along resistant shores and sterile barrier beaches elsewhere, notably around islands and headlands and where coastal currents are setting into inlets. The more marine birds are liable to gather to nest here and feed offshore. The eroded material tends to be washed into sheltered inlets and deposited there with the fertile detritus brought down by rivers and precipitated on contact with salt water, to form a stable, accreting shore exposed to greater tidal fluctuations, and with a richer intertidal life. In such situations, the shore builds up to form salt marshes, and lagoons become impounded to provide breeding sites for a larger community of coastal birds, while it becomes difficult for birds to see the fish offshore because the water is turbid. The ecological pattern summarized in Fig. 2 is repeated in this way all up the coast of Europe, reaching its climax in the North Sea with vast seabird colonies overlooking the inflow of Atlantic water in the northwest, and huge mudflats supporting a large part of the European shorebird and wildfowl population in the southeast (Bourne, 1974, 1976a).

BIRDS AT SEA

Birds have a limited number of options for exploiting the sea. They can feed along the shore, which was doubtless the primitive situation and which I would no longer include within my terms of reference if a number of particularly versatile and successful groups such as the gulls did not still do it. Or they can feed from the air or in the water. Prolonged flight requires a long wing and a light build to permit economical soaring incompatible with easy maneuvering in the water, whereas agile swimming requires a streamlined muscular build with strong legs set far back and short wings to reduce drag, which make aquatic birds clumsy in the air, while neither type is very agile on land. The strategy or combination of strategies adopted varies with circumstances, the aquatic habit proving more successful where many birds gather to compete for dense but deeply-swimming food, whereas the aerial habit is more successful where the birds are feeding over both land and sea or are seeking widely but thinly dispersed food. Some groups, such as the sulids and shearwaters, clumsily combine the two habits (Bourne, 1976b, Brown *et al*, 1978).

Within these broad categories of adaptation, seabirds may adopt a variety of hunting techniques analyzed by Ashmole (1971). They include the collection of inert or drifting foods, stalking and surprising or pursuing agile prey, its capture where it is brought to them by currents or submarine predators, parasitism, and scavenging. Different age groups and even sexes within the population may behave differently. While the gulls show an exceptional amount of individual variation in their feeding behavior, possibly one reason for their success, clumsy young birds commonly feed differently from the more agile adults (Phillips, 1962). Similarly the small, agile male Blue-footed Boobies *Sula nebouxii* feed differently from the large, clumsy females (Nelson, 1978). Young seabirds commonly migrate further than adults, and may not return to the breeding area for several years, gathering elsewhere in the breeding season. This not only helps reduce intraspecific competition for food between the generations in the breeding area, but also leads to a dispersal of the population of large, long-lived species with a low reproductive rate at a time when a large part of it is dangerously prone to concentrate at a few overcrowded breeding places, where they are vulnerable to purely local disasters.

I have already compared and contrasted the seabird communities of two subtropical upwelling areas on opposite sides of Africa and discussed the way in which they fit into the general pattern of seabird distribution (Bourne, 1963), and they have been studied in detail by Bailey (1971) and Brown (1979). Now that more information is becoming available it may also be useful to consider the situation in the northern oceans, summarized in the Appendix. In the first place, if we take the distribution of seabirds as a whole, summarized in Table 1, it will be seen that while by far the richest community is found in the circumpolar southern ocean, with over a hundred breeding species overall (depending how they are classified), the next richest community is found in the eastern North Pacific with 54 species, followed by the eastern North Atlantic with 37, and the tropical oceans with only about 30. Thus the northern oceans are by no means a barren habitat compared even with the southern hemisphere, supporting in excess of 100 million birds (see the Appendix)—half of them endemic large auks to match the southern penguins and more than an eighth each gulls, small auks, and storm-petrels, with nearly as many petrels, mainly Northern Fulmars (*Fulmarus glacialis*), and a residue of cormorants and Northern Gannets (*Morus bassanus*).

It is notable that while many southern seabirds have a circumpolar range, and there is a considerable similarity between the seabird communities of the tropical oceans, the birds of the opposite sides of each tropical ocean are often more similar to those of the adjacent parts of neighboring oceans than they are to each other. Thus, for example, the birds of the eastern tropical Pacific are more similar to those of the western Atlantic than to those of the western Pacific, while the birds of the western Pacific have a closer resemblance to those of the Indian Ocean than to those of the east Pacific (Bourne, 1976b, table 1). This is presumably a consequence of the free communication that existed between the tropical oceans in the geologically recent past, and the difficulty experienced by many species in crossing the central expanse of open ocean to establish colonies under ecologically different conditions on the far side, especially in the wide east-central Pacific. It is also notable that the South Atlantic has several species found in the Indian Ocean but not the North Atlantic, notably the Greater and Lesser Frigate birds (*Fregata minor* and *F. ariel*) and the Trinidad Petrel (*Pterodroma arminjoniana*) on South Trinidade, which suggests the existence of a warm-water connection south of the Cape of Good Hope in the past; there were once even more Indian Ocean species on St. Helena (Olson, 1975).

In contrast to the situation in the tropics, where water gaps appear to have formed a more important isolating mechanism than pres-

TABLE 1
Distribution of Breeding Seabirds

Group	Southern Ocean	Indian Ocean	Tropical Pacific		Tropical Atlantic		North Pacific		North Atlantic		Total
			W	E	W	E	W	E	W	E	
Penguins	13	—	—	2	—	—	—	—	—	—	15
Albatrosses	9	—	—	1	—	—	3	2	—	—	13
Petrels	41	6	9	2	3	1	6	7	2	6	56
Storm-petrels	5	—	1	5	—	1	6	8	1	4	21
Diving-petrels	3	—	—	1	—	—	—	—	—	—	4
Tropic-birds	—	3	2	1	2	2	—	—	—	—	3
Frigate-birds	—	3	2	2	3	2	—	—	—	—	5
Sulids	2	4	3	5	3	3	—	—	1	1	9
Cormorants	16	4	1	4	1	2	4	4	2	2	28
Skuas	2	—	—	—	—	—	1	1	1	2	3
Gulls	7	2	1	3	—	1	7	12	6	10	33
Terns	10	11	12	6	14	9	3	5	6	5	37
Small alcids	—	—	—	—	—	—	8	9	1	1	11
Puffins	—	—	—	—	—	—	3	3	1	1	4
Black Guillemots	—	—	—	—	—	—	2	1	1	1	3
Large auks	—	—	—	—	—	—	2	2	4	4	4
Total	108	33	31	32	26	21	45	54	26	37	249
Percent	43	13	12	13	10	8	18	22	10	15	100
Percent of same species in ocean:											
to west		27	61	28	46	68	22	56	56	69	
to east		56	29	37	58	64	68	30	93	25	

ent dry land, there is a greater similarity between the seabird communities of opposite sides of the two northern oceans than there is between the adjacent parts of different oceans, despite the fact that they once formed part of a single Tethys Sea, were in communication until comparatively recently through the Strait of Panama, and still are through the Arctic Ocean. It would appear that while the tropical oceans are comparatively uniform in character, the differences between the northern oceans have had a much more marked influence on the manner of development of their seabird communities. It is notable that in both of them the greatest number and diversity of birds are found in the east, whereas if we ignore the influence of the Humboldt Current in encouraging the establishment of a cool-water avifauna off Peru, in the tropics the largest community is found in the west of each ocean.

In general the North Pacific is large, deep, and geologically ancient, with a well-developed wind and current system at sea, but with poorly developed continental shelves. While it has a large and varied seabird community, this includes a preponderance of either coastal or pelagic types, notably large endemic radiations of plankton-eating alcids in the north and fork-tailed *Oceanodroma* storm-petrels in lower latitudes, and a smaller one of cephalopod-eating albatrosses out at sea, though it has comparatively few large fish-eating auks and no fish-eating gannets. In contrast the North Atlantic is a smaller, geologically recent ocean with wide continental shelves and a rather confused wind and current system extending into the Arctic Ocean. It has only one rather distinct endemic small alcid in the Arctic, and an even more distinct endemic storm-petrel in western Europe, to compare with the large radiations of these two groups in the North Pacific. But on the other hand, until the Great Auk (*Alca impennis*) was exterminated by man, the North Atlantic had two large fish-eating auks in addition to the two also found in the North Pacific, and a highly conspicuous gannet in the place of the North Pacific albatrosses, which were once present but died out at the end of the Tertiary. I find it rather odd that in the course of his comparison of the alcid communities of the two oceans Cody (1973) did not notice these much more fundamental differences.

While the pattern of water circulation and bird distribution in the higher latitudes of the northern oceans is to some extent a mirror image of that found in lower latitudes, or, to be precise, the top half of the figure-eight, there are some interesting differences. While cold water from the polar regions now enters the area on the surface in the west and sinks instead of welling up from the ocean depths in the east, with much water mixing again leading to a high marine productivity supporting a large bird population, the surface water emerging from the area of mixing flows east before the westerlies instead of west before the trade winds. In the Atlantic it then mixes with the European coastal water in frontal regions offshore and in the centers of the inlets of the region in the way already described (Fig. 2), before flowing up the coast of Europe into the Arctic Ocean. Infrared satellite photographs suggest that there is an fact a good deal of upwelling here, cooling the surface water where the prevailing west wind blows offshore along the east coast of Britain and the archipelagos to the north, which may help explain the occurrence of even larger concentrations of breeding seabirds here than in the cool current area in the north-west Atlantic (see the Appendix).

The ecological relationships between species in these northern seabird communities are both complex and variable. Off Britain in summer many species may be found taking the same foods, such as sand-eels (*Ammodytes* sp.,) and small clupeid and gadoid fish (Pearson, 1968), often feeding together in different ways over the same fish shoals, but the food of one species, such as the Atlantic Puffin (*Fratercula arctica*), is likely to vary over the course of time with effects on the welfare of its young (Harris and Hislop, 1978). This now seems most likely to explain the periodic fluctuations in its numbers, which over a long period appear to bear a reciprocal relationship to those of another more southerly fish-eating species, the Manx Shearwater (*Puffinus puffinus*) (Bourne and Harris, 1979). There is still little information about what happens when the competition for a declining food supply becomes more intense, in the winter, and it seems possible that differences in feeding technique and pattern of dispersal of the type debated by Cody (1973) and Bedard (1976), and also the activity of the fishing industry in providing extra food (Bourne, 1966), may then become more important. For example, in the North Atlantic, the Common Murre or Guillemot (*Uria aalge*) tends to remain comparatively sedentary, while the structurally similar Razorbill (*Alca torda*) tends to migrate south, and the Puffin disperses at sea at that time (Mead, 1974).

While seabird ecology is probably not as simple as is sometimes suggested, it is possible to discern some trends. One is toward the concentration of breeding adults (but not their young) at the colonies—which may be few in number for pelagic species, but more numerous and less stable for coastal ones—at the most suitable season for breeding, which in high latitudes is normally the summer. However, it may be noted that the North Pacific albatrosses in particular nest in the lowest latitudes of their range in the winter. Many different factors could combine to explain this, including a southern origin for the birds, an absence of suitable breeding sites farther north, and the need to have the young fledged in time to take advantage of the summer increase in food supply; some of the subtropical gadfly petrels of the genus *Pterodroma*, which also come from the south and have long breeding cycles, behave similarly.

One consideration revealed by the concentration of birds at the breeding colonies, and especially by the amount of time that they spend sitting about idly displaying there, is that food must be superabundant in the vicinity. Indeed, they can often be seen to collect as much as they can use nearby in a few minutes, and clearly often the only factor limiting their numbers is overcrowding (Ashmole, 1963). Their frequently high breeding success and the usual absence of any adult mortality not due to predation, accidents, and disease provide further evidence for this. It is now becoming evident from beach surveys that in fact most mortality occurs outside the breeding season, and in high latitudes in the late winter. Originally it was usually attributed to bad weather, which is certainly sometimes important both for itself and for bringing bodies ashore, but normal birds are adapted to survive it. It is becoming increasingly clear that there are usually underlying factors to explain such mortality, such as a food failure at sea, disease, poisoning by toxic micro-organisms, losses in fish nets, and pollution by oil or toxic chemicals (Bourne, 1976c), though these are also usually local phenomena whose effect on widely dispersed species can be overrated.

Another consideration revealed by a closer acquaintance with birds at sea is that the interpretation of their ecology in terms of a zonal type of distribution of groups of specialized feeders, such as I described initially, is often an oversimplification. Marine phenomena such as upwelling tend to be very patchy, especially along an irregular coastline such as that of western Europe, and the distribution of seabirds is liable to become even more patchy as a result of their tendency to gather to feed socially together over concentrated sources of food such as fish shoals and around fishing boats. In such circumstances, while the idea of a zonal type of distribution may still remain a useful concept, that of an association of birds characteristic of a specific situation may sometimes be more appropriate.

Thus, off northern Britain it is possible to distinguish a group of species which are most numerous in summer in limited areas close to the frontal developments off the west coast and in the center of inlets, where they feed on plankton and small fish—a group which includes the storm-petrels, Manx Shearwater, and Atlantic Puffin; an association of widespread mobile aerial plankton eaters commonest out at sea, notably the Northern Fulmar and Black-legged Kittiwake (*Rissa tridactyla*); an association of widespread species feeding on larger fish which are most numerous offshore, including the large auks and Gannet; and an association of species feeding along the coast, including the other gulls, the terns, the cormorants, and the Black Guillemot (*Cepphus grylle*). However, not only do some of these range very widely, but also in recent times a cross section of the more aerial species, including all the gulls, the fulmar, the Gannet, and some of the shearwaters, have taken to feeding behind fishing boats, though most of the more aquatic species are still scarce there.

The situation is still developing, and not only has the number of scavenging Gannets continued to increase in recent years, but also other more aquatic species such as the Common Murre and the Shag (*Phalacrocorax aristotelis*) are beginning to show an interest in such opportunities in some areas as well; it would be useful to have more comparative information from other parts of the world. At the present time the activities of fishermen are clearly beneficial to birds in western Europe, making food from the depths available in the surface waters, and all the more conspicuous scavengers are increasing in numbers. It is possible that in the course of time, with the development of industrial fishing and the more efficient use of fish offal which is at present discarded, the situation may be reversed, as it has been off Peru (Schaefer, 1970; Paulik, 1970) and South Africa (Crawford and Shelton, 1979), especially if the birds take nearly a third of the marine fish production, as calculated by Furness (1978). (But it seems possible that some of the factors he used, such as the feeding range, were underestimated, and that it is really much less.)

SEABIRDS ASHORE

It is well-known that seabirds tend to select certain characteristic nest sites which provide the maximum possible security without leading to unnecessary interspecific competition. There has been less discussion of the factors leading to the location of colonies. Often, of course, they are the only possible sites from which the birds can reach a particular food supply, as with many oceanic islands. Alternatively, the birds may escape the attention of predators by selecting at random from many possible sites, as when they disappear into South American deserts to breed. Frequently, however, there are certain overriding geographical considerations which determine what sites are available and how the birds can make use of them. For example, coral reefs will only grow above a certain water temperature and then they line all exposed shores, while in the wetter parts of the tropics all dry land is covered with vegetation, so that tropical seabirds are often compelled to nest on coral reefs or in vegetation in a way that would be impossible or hazardous in higher latitudes.

If we restrict ourselves to the consideration of the situation in high latitudes, seabirds again have a limited number of options. There are larger areas of potential breeding terrain in the northern hemisphere, but most of them are infested with a variety of predators, notably foxes, which render them unsafe. Therefore the birds are compelled to use such sites as offshore islands and sandbanks, and mainland cliffs, marshes, and moors, where predators cannot reach or find them. The situation was initially rather different in the southern hemisphere, where the natural sites were fewer but normally free of terrestrial predators (although the weather is usually even worse than in the northern hemisphere). It would appear that by far the worst harm caused by man to seabirds has been the introduction of alien predators to innumerable such places.

Within these limits the distribution of seabird breeding sites is likely to be determined by geological processes. Virtually the only breeding places available for most highly oceanic species are either volcanic oceanic islands or cliffs on exposed mainland coasts. Either is likely to have steep, unstable slopes and a life shorter than that of a bird species before it is eroded away, so that the bird must nest in some insecure niche and hope that an alternative site appears in time. The result is the familiar type of overcrowded seabird colony in which each species tenaciously clings to its own specialized corner, typically inhabited by the Alcidae; though members of several other groups also occur. It is notable that while the larger species usually nest in the open, presumably because they cannot find enough large safe holes, the smaller ones prefer holes, where they are safe from aerial predators and the weather. There is much room for speculation to what extent the availability of such sites is an important factor limiting seabird numbers in some areas.

In sharp contrast to this situation, more coastal species live in a milder environment where geological processes are more likely to lead to the deposition of sandbanks and formation of marshes than the upheaval of volcanic islands and erosion of cliffs, so that a different strategy is required. While there is no longer permanent security anywhere, temporary refuges may be found in many different places with the seasonal appearance and dissolution of islets and pools, and groups of birds now disperse to settle at any of a variety of sites and continue to use them as long as the site persists and remains undisturbed. Therefore, in contrast to the pelagic species, many gulls, terns, and Pelecaniformes have developed as mobile, opportunistic breeders, prepared to move at short notice among islets, cliffs, trees, beaches, tidal marshes, swamps, barren ground, and even artificial structures, though it appears few of them use burrows, which require solid terrain, take longer to establish, and can act as traps.

These familiar but little-considered phenomena raise a number of incidental problems. There is room for more study of the extent to which precise breeding-site preferences, and limitations on the supply of sites, are important factors limiting seabird numbers, the extent to which this has been affected by human activity (including the introduction of predators to undisturbed sites), and whether more could be done to rehabilitate lost sites or create alternatives. Initially, man caused most damage to seabirds simply by slaughtering them, and while this is now gradually being brought under control in civilized regions, the birds are confronted by two major new threats, the loss of their food supplies at sea and breeding sites on land. It seems doubtful whether ornithologists will ever be able to exercise much influence over world fishery policy, which seems likely to converge on the maintenance of sustained yields for birds as well as men in any case, but it seems possible that much more could be done for the welfare of often depleted local seabird populations and individually threatened species by more attention to the management of breeding sites (Bourne, 1972).

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COMMENTS

Nisbet: Do you have any opinion as to whether predation limits distribution of birds at sea? If a murre dives above a school of predatory fish, why doesn't it get eaten?

Bourne: There are a lot of difficulties to this. One used to assume that all the bodies of birds that died washed up on beaches. Looking at the evidence more critically, the things which wash up which aren't oiled usually seem to be fresh, so one has the impression that dead birds may not last very long at sea. We simply don't know what number of birds are living at sea, except that obviously they have a very good survival there. If you look at murre population dynamics and allow for the numbers that get killed immediately offshore by things like oil pollution and nets, they obviously must live almost indefinitely out at sea, so that there can't be much mortality over things like fish shoals. I've seen an account of a couple of Shags being killed by Gannets diving over a particularly dense shoal, but most of the time there seem to be very few accidents in these natural feeding flocks. Presumably the birds are obliged to take a certain amount of care. One of the suggestions was that one should go skin-diving amidst one of these flocks. However, one might have certain second thoughts about Gannets plunging in from 500 feet and Killer Whales underneath. Does one really wish to get mixed up in this particularly hectic-looking melée? I have the impression that natural mortality at sea is extremely low, that most of the predators would not find it very safe to depend on the supply of birds at sea because they are thinly distributed.

Nisbet: Could that be why not many tropical seabirds sit on the water where there are sharks?

Bourne: Yes, exactly. I think the other reason tropical seabirds do not often sit on the water is that the food is pretty scattered and they need to have high food density for an aquatic mode of approach to pay. Only when the food is dense do seabirds take to aquatic feeding as a major strategy. They do it off Peru, I think. There are aquatic feeders there—diving petrels and penguins.

Austin: And our lovely terns just don't go in at all. Sooty Terns, we believe, can't swim, they can barely float.

Nisbet: Does the floating oil collect in the slick at a front, or does the wind drift move it faster than the water current moving toward the front?

Bourne: My own impression is that the major consideration with floating oil is drift with the wind. Probably this applies to fronts as well. We only see these formed in calm weather in summer. The vast quantities of floating oil that Thor Heyerdahl saw from his raft drifting across the Atlantic are being interpreted to imply that the entire Atlantic is covered with tar balls. An alternative interpretation is that all the floating objects in the tropical Atlantic arrive at convergences, that both tar balls and raft were floating together along a convergence, and that he was seeing the maximum concentration of oil and not a random sample.

APPENDIX
The Breeding Seabirds of the Northern Seas

Area	Alcids Large	Medium	Small	Petrel	Storm-petrels	Gulls Large	Small	Cormor-ants	Gannet	Total
North France	2	—	—	+	1	85	2	4	6	100
Channel Islands	1	—	—	—	2	9	+	1	6	19
Southern England	11	—	—	3	2	63	10	5	—	94
Total English Channel	14	—	—	3	5	157	12	10	12	213
West England & Wales	54	+	—	300	10	220	18	3	32	637
Eastern Ireland	112	+	—	10	+	59	24	2	+	207
Total Irish Sea	166	+	—	310	10	279	42	5	32	844
East Scotland	324	1	—	13	—	202	283	7	18	848
East England	45	—	—	3	—	10	86	1	+	145
Netherlands	—	—	—	—	—	66	—	3	—	69
West Germany	2	—	—	+	—	37	1	+	—	40
East Germany	—	—	—	—	—	2	—	—	—	2
Poland, Lithuania, Latvia	—	—	—	—	—	1	—	—	—	1
Esthonia	—	+	—	—	—	7	—	—	—	7
Finland	2	3	—	—	—	14	—	—	—	19
Sweden	24	15	—	—	—	150	+	+	—	189
Denmark	3	1	—	—	—	135	+	1	—	140
South Norway	84	10	—	2	—	208	196	26	1	527
Total North Sea & Baltic	484	30	—	18	—	832	566	38	19	1987
Western Ireland	31	1	—	71	100	53	61	45	43	405
Western Scotland	165	+	—	287	40	81	62	14	26	675
North Norway	2682	34	—	+	+	450	624	64	+	3854
Total Atlantic coasts	2878	35	—	358	140	584	747	123	69	4934
Outer Hebrides	500	1	—	125	100	54	61	45	43	929
Orkneys	360	5	—	94	50	29	256	8	8	810
Shetlands	400	5	—	134	50	15	86	18	20	728
Faroes	1466	8	—	1080	280	150	346	12	8	3350

Appendix (continued)

Area	Alcids Large	Medium	Small	Petrel	Storm-petrels	Gulls Large	Small	Cormorants	Gannet	Total
Jan Mayen	50	+	1	50	—	5	1	—	—	107
Bear Island	300	1	50	110	—	1	200	—	—	662
Total Atlantic Islands	3076	20	51	1593	480	254	950	83	79	6586
TOTAL W. PALEARCTIC	6618	85	51	2282	635	2106	2317	259	211	14564
Murman coast	60	1	—	—	—	8	30	1	—	100
Novaya Zemlya (W. coast)	2000	10	10	5	—	17	20	—	—	2062
Franz Josef Land	200	30	500	20	—	5	20	—	—	775
Other regions	—	1	—	—	—	5	—	—	—	6
Total Barents Sea	2260	42	510	25	—	35	70	1	—	2943
Total White Sea	1	2	—	—	—	10	—	—	—	13
Total Kara Sea	50	3	1	—	—	7	7	—	—	68
Svernaya Zemlya (E. coast)	—	30	150	—	—	1	15	—	—	196
Eastern Taimyr	60	2	—	—	—	1	30	—	—	93
Novosibirisk Is. (W. coast)	30	2	—	—	—	2	50	—	—	84
Other regions	—	—	—	—	—	5	—	—	—	5
Total Laptev Sea	90	34	150	—	—	9	95	—	—	378
De Long Is.	40	40	—	—	—	1	45	—	—	126
Wrangel I. (W. coast)	40	5	—	—	—	1	10	1	—	57
Other regions	—	1	—	—	—	6	1	—	—	8
Total East Siberian Sea	80	46	—	—	—	8	56	1	—	191
Wrangel I. (E. coast)	60	10	—	—	—	1	20	1	—	92
North Chukotsk coast	50	10	20	—	—	10	10	20	—	120
Total Chukotsk Sea	110	20	20	—	—	11	30	21	—	212
TOTAL N. PALEARCTIC	2591	147	681	25	—	80	258	23	—	3805

Ratmanov Is.	10	1	200	—	—	1	1	1	—	214
Komandorsky Is.	1600	10	7	2500	3	1	80	20	—	4221
E. and S. Chukotsk coasts Koryasky peninsula East Kamchatka	300	10	50	2	—	10	100	50	—	522
Total Bering Sea	1910	21	257	2502	3	12	181	71	—	4957
Kuriles	1500	20	50	1000	1000	20	400	200	—	4190
West Kamchatka	5	1	—	—	—	5	—	—	—	11
N. shore Okhotsk Sea	1000	10	10	—	—	20	?	100	—	1140
Shantarsky and Iony Is.	500	4	30	100	—	5	60	5	—	704
Sakhalin (N. and E.)	720	3	1	5	1	3	4	40	—	777
Total Okhotsk Sea (inc. E. coast Kuriles)	3725	38	91	1105	1001	53	464	345	—	6822
Sakhalin (W. coast)	17	1	—	—	—	1	10	5	—	34
Primorye Coast	30	5	—	—	1	5	5	30	—	76
Total Japanese Sea	47	6	—	—	1	6	15	35	—	110
TOTAL E. PALEARCTIC	5682	65	348	3607	1005	71	660	451	—	11889
TOTAL PALEARCTIC	14891	297	1080	5914	1640	2257	3235	733	211	30258
ICELAND	10000 +	20 +	+	1000 +	10 +	115	1000 +	13	40	12200+
TOTAL EAST NEARCTIC	10478	?	?	1072	?	500 +	234	56	65	12405
ALASKA	15700	1000	10000	2000	9000	530	2750	250	—	41230
TOTAL NORTHERN SEAS	52000 ?	2000 ?	12000 ?	10000 ?	14000 ?	5000 ?	7500 ?	1500 ?	316 ?	105000 ?

Totals in thousands of breeding individuals; those for north and east Palearctic from Uspenski (1959), those for Iceland estimated by Prof. A. Gardarsson, those for east Nearctic modified from Brown et al (1975), those for Alaska from Sowls et al (1978), with an allowance in the final total for additional birds in roughly the same proportions in Spitzbergen, western North America and Japan. Large auks include *Alca torda*, *Uria* sp., *Fratercula* sp., *Lunda cirrhata*, and *Cerorhinca monocerata*; medium auks *Cepphus* sp., *Synthliboramphus* and *Brachyrhamphus* sp.; small alcids *Alle alle*, *Ptychramphus aleuticus*, *Cyclorrhynchus psittacula*, *Aethia* sp.; petrels include *Fulmarus glacialis* and *Puffinus puffinus*; storm-petrels *Hydrobates pelagicus* and *Oceanodroma* sp.; large gulls *Larus hyperboreus*, *L. glaucescens*, *L. argentatus*, *L. fuscus*, *L. marinus* and *L. schistisagus*; small gulls *L. crassirostris* and *Rissa* sp.; cormorants include *Phalacrocorax carbo*, *P. auritus*, *P. aristotelis*, *P. pelagicus*, *P. urile* and *P. capillatus*; while the Gannet is *Morus bassanus*. A comparatively small number of birds breeding inland were not covered by the surveys.

THE PELAGIC ECOLOGY OF SEABIRDS*

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Abstract

Recent developments in the study of the pelagic ecology of seabirds are described, with particular emphasis on work off eastern Canada and in the eastern Canadian Arctic. Quantitative mapping can be used to provide insights into factors controlling seabird distributions. The distributions of Cory's Shearwater (*Puffinus diomedea*) and the Greater Shearwater (*P. gravis*) in the northwest and southwest Atlantic are compared; the very different summer and winter pelagic habitats of Wilson's Storm-Petrel (*Oceanites oceanicus*) are described. It is suggested that the distributions of the Northern Fulmar (*Fulmarus glacialis*) and the cold-water zooplankton fauna off Newfoundland may be controlled by a common factor. Dovekie (*Alle alle*) winter distributions are related to an area of vertical turbulence on the western slope of the Grand Banks, and summer distributions to high-latitude areas where there is an early "biological spring." On a finer scale, the feeding areas of Thick-billed Murres (*Uria lomvia*) from a colony in Hudson Strait are described; birds were flying at least 75 km to feed.

The problems of making detailed correlations between seabird distributions and oceanographic factors are discussed. The use made by Greater Shearwaters and Red Phalaropes (*Phalaropus fulicarius*) of tide rips in the Bay of Fundy is described, and the results of interdisciplinary work relating these birds to physical and biological oceanographic factors are summarized.

The possibilities of using quantitative seabird data to define, compare, and contrast pelagic seabird communities, and to link these with zooplankton communities, are discussed.

Most work on seabird ecology has been done on breeding birds, and a great deal is now known about breeding success, feeding ecology, population dynamics, and so on, during the breeding season. Yet seabirds spend the greater part of every year away at sea, and we know very little about their distributions, let alone their ecology, at such seasons. The reason pelagic studies have lagged so far behind is basically a logistic one. It is only with the recent boom in oceanographic research that ornithologists have been able to get to sea often enough to collect the basic information on seabird distributions necessary for an understanding of the birds' pelagic ecology, and the same boom has produced the framework of oceanographic knowledge which they need in interpreting these distributions. Even so, although work on the pelagic ecology of seabirds has expanded greatly within the last 15 years, the subject is still only at the stage that studies of terrestrial ecology reached 50 years ago.

This paper examines, in a fairly speculative way, the preliminary results of these investigations. It is based primarily on the work which the Canadian Wildlife Service has been doing in eastern Canadian waters since 1969 (Brown, Nettleship *et al.*, 1975; Brown, 1977). Most of this has been done from oceanographic vessels, though we have recently developed an aerial census technique—a system which allows wider, more frequent and more detailed coverage than is usually possible from ships (Johnson *et al.*, 1976; Nettleship and Gaston, 1978). The quantitative base for our shipboard observation is the number of birds seen during a standardized 10-minute watch, and is modelled on the Smithsonian Institution's POBSP survey

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(King, 1974). We now have reasonably good map coverage all year for the waters off Atlantic Canada, but there is still much to be done in the eastern Arctic.

The quantitative mapping of distributions is of course only the first step toward an understanding of the birds' pelagic ecology. Even so, the maps can provide insights into the factors which may influence those distributions.

1. Cory's Shearwater (*Puffinus diomedea*) and the Greater Shearwater (*P. gravis*) are two large shearwaters which are non-breeding visitors to eastern North American waters during the summer. The maps show that their distributions have virtually no overlap: Cory's is a bird of the warm slope water at the edge of the Gulf Stream, while the Greater occurs in the cooler waters to the north (Brown, 1977: maps 2 and 3). This segregation of two similarly sized, closely related species is what one would have predicted from Lack's (1971) competitive exclusion principle, although differences in foraging technique make one wonder about the extent to which the two could actually be competing for food (Brown *et al.*, 1978). Their preferred habitats, as indicated by surface water temperatures, seem very similar in both the North and South Atlantic (Brown, Cooke *et al.*, 1975; Brown, Nettleship *et al.*, 1975). This may seem obvious, but in fact it is not true of all trans-equatorially migrating seabirds. By contrast, Wilson's Storm-Petrel (*Oceanites oceanicus*) breeds in the Antarctic and Subantarctic but "winters" in the northwest Atlantic at the warmer edge of the Boreal Zone. The reasons for this striking seasonal discrepancy are not yet known.
2. Off the Atlantic coast of Canada, Northern Fulmars (*Fulmarus glacialis*) are commonest in waters influenced by the cold Labrador Current. The southern edge of their pelagic range retreats some 500 miles northward between May and September (Brown, Nettleship *et al.*, 1975); this withdrawal coincides with a withdrawal of cold-water zooplankton species (Vladimirskaya, 1965). Further investigation might well show that birds and zooplankton are in some sense part of the same marine community, and that both are reacting to the same seasonal changes in pelagic habitat.
3. Dovekies (*Alle alle*) are common off eastern Canada in winter, yet they are by no means uniformly distributed. Fig. 1 shows the situation on the southern Grand Bank early in 1971. Unlike murres (*Uria* spp.), which were fairly evenly distributed over the Bank and both western and eastern slopes, the Dovekies were concentrated over the western slope. In this area the bottom rises abruptly from 2000 m to 100 m, and this immense cliff stands squarely across the path of the Gulf Stream. It seems likely that the vertical turbulence as the current flows up and over it brings food up into the surface layers and into the Dovekie's reach, much as tide rips do in the Bay of Fundy (see below).
4. In some cases the distribution of colonies can give some clues on pelagic factors important in the birds' ecology. Dovekies breed in the high Arctic from northwest Greenland east to Severnaya Zemlya (Dement'ev and Gladkov, 1968; Fisher and Lockley, 1954; Norderhaug *et al.*, 1977; Salomonsen, 1950). The largest colonies tend to be the most northerly, and comparison with an ice atlas (*e.g.* Anon., 1958) shows that these are either in waters close to pack-ice which

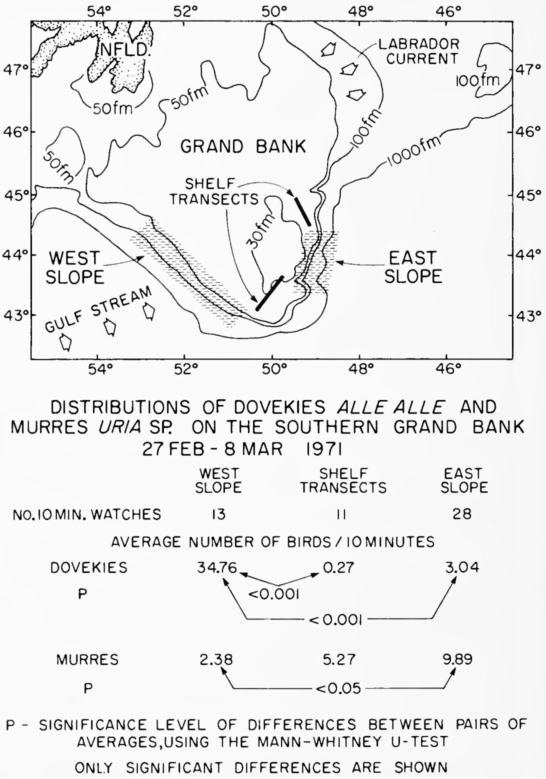

Figure 1. Dovekie (*Alle alle*) and murre (*Uria* sp.) distributions on the southern Grand Bank.

> never freeze (northern Baffin Bay, west Spitsbergen), or in areas which freeze but are more or less clear of ice by the last half of July, when the chicks hatch. This is an early break-up period for those high latitudes. It implies that the "biological spring," in which zooplankton biomass suddenly increases tenfold, will also be early; it occurs in July on the ice-free Greenland side of Davis Strait, but as late as September on the ice-bound Canadian side (Pavshtiks, 1968). So it seems that the timing of hatching and the siting of the colonies are linked to the presence of an abundant food supply early in the short high-Arctic summer. The fact that daylight is continuous at these latitudes would allow thorough exploitation of that food supply, and the birds do indeed appear to forage throughout the 24 hours (*e.g.* Brown, 1976).

These are all rather general points. However, really detailed, fine-grain mapping can yield a great deal of information, especially if one notes behavior as well as numbers. Flight direction and the percentage of birds sitting on the water (and therefore potential feeders) can be very useful in locating important feeding areas and in estimating the foraging range of breeding birds. Fig. 2 gives an example: it shows the average numbers of Thick-billed Murres (*Uria lomvia*) seen at various points on a transect past the very large colony at Digges Island/Cape Wolstenholme, in Hudson Strait, along with directions of flight and proportions of sitting birds. On the days of the transect most of the birds were evidently foraging west or northwest of the colony. The largest numbers, and the highest percentage of sitting birds, were just north of Mansel Island; the temperature and salinity differences in that area suggest that the birds were attracted to a boundary between water types, where food may be concentrated (*e.g.* Pingree *et al.*, 1974). The flight directions clearly indicate that these were birds from the Digges colony. One may doubt whether they could have been flying 75 km out to Mansel Island to collect food for the chicks which must have been on the colony at that time (see Tuck, 1961). But it is not out of the question; murres carrying fish—presumably for chicks—have been seen returning to Prince Leopold Island, Lancaster Sound, from distrances as great as 60 km (Nettleship and Gaston, 1978: Fig. 16). The fact that murres can forage at such ranges shows the need for a re-examination of the geographical scope of environmental impact surveys, for example, and Cody's (1973) hypotheses on the structure of alcid species communities.

The next stage in trying to understand something about the pelagic ecology of seabirds is to try to make some direct links between the distributions of the birds and of oceanographic factors, but in more specific ways than in the scenarios outlined above. At the physical oceanographic level this is fairly simple, if not very informative. Water types can be defined by their temperature/salinity ratios (*e.g.* Pickard, 1971), much as terrestrial habitats can be defined, for example, by the acidity of the soil. Brown, Cooke *et al.* (1975) have linked the distributions of certain seabirds to those of water types in the Chilean fjords, and Pocklington (1979) has done the same for much of the Indian Ocean. This does not necessarily mean that the birds are responding to temperature or salinity as such, but that they are part of a biological community which can be defined by these parameters. The actual link is presumably some prey organism. Unfortunately, attempting links at the biological oceanographic level is much more difficult. To begin with, it requires an interdisciplinary approach. But oceanographers are still reluctant to think of seabirds as legitimate subjects for research, so the initiative has to come either from an ornithologist, who usually lacks the necessary background, or from an ornithologically-minded oceanographer, who usually lacks the time. Moreover it is usually impractical to collect birds for their stomach contents from a large oceanographic ship, or to collect fish and plankton precisely where the birds are feeding. Collections of both kinds can easily be made from a small boat (*e.g.* Bédard, 1969; Hartley and Fisher, 1936), but this usually limits one to inshore areas, and thus to coastal species, or to pelagic species in the breeding season only.

Canadian Wildlife Service work in the Bay of Fundy shows what one can expect to come out of such an interdisciplinary approach (Brown, in prep.). In late August large flocks of "wintering" Greater Shearwaters and post-

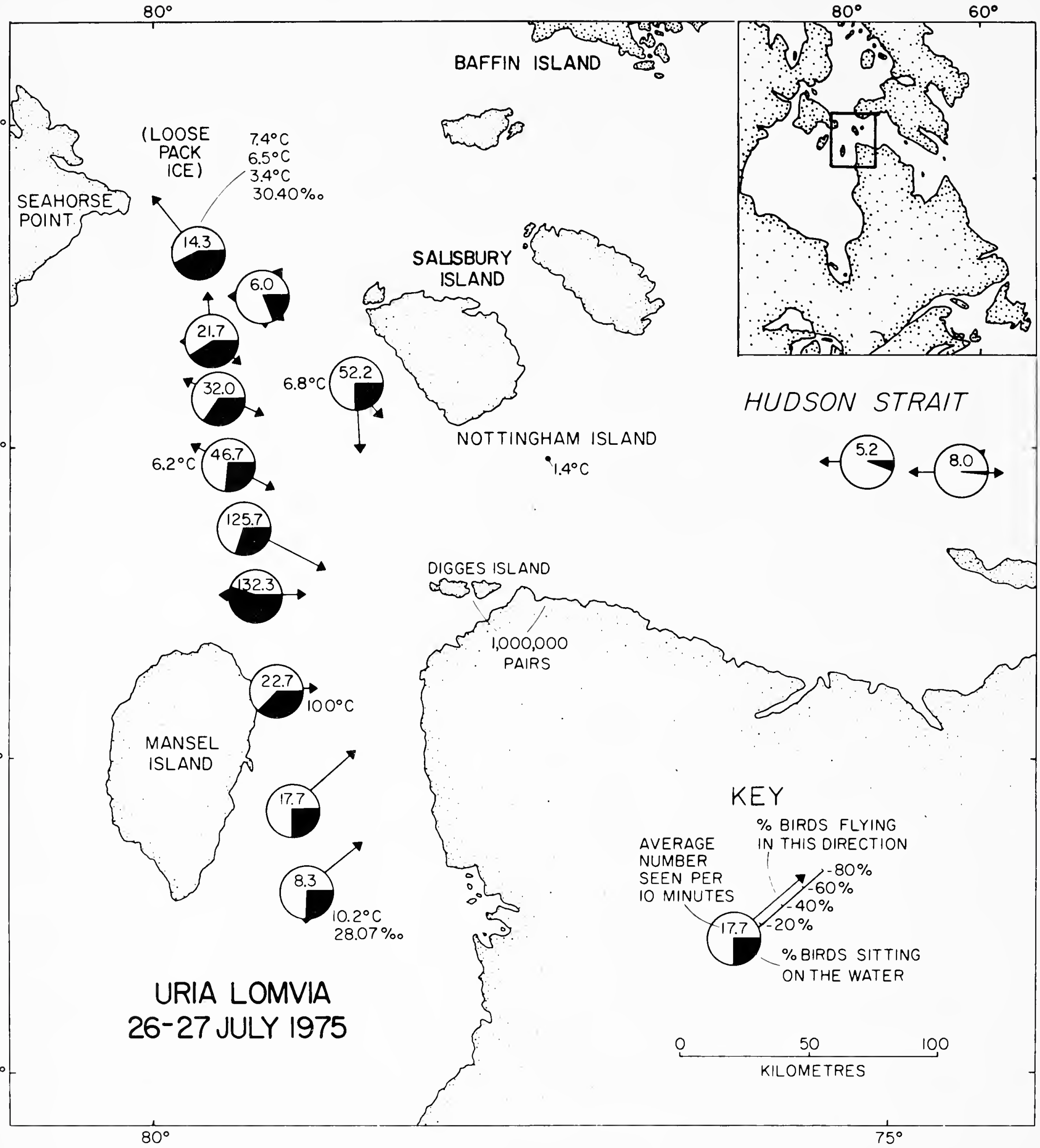

Figure 2. Distributions of Thick-billed Murres (*Uria lomvia*) in western Hudson Strait, as observed from a ship. The two easternmost symbols refer to observations made on 26 July; the remainder were made next day. The observations immediately west of Nottingham Island were made at first light; birds were already returning to the colony, and may have been feeding at night. Averages are based on at least three 10-minute watches. Temperatures (°C) and salinities (‰) refer to surface water.

breeding Red Phalaropes (*Phalaropus fulicarius*) assemble 5-10 km off Brier Island, Nova Scotia. The birds are attracted to an area of turbulence caused when strong tidal streams run up against steep underwater ledges which reach almost to the surface. This creates a "tidal pump" which brings cool bottom water and abundant copepods up to the surface. Both drift downstream until the cool water sinks beneath the warmer surface water offshore, leaving the copepods trapped at the edge of the convergence line. Red Phalaropes feed on the copepods in the two areas where these are most abundant—immediately over the "pump" and in the convergence line. Both areas are easily identified by the presence of "streaks" of calm water at the surface. The birds rarely feed away from the "streaks," and it is interesting that they feed in similar areas out at sea where food may be locally concentrated: at the offshore oceanic front off Senegal, for example, and in Langmuir circulation cells off Peru (Brown, 1979 and unpublished; see also Pollard, 1977). Meanwhile swarms of the euphausiid *Meganyctiphanes norvegica* also appear at the surface, apparently following the copepods and feeding on them. These are fed on in turn by the shearwaters and by Great Black-backed and Herring Gulls (*Larus marinus* and *L. argentatus*, baleen whales, Mackerel (*Scomber scombrus*), Herring (*Clupea harengus*) and Short-finned Squid (*Illex illecebrosus*); on occasion, the birds also take the fish and squid. In short, the "tidal pump" and the copepods are the physical and biological bases of a short food chain supporting a marine community of which the seabirds are an integral part. A comparable "pump"-copepod-euphausiid system exists across the Bay in Head Harbour Passage, New Brunswick, but the community it supports shows two intriguing differences from Brier Island—for as yet unexplained reasons Bonaparte's Gulls (*Larus philadelphia*) replace the shearwaters, and there are Northern Phalaropes (*Phalaropus lobatus*) instead of Red. The investigation is continuing.

Quantitative information on seabirds at sea can be used for more than just the preparation of distribution maps. One can use it to define objectively groups of species which regularly occur together, just as Fager (1957) and Fager and McGowan (1963) have done for zooplankton communities. If one applies Fager's "index of affinity" to the seabird species which occur together in 10-minute watches, it appears that, for example, the offshore summer seabird community in Baffin Bay includes only four species: Northern Fulmar, Black-legged Kittiwake (*Rissa tridactyla*), Thick-billed Murre, and Dovekie. These are, respectively, a larger and a smaller surface feeder and a fish- and a plankton-eating diver. Such a segregation is to be expected on the basis of Lack's (1971) principle of competitive exclusion of species with similar diets; it is also clear that Arctic marine habitats are as species-poor in birds as are those on land. It would be worth using this technique to define other seabird communities in order to compare and contrast them; how, for instance, does the Baffin Bay community compare with the equivalent seabird community in the Antarctic? One might also gain some insights into possible key food species by calculating "affinities" for a combined species pool which included both the plankton collected in surface tows and the seabirds seen during those tows. I have in fact begun to do this, but the results so far are inconclusive.

Finally, quantitative information will eventually provide estimates of seabird biomass, and it will be particularly useful to be able to take non-breeding migrants into account, and also periods outside the breeding season. I do not think we yet know enough about the correction factors needed to convert the existing data into any *absolute* estimate of population size and hence of biomass of birds at sea. But we can make rough *relative* estimates of biomass simply by multiplying the average numbers of each species seen per 10-minute watch by its weight, and use these to compare seabird communities in different areas. For example, the relative biomass of seabirds in the Senegal upwelling is only about 6 kg/10 minutes, against more than 100 kg for the Benguela Current, the comparable upwelling in the South Atlantic (data calculated from Brown, 1979; Jehl, 1973; Summerhayes *et al.*, 1974). At first sight the difference is not too surprising, since off Senegal the tertiary productivity of the fish on which most seabirds feed is at most 15% of the figure for Benguela (Cushing, 1971). But this cannot be the whole explanation. Productivity at the southern, least productive end of the Peru upwelling is similar to that off Senegal, yet that area supports a relative seabird biomass of at least 24 kg/10 minutes. For some reason, seabirds are not using the Senegal upwelling to full capacity.

Why not? The answers will require a "whole ocean" approach—an appreciation not just of the immediate situation off Senegal, but of all the potential food resources available to seabirds over the whole of the North and South Atlantic. Obviously we do not yet know this. But one of the factors must be the lack of suitable nest sites in the Senegal area; alone of the four major eastern boundary upwellings, it has no significant population base of breeding birds. Timing is another factor; the Senegal upwelling occurs in the first three months of the year, and this is probably too late to be of much use to wintering northern hemisphere seabirds. The availability of richer feeding areas in the Benguela Current and on the Patagonian Shelf and off eastern North America perhaps explains why southern hemisphere seabirds do not use it. There must be many other possibilities. But I quote this speculative scenario as an example of some of the questions we will ask, and answers we will receive, as the study of the pelagic ecology of seabirds develops further. Comparisons of biomass between seabird communities are outlined, with particular reference to an apparent under-exploitation of the Senegal upwelling by seabirds.

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COMMENTS

Bourne: I should like to congratulate Dick Brown on what he has been doing. He has clearly found a very useful situation in the Bay of Fundy. I meant to mention these situations where you have an estuary with a considerable tidal fall and a rich productivity offshore. Stuff gets swept into the estuary with the tide and made available. We have this in northeast Scotland in the Ythan Estuary which supports a large tern colony. The terns feed largely on shoaling fish which get swept in and out of the estuary with the tide so that they are made available to the birds.

You were mentioning West Africa. I think there are enormously rich seabird colonies on the Banc d'Arguin in Mauritania which is immediately inshore from this area of upwelling. I would suspect that a lot of the biological material produced offshore in the upwelling is swept in over the shallow banks surrounding it to become available to the bird colonies there.

Brown: Yes, I agree, but I should also say that a better example would be Southwest Africa or Peru. The Banc d'Arguin colonies are minuscule. You have few birds off Senegal simply because there is no breeding base—just a few small rocks where the birds breed, some rather shifting sand banks subject to hyena predation, and this is about it. So the Senegal area, as you say, has potential richness but has to depend on migrant birds who have other more attractive places to breed.

POPULATION AND COLONY-SITE TRENDS OF LONG ISLAND WATERBIRDS FOR FIVE YEARS IN THE MID 1970s*

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ABSTRACT

This paper reports the general results of a helicopter survey/census taken for several days each June from 1974–78, inclusive, of the entire shoreline of Long Island, New York, excepting Fisher's Island. Censused were 15 common species of herons, egrets, ibises, gulls, terns, and skimmers, with a collective population for Long Island varying between 33,000 pairs (1978) and 42,000 pairs (1975). In 1975 Gull-billed Tern was found breeding for the first time north of New Jersey, and the first known nesting of Laughing Gull on Long Island since 1900 was proved in 1978. Major and previously undetected heronries were found at Huckleberry Island in Long Island Sound off New Rochelle, on South Brother Island in the East River near the Triboro Bridge, on Robins Island in Peconic Bay, and on Plum Island in Block Island Sound off Orient Point. New gulleries were found in North and South Brother Islands in the East River, and on Huckleberry Island. The only major new tern colony found was a marsh colony at Lane's Island in Shinnecock Bay.

It was determined that the bulk of Long Island's breeding herons (between 78% and 92%) was concentrated in the marshes on the south shore of Long Island west of Fire Island Inlet. Years of occupancy as well as the minimum and maximum numbers of each species are given for the main southwestern Long Island heron area, as well as for each of the seven other known Long Island colonies. Similar data are given for the eight largest Common/Roseate Tern and Black Skimmer colonies in the Long Island area, and for the nine major Herring/Great Black-backed Gull breeding areas. Brief mention is made of the still-obscure Long Island status of Yellow-crowned Night Heron, and, although discussion is deferred to another paper, the locations of individual colonies in the major southwestern heron area are presented on a map.

An updated analysis of the population size and health of each of the 15 common species, with largest concentrations, new colonies, and numbers of colonies where each occurs, is also given. Among waders, Snowy Egrets and Glossy Ibises were the most numerous: Black-crowned Night Herons and Snowy Egrets occurred in the greatest number of colonies; Cattle Egrets, Little Blue Herons, and Louisiana Herons had the smallest populations and most restricted distributions. It appears that between 1974 and 1978 the Long Island Black-crowned Night Heron population was only about 25% of what it was in the mid-1930s, and maximum (and average) colony size was significantly smaller, although breeding pairs and numbers of colonies increased steadily during this study.

Herring Gull populations peaked in 1975, and from 1976–78 dropped markedly, apparently following a similar trend in New England some years earlier. They are concentrated in 11 major breeding areas, the largest of which is on Gardiner's Island. Great Black-backed Gull's Long Island center of distribution (73%–86% of all pairs) is also on Gardiner's Island, that site being one of the largest aggregations of breeding Black-backs in the eastern United States.

Common Terns on Long Island, unlike in New England, appear to be either holding their own or increasing slightly in both numbers and colonies occupied, and colony size maxima in the present

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*This paper is dedicated to the memory of LeRoy Wilcox, pioneer student of Long Island's waterbirds, who will be remembered fondly and with respect by those privileged to have known him.

study period had been exceeded previously only three times. Six large colonies accounted for between 66% and 84% of the Long Island population each year. Roseate Tern was the one species highlighted as being in serious decline: in the five years of this study, its numbers dropped from about 1,900 pairs to about 600 pairs, and number of occupied sites from 11 to seven; almost all Roseates are now concentrated in one colony on Great Gull Island, whose numbers have also been dropping. Least Tern, on the other hand, may never have been more numerous on Long Island, and its largest known colonies occurred during this study period. Black Skimmer has apparently been holding steady on Long Island in recent times, in terms of both number of breeding pairs and colonies occupied. The first marsh-nesting skimmers on Long Island were also reported.

Detailed population analyses of several groups revealed Herring Gulls in nine major Long Island breeding areas were uniformly declining after 1975, while Black-back colonies were behaving with weak (if any) coordination. Herring Gulls were more evenly distributed throughout Long Island in their nine major colony areas, but Black-backs were concentrated on Gardiner's Island. Herring Gulls peaked in 1975 and then began to decline, and although Black-backs peaked in 1977 they were apparently neither increasing nor decreasing. Empirical regression analysis of the Herring Gull data from all colonies from 1976–78 produced a significant exponential decay equation, which predicts the disappearance of Herring Gull as a Long Island breeding bird in some 50 years should the decline continue unabated (a most unlikely occurrence).

This study also determined that about 20% of all Long Island Common Terns were nesting in marshes in 1974–78, although no reproductive success data were taken. Marsh colony sites appeared to be remarkably stable year-to-year, and some were unexpectedly large. A portion of the Long Island Roseate Tern population also nested in marshes, but was manifestly unsuccessful: 31% in 1974 declined to 0% in 1978. Regression analysis confirmed that for the five years the number of marsh-nesting Common Terns each year was significantly related to the entire Long Island population each year, suggesting that a shortage of preferred non-marsh habitat was forcing Long Island's Common Terns into the marshes for nesting. In 1977, marsh colonies were significantly smaller on both Long Island and in New Jersey than were non-marsh Long Island colonies; several possible explanations are advanced. Finally, annual numbers of breeding Common Terns regressed on tidal prisms of the four major disturbed inlets on Long Island's south shore confirmed a predicted positive relationship, which we interpret to mean that the fish food supply produced by tidal flux at these inlets is largely responsible for determining the number of breeding pairs of terns supportable in colonies adjacent to those inlets. Individual-year analyses of the same data found even more significant relationships in three of the five years but no correlation in two; explanations for these differences are presented.

Least Terns were found in unexpectedly large numbers in two areas—Peconic Bay and the central Long Island north shore. Combined, these two sites accounted for between 55% and 70% of the total Long Island population each year. Birds in the two areas were using different breeding strategies, occurring in few and large colonies on the north shore, but in many and small colonies on Peconic Bay.

I. INTRODUCTION

In the early and mid 1970s attention was focused on populations of colonial waterbirds inhabitating coastal areas of the eastern United States by a variety of factors: severe coastal erosion and plans to "stop" it, the Coastal Zone Management Act, the possibility of offshore oil drilling and attendant onshore sites, and the development of several National Seashores and National Recreation Areas. Because of the last, we became aware that no one really knew the breeding waterbird populations of even such allegedly well-studied areas as Gateway National Recreation Area (including Jamaica Bay Wildlife Refuge, Sandy Hook, Hoffman and Swinburn Islands, Breezy [Rockaway] Point), and Fire Island National Seashore (including within its boundaries, or immediately adjacent, the Moriches and Fire Island Inlet Islands). Consequently, in early June 1974 we undertook to estimate the entire Long Island colonial waterbird population, using a helicopter during a period of a few days in order to reduce population count differences due to time lag, renesting, etc., and to take advantage of a brief overlapping period when all species would likely be at their nests. In this way we hoped to not only place the waterbird resources of Gateway and Fire Island in a regional perspective, but to also obtain for the first time ever a delineation of all the species, colonies, and individuals of waterbirds breeding on Long Island.

In 1974 we surveyed and censused (for distinctions between those terms, see Buckley and Buckley, 1976) the entirety of Long Island in two days (10, 11 June). The results indicated that much more information would be obtained were the same observers to conduct the survey/census another year in a slightly more relaxed three days. This was done on 9, 10, 11 June 1975. Inevitably, the census was repeated in 1976 (7, 8, 9 June), 1977 (1, 3, 4 June), and 1978 (12, 14, 15 June). While detailed analysis of the copious data obtained over the five years will take considerable time, it was felt important to bring some highlights to the fore in one overview paper.

The present paper is designed primarily to do three things: (1) provide the first picture, across five years, of most breeding Long Island colonial waterbirds; (2) update the rapid explosion that herons and ibises are undergoing on Long Island, while filling out the picture for gulls and terns; and (3) make minor corrections for some figures presented in *American Birds*, resulting from changes in conversion factors (see below) and in a few cases, errors in arithmetic. The information presented here materially updates (and occasionally corrects) Bull (1974) and, when read in conjunction with Bull (1964), emphasizes the astounding changes that have recently taken place in Long Island waterbird populations, especially among herons and ibises. Comparison of some of our tern-skimmer census results with those of Duffy (1977) emphasizes how essential it is to attempt to census all colonies simultaneously at the optimal time of year. Buckley, Gochfeld, and Buckley (1977) have already demonstrated the ability to assay with about ± 15% and ± 5% accuracy, respectively, the breeding populations of both Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*) across an entire season with data taken during only a single helicopter census at the optimal time *i.e.*, early June. We believe this approach, with refinements, can be used for most, if not all, colonial waterbirds breeding in the Northeast.

We should stress that in the studies reported here we have completely avoided the question of colony productivity/success, relying instead on detecting changes by viewing the entire population almost simultaneously once each year over the course of several years. While our data cannot be readily obtained other than by brief, intense helicopter survey/census, they are no substitute for, and *must* be viewed in conjunction with such long-term individual colony studies as the Common-Roseate Tern (*Sterna dougalli*) work of Hays, LeCroy *et. al.* on Great Gull Island, of Gochfeld on the Jones Beach strip, and of Ford in the Captree gullery. Detailed in-colony studies on a smaller scale, such as those by Houde (1977a, b) on tern and gull interaction at Hicks Island, and Post and Gochfeld (1979) on tern demography at Breezy Point, are essential for providing details to explain trends and movements detected during extensive aerial survey/censuses.

II. Materials and Methods

From 1974–77 we surveyed the entire coastline of Long Island (except Fisher's Island), including all salt marshes, major tidal rivers and creeks, and barrier and spoil islands, as well as Sandy Hook in New Jersey, Hoffman and Swinburn Islands in lower New York Harbor, and the group of unnamed islands off New Rochelle, Westchester County, and north of City Island, Bronx County. In 1978 coverage was extended to include all islands in the East River between Brooklyn/Queens and Manhattan/Bronx. The survey/census followed the route indicated in Fig. 1. A five-passenger Bell Jet Ranger II turbine-powered helicopter seated the pilot (right side) and one observer in the front seat, with one observer at each window in the back seat. Once a colony was located from a cruising altitude of 250-300 ft. (50-70 mph speed), it was circled until observers on both sides of the aircraft were able to obtain whole colony counts or estimates (done by multiple section-counts or section-estimates in large colonies). All potential areas were investigated, even if known to be colony-free in the past. Marshes were quartered in a regular grid and beaches run linearly, at low altitudes (20–40 ft.) and low air speeds (20–50 mph) in order to detect isolated Common Tern/gull colonies and

Least Tern (*Sterna albifrons*) colonies, respectively. The area of weakest coverage was along the north shore of Shinnecock/Quantuck/Moriches/Great South/South Oyster/Hempstead Bays, where development was greatest and likely habitat scarcest. Nonetheless, it is possible that some night-heronries, and possibly even a few "white" heronries, were missed, although we know of no ground-reported heronries we failed to detect aerially in the five-year period, except South Brother Island (see below). We probably missed occasional small Least Tern colonies; might have missed small or incipient night heron/Glossy Ibis (*Plegadis falcinellus*) colonies (they are exceedingly difficult to detect except at very close range), and probably missed a few isolated pairs of Common Terns and Herring Gulls (*Larus argentatus*). Counts of Yellow-crowned Night Herons (*Nyctanassa violacea*) and Green Herons (*Butorides striatus*) are not analyzed here: the former because they breed as scattered single pairs or in small colonies (frequently on the mainland of Long Island and often in back yards), the latter because they are not colonial. Both species do occur in small numbers in mixed heronries, but even there only Yellow-crowns were systematically tallied. We do not purport to have censused that species adequately, so the few data we show represent only those occurring in mixed heronries; the interpretation of those figures is open. When mixed tern colonies were large and conditions permitted, we landed and obtained data on foot, reconciling those figures with aerial estimates after takeoff.

It must be stressed that disturbance caused by the helicopter's close approach (and even its landing) was minimal, and we even found a disconcerting amount of habituation on the part of herons and Least Terns, which tolerated increasingly closer approaches each year before they flushed. Certainly helicopter censusing results in only very brief disturbance, as people do not normally enter the colony (thereby leaving no trails for mammalian predators to follow) and no nests, eggs or young are disrupted. General population health and repeated occupation of colony sites over the five-year study period support the negligible impact of helicopter censusing. Kushlan (1979) experimentally demonstrated no differential impact between censusing by fixed-wing and rotary-wing (helicopter) aircraft on Everglades heronries, and observers using helicopters are in general agreement about the low level of disturbance

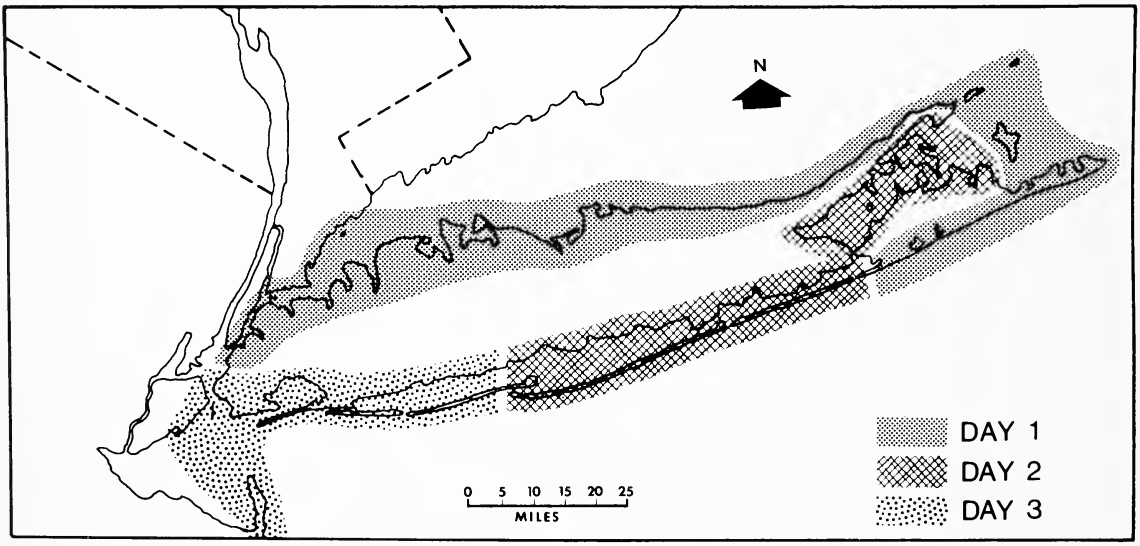

Figure 1. Areas covered on successive days of 1975–1978 helicopter survey census of Long Island area. Exaggerated gaps between days are for graphic purposes only; coverage was total and frequently overlapped. 1974 coverage was in 2 days, but breakout not depicted.

they cause so long as some degree of habituation has taken place. Buckley and Buckley (*in prep.*) contrast the pros and cons of surveying and censusing by fixed- and rotary-wing aircraft.

At each colony, data were taken in the form of the total number of adults per species in attendance. Multiplicative conversion factors were then applied to those counts in order to estimate numbers of breeding pairs—the only kind of data presented in this paper unless specifically noted otherwise. For Common and Roseate Terns, we used a conversion factor of × 0.92 as determined in Buckley, Gochfeld and Buckley (1978), as we did for Least Terns (cf. × 0.90 used by Duffy [1977]); for Black Skimmers we used × 0.5, as our own observations as well as those of Gochfeld (pers. comm.) indicated that generally both members of the pair were in attendance when we censused. The same factor was used in New Jersey by Buckley (1978) and for the entire Northeast coast by Erwin (1979). Owing to uncertainties about actual adult/pair numbers in the colony, plus a general feeling among Northeast heronry workers that one adult corresponds to one breeding pair, heron and ibis counts were converted to pairs by multiplying by 1.0. For the same reason, Herring Gull and Great Black-backed Gull (*Larus marinus*) counts were also converted by a factor of × 1.0. An especially great effort was made to count/estimate either actual gull nests or pair-members standing at a nest or in a territory. Gull figures may thus more properly be considered as representing nests or occupied territories, the only exception to the data-in-pairs generality. The numerical average of all observers' converted figures is the final figure used for each species in each colony.

The question of what constitutes a colony is a vexing one (see Buckley and Buckley 1980 for a longer discussion). For purposes of this analysis, a colony had to contain three or more pairs, even of mixed species. Thus two pairs of Herring and one pair of Great Black-backed Gulls together were scored as a colony, but if the two pairs were widely separated from the one, neither would be counted as a colony. For purposes of listing species occurrence within a colony, no species minimum was required, provided the colony itself consisted of three or more pairs. For these analyses, ibises are included among "herons" and skimmers among "terns." Least Terns, however, were treated as separate from the other terns. Sites occupied (pertinent in discussion of Least Terns) are just that, even if only by one pair.

At what point a colony is to be considered composed of two or more "subcolonies," or if the units are discrete enough to be scored as separate colonies, may be the knottiest problem of all. Generally speaking, if two groups were on separate bay marsh islands, or at opposite ends of one island, they were regarded as two colonies. If the groups were separated only by virtue of habitat discontinuities and were reasonably close (<½ mi. or <0.8 km appear to be good "working" distances), they were generally considered subcolonies. The most conservative approach in data-taking—to divide the populations as finely as possible, combining them later as needed—has generally been followed here. A few arbitrary decisions were made for convenience (*e.g.*, Gardiner's Island gulls were divided into six colonies [Great Pond, Tobaccolot Pond, Bostwick Point, Home Pond, eastern cliffs, and western cliffs]. Generally discrimination between most colonies was obvious, and further discussion is out of place here.

Statistical analyses, generally performed on pre-programmed cards for the Hewlett-Packard models HP-65 and HP-97, included t-test, two-way ANOVA without replications, Friedman two-way ANOVA by ranks, least-squares linear regression and least-squares exponential curve fitting. Assumptions necessary for use of parametric analyses were deemed met and were not explicitly tested for; while these assumptions may not be warranted, deviations due to non-uniform variances (the most likely kind in these data) are believed by most statisticians not to affect severely the tests used here, most of which are reasonably robust (cf. Sokal and Rohlf, 1969).

III. QUALITATIVE RESULTS

A. *New species.* The five years of surveying turned up two new species of breeding colonial waterbirds on Long Island: two pairs of Gull-billed Terns (*Gelochelidon nilotica*) in a Common Tern/Black Skimmer colony on Black Banks Island in marshes northwest of Jones Beach in 1975, 1976, and 1978 (Buckley, Buckley, and Gochfeld, 1975), and one pair of Laughing Gulls (*Larus atricilla*) in the same place in 1978 (Buckley, Gochfeld, and Buckley, 1978). Gull-billed Tern was new as a New York State breeder, while Laughing Gull had been extirpated in the late 1800's, with no proven nesting after 1900. Both species had been expected to breed, presaged by the presence of paired adults during several previous breeding seasons. Another Gull-billed Tern was flushed off a nest in the Silver Hole Marsh tern colony at Jamaica Bay Wildlife Refuge in 1976, although its fate was unknown. Up to three pairs of adults have been seen on the East and West Ponds at the Refuge from 1976–79, although no additional nests have been located. The Black Banks Island pairs were apparently not present in 1979 (PAB: pers. obs. 28 June), although one or two pairs were reported in S. Hempstead Bay marshes, with apparently no nest located (M. Gochfeld, pers. comm.). No Laughing Gulls were at the Black Banks Island site on 28 June 1979, although greater than normal numbers of adults in the marshes north of the Jones Beach strip (R. Paxton, pers. comm.) suggest that some are again breeding.* Another expected new marsh breeder on Long Island, Boat-tailed Grackle (*Cassidix major*), may have nested in or near the heronry on Pearsall's Hassock, Lawrence Marsh, in May-June 1979 (T. H. Davis, pers. comm.). Two additional new colonial nesters are anticipated any year: White Ibis (*Eudocimus albus*) and Forster's Tern (*Sterna forsteri*). While the former may take up residence in one of the south shore heronries accessible by road, the latter will almost certainly not be found unless by chance or by continued helicopter surveying of all tidal salt marshes. At present, Long Island marks the known northern breeding limit for Gull-billed Tern (and Boat-tailed Grackle, if it actually nested).

In a somewhat different category is Double-crested Cormorant (*Phalacrocorax auritus*). Now breeding south of Cape Cod Bay (south shore of Cape Cod and rocky islands in Rhode Island), breeding-plumaged adults of this species have been occurring in increasing numbers each summer in two widely separated Long Island area locations: Gardiner's Island and Hoffman-Swinburn Islands. In 1972 (Erwin, ms.), 30 pairs were reported from an undisclosed location on the Connecticut shore, and Drury (1973) found them in small numbers in "eastern Long Island Sound." It is thus not surprising that in 1977, Proctor (*in* Erwin, 1979) found a small colony (65 pairs) at Hungry Point on Fisher's Island, New York, off New London, Connecticut. We expect that Double-crested Cormorants will probably be found nesting soon in Herring Gull colonies (cf. Drury, 1973) on Gardiner's Island, or on Hoffman or Swinburn Islands in Lower New York Bay—possibly in both locations.

B. *New colony sites.* Several previously unknown colonies or colony areas of gulls, herons, and terns, indicated on Figs. 2 and 3 and Tables 1 and 2, were located during the study period.

1. *Heronries.* A heronry on *Huckleberry Island* (Fig. 4) probably accounts for many egrets and night herons seen in lower Westchester and on the opposite shore of Long Island. Its nearest neighbors are on the Norwalk, Connecticut islands (22 miles northeast), at Stony Brook Harbor (30 miles east), and in the East River at the newly found South Brother Island colony 8 miles southwest (see below). Its size suggests a moderately old colony in an area where none had previously been known. The absence of Glossy Ibis, Cattle Egret (*Bubulcus ibis*), and the small dark herons (Louisiana and Little Blue Herons) (*Hydranassa tricolor* and *Florida caerulea*) is not unexpected, as these all occur in only a few heronries in the New York City area.

The day the Huckleberry Island heronry was first found (9 June 1975) we flushed a recently

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*After this paper had been written, P.W. Post discovered in 1979 a new colony of 12–15 pairs of Laughing Gulls at JoCo marsh in Jamaica Bay (Post and Riepe 1980); by June 1980 this colony had mushroomed to 235 pairs (Buckley and Buckley *in prep.*).

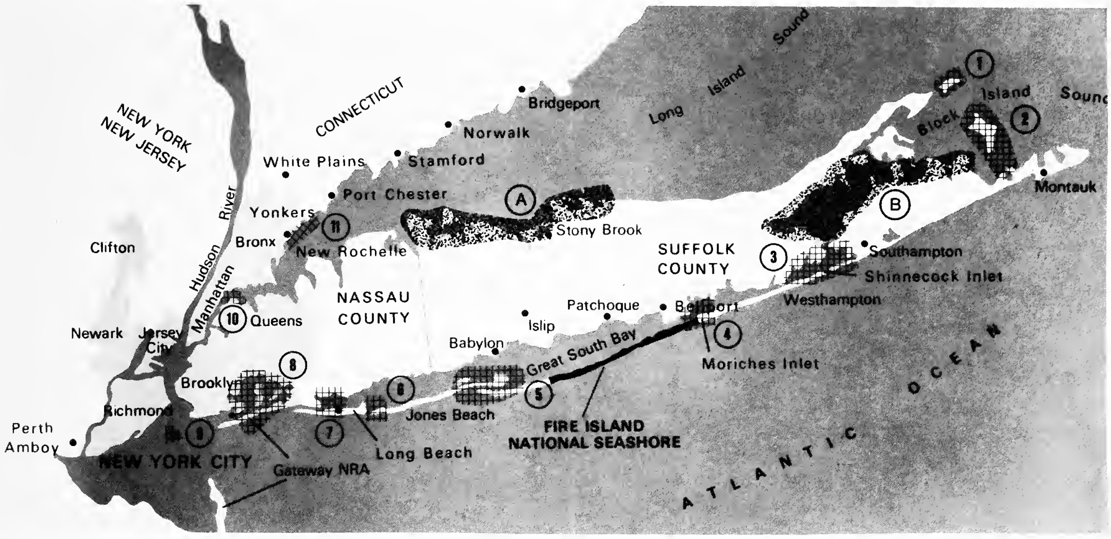

Figure 2. Cross-hatching: Eleven major Herring/Great Black-backed Gull breeding areas discussed in text. Data for Tables 6 and 7 are from areas 1–9 only. For identification of all 11 breeding areas, see Table 2. *Stippling:* major Least Tern breeding areas on Long Island; A: north-central shore of Long Island, B: greater Peconic Bay. For additional information see Table 2. All sites for period 1974–1978.

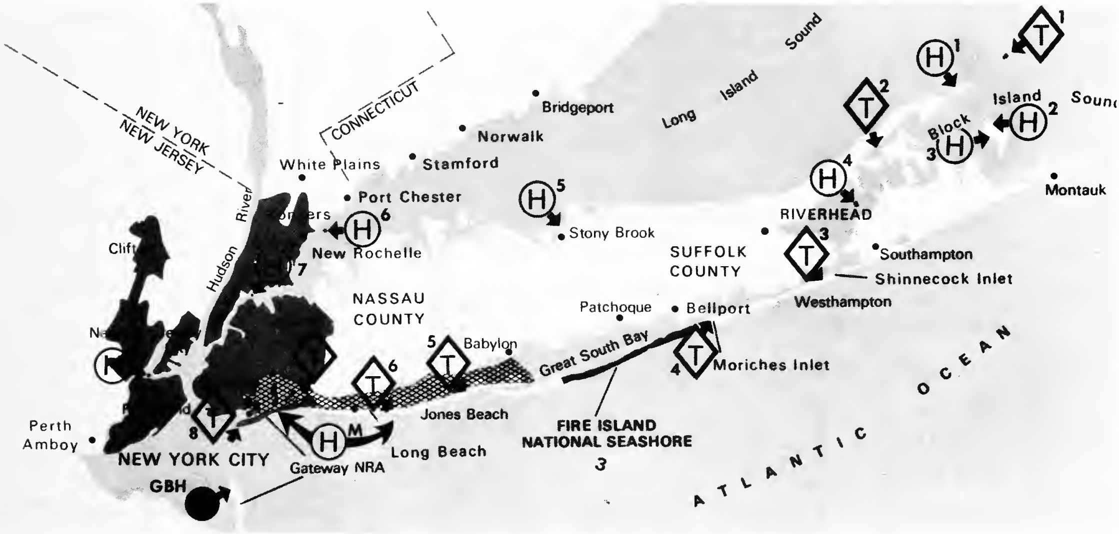

Figure 3. Major terneries (T) and all heronries (H) known from Long Island area in the period 1974–1978. For identification of individual colonies, refer to Table 1. H^m = area of heronry concentration in south shore marshes on western Long Island; see Figure 11 for greater detail. GBH = Great Blue Heronry at Sandy Hook, New Jersey. For identification of individual terneries and heronries, see Table 1.

TABLE 1

Identification of Tern Colonies (T) and Heronries (H) of Fig. 3

T^1:	Great Gull Island, Suffolk Co.
T^2:	Port of Egypt, Southold, Suffolk Co.
*T^3:	Lane's Island, Shinnecock Bay, Suffolk Co.
T^4:	West Inlet Island, Moriches Inlet, Suffolk Co.
T^5:	Cedar Beach, Jones Beach Strip, Suffolk Co. (Fire Island Inlet)
T^6:	West End, Jones Beach State Park, Nassau Co. (Jones Inlet)
*T^7:	Jamaica Bay Wildlife Refuge, Queens Co.
T^8:	Breezy Pt., Rockaway Peninsula, Queens Co. (Rockaway Inlet)
H^1:	Plum Island, Suffolk Co.
H^2:	Bostwick Pond, Gardiner's Island, Suffolk Co.
H^3:	Home Pond, Gardiner's Island, Suffolk Co.
H^4:	Robins Island, Peconic Bay, Suffolk Co.
H^5:	Long Beach Pt., Stony Brook Harbor, Suffolk Co.
H^6:	Huckleberry Island, Long Island Sound, Westchester Co.
H^7:	South Brother Island, East River, Bronx Co.
H^8:	Shooter's Island, Kill Van Kull, Hudson Co. N.J./Richmond Co. N.Y.
H^m:	Major heronry area on southwestern Long Island

*Salt marsh colony

TABLE 2

Identification of Numbered Gull Colony Clusters of Fig. 2

1:	Plum Island, Orient Point, Suffolk Co.
2:	Gardiner's & Hicks Islands, Block Island Sound, Suffolk Co.
3:	Shinnecock Bay, Suffolk Co.
4:	Moriches Inlet, Suffolk Co.
5:	Fire Island Inlet, Suffolk Co.
6:	Jones Inlet, Nassau Co.
7:	Lawrence Marsh (Hewlett Bay), Nassau Co.
8:	Jamaica Bay, Queens & Kings Co.
9:	Hoffman & Swinburn Islands, Lower New York Bay, Richmond Co.
10:	North & South Brother Islands, East River, Bronx Co.
11:	Huckleberry Island complex, Bronx & Westchester Cos.

fledged (tufts of down still clinging to the occiput) Great Blue Heron (*Ardea herodias*) from the colony, leading to the false hope that species might be nesting there, but no other Great Blue was ever seen there again. Breeding herons on Huckleberrry Island were nesting in tall (up to 40 ft.) trees, and most nests appeared to be placed above 5 ft.

South Brother Island, in the East River just north of Hell Gate (the confluence of the East River, Long Island Sound, and the Harlem River; Figs. 5 and 6) was both the most disconcerting find—coming as it did in the last year of the study—and the most rewarding—confirming a suspicion of Buckley and Kane (1975: 131) that "an undetected roost/heronry [lay] between the known ones at Jamaica Bay Wildlife Refuge and the Hackensack Meadows—possibly on Rikers Island in the East River." Rikers Island is 1200 ft. from South Brother Island. As on Huckleberry Island, no Glossy Ibis or small dark herons were seen, and Snowy Egret (*Egretta thula*) and Black-crowned Night Heron (*Nycticorax nycticorax*) were dominant. Unexpectedly, some 30 pairs of Cattle Egrets were also present, possibly the same birds that feed in the Hackensack Meadows. This is presently the largest breeding concentration of Cattle Egrets in the area, virtually doubling the known population and bringing to three the known regular colonies on Long Island. The dominant tree on heavily vegetated South Brother Island was *Ailanthus* (tree-of-heaven), with a thick catbrier/Virginia creeper/poison ivy understory. Nests were apparently placed from ca. 5 ft. to 20 ft., concentrated in a hollow in the center of the island. Judging from its size, this too is likely a well-established colony. Nearest colonies are Huckleberry Island, Jamaica Bay (12 miles southeast), and Kearny, New Jersey (14 miles southwest).

Robins Island in Great Peconic Bay, and *Plum Island* off Orient Point, were also apparently not known to harbor heronries prior to our discovery of them in 1975 and 1974 respectively. The size and composition of the Robins colony suggest that 1975 was the first year of its existence, while the mixed-species character of the Plum Island colony leads one to believe it has been there for some time. Robins Island is covered by mature hardwood forest, with nests located up to 30 ft. high in trees surrounding a pool on its northwest corner. Robins Island is the eastern Long Island colony nearest to those further west, being 50 mi. northeast of Seganus Thatch, and 40 mi. east of Stony Brook Harbor; Gardiner's Island is 20 mi. east. The Plum Island heronry is in tall bushes and low trees in the midst of a shallow, flooded area on the southwestern side of the island (Fig. 7). The nearest other Long Island heronries are on Gardiner's Island 5 mi. southeast, and Robins Island 30 mi. southwest. Because, apart from southwestern Long Island, the Plum and Gardiner's Island colonies harbored the only Glossy Ibis, and Plum Island the only Little Blue or Louisiana Herons (with one exception), we believe the Gardiner's Island-Plum Island heronries form one breeding population.

Figure 4. Huckleberry Island heronry/gullery, in Long Island Sound off New Rochelle, Westchester County. Looking south, picture was taken in June 1978. Arrow marks City Island, Bronx County.

Figures 5 and 6. North (N) and South (S) Brother Islands, in East River just north of Hell Gate and Triboro Bridge. Photos looking southwest, taken June 1979. Arrows indicate World Trade Center towers.

2. *Gulleries*. Two new Herring/Great Black-backed breeding areas were located, *Huckleberry Island* in 1975 and *North and South Brother Islands* in 1978. Huckleberry Island (Fig. 4), first had Herring Gulls in 1976 (four

Figure 7. Plum Island heronry/gullery, looking west towards Orient Point. Arrow marks heronry; main gullery is in open area out of view to the left of picture. Photo taken June 1978.

pairs), which increased to 27 pairs by 1978; the first pair of Great-backed Gulls in 1977 increased to two pairs in 1978. Gulls nested near and among bushes on the bare rocks around the edge of the island. The nearest gull colonies are on North and South Brother Islands, and possibly in the Greenwich, Connecticut area some 14 mi. northeast, where the first reported Herring Gull nest was located in 1978 (Smith *et al.,* 1978: 1143–44).

Both North and South Brother Islands (Figs. 5 and 6) supported gull colonies, while only South Brother had a heronry. In 1978, the year of discovery, an estimated 113 pairs of Herring Gulls and 8 pairs of Great Black-backs were nesting on South Brother, while 135 Herring Gull nests and 5 of Black-backs were found on North Brother. Nests ringed the bare soil and exposed rocks between the high-tide line and dense central vegetation on South Brother (Fig. 8), while on North Brother they were scattered in the open grass and shrubs around and between the buildings, as well as on various parts of the buildings including roofs (Figs. 9 and 10). The nearest gulleries to the Brother Islands are on Huckleberry Island, on Hoffman Island, and in Jamaica Bay; distances to these colonies have already been given.

3. *Tern colonies.* No significant new tern or skimmer colonies were located during this study, with the exception of the precarious

Figure 8. South Brother Island, East River: closeup of Herring Gull nesting sites in sandy area between high-tide line (near rocks) and heavily vegetated center of island. Photo taken June 1978.

Figure 9. Open grassy portion of North Brother Island gullery, looking southwest in June 1979. Arrow marks gull nest.

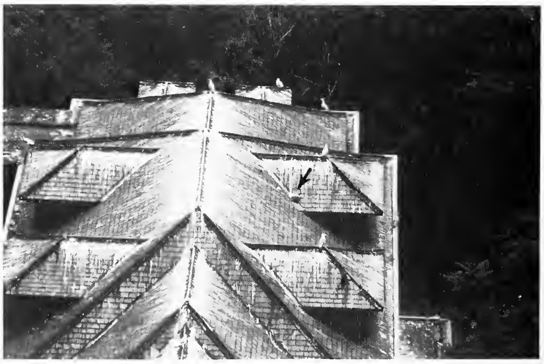

Figure 10. Roof-nesting Herring Gulls on North Brother Island, June 1979. Arrow indicates incubating bird.

Lane's Island Common/Roseate Tern and Black Skimmer marsh colony, discussed in Section IV. Likewise, while no major new Least Tern colony was found, previous workers had drastically underestimated the numbers nesting on the central North Shore, and along Peconic Bay (*sensu lato*). These populations will also be discussed in Section IV.

C. *Unexpected distributions and miscellany.*

1. *Herons.* The virtual restriction of small dark herons to southwestern Long Island, to which Glossy Ibis were almost but not quite as restricted (*cf.* Tables 3 and 4), was striking. The reasons for this distribution, beyond mere marsh acreage requirements, are not at all clear at this time and deserve investigation. Cattle Egrets breeding on Long Island appeared to occupy a rather narrow niche, being terrestrial feeders along airport runways (Kennedy Airport, "served" by the Ruffle Bar and Pearsall's Hassock colonies) or on landfills (in the Hackensack Meadows, "served" by the South Brother Island colony). Occasional pairs have nested at Jones Beach, feeding along the grassy parkway medians and shoulders, but they have not persisted. Long Island's vestigial dairy herds have never supported a Cattle Egret population, rather in contrast to the situation in New Jersey and farther south, and for reasons unknown.

We have the nagging feeling that there is

TABLE 3

Maximum and Minimum Counts of Herons and Ibis at the Nine Major Areas of Fig. 3

Numbers in brackets are the years each species was present in each colony; dashes indicate non-occurrence in 1974-78. GE: Great Egret; SE: Snow Egret; CE: Cattle Egret; LBH: Little Blue Heron; LAH: Louisiana Heron; BCNH: Black-crowned Night Heron; GI: Glossy Ibis; H^m: area of heronries depicted on Fig. 11.

	GE	SE	CE	LBH	LAH	BCNH	GI
H^1	2-26 [5]	20-135 [5]	—	1,2 [2]	1 [1]	6-45 [5]	5-10 [5]
H^2	1 [1]	1-13 [5]	—	—	—	30-100 [5]	1-5 [5]
H^3	—	12,50 [2]	—	—	—	1,4 [2]	1,3 [2]
H^4	—	1-2 [4]	—	—	—	20-48 [4]	—
H^5	1-5 [4]	25-128 [5]	—	—	1 [1]	40-92 [5]	—
H^6	3-14 [4]*	5-44 [4]*	—	—	—	8-31 [4]*	—
H^7	—	80**	30**	—	—	76**	—
***H^8							
H^m	187-404 [5]	610-1314 [5]	14-36 [5]	9-32 [5]	7-18 [5]	295-443 [5]	455-883 [5]

*Colony not found until 1975
**Colony not found until 1978
***Colony not censused

TABLE 4

Distribution of Breeding Pairs of Waders on L.I. in 1974-78

"Southwestern L.I." refers to main breeding area west of Fire Island Inlet on south shore: the cross-hatched area of Fig. 3, and the entirety of Fig. 11.

	1975 pairs/percent	1975 pairs/percent	1976 pairs/percent	1977 pairs/percent	1978 pairs/percent
Southwestern L.I.	1641/84%	2249/88%	2663/92%	2722/87%	2240/78%
all others	324/16%	301/12%	244/ 8%	425/13%	647/22%
TOTAL LONG ISLAND	1965	2550	2907	3147	2887

still an undetected "white" heronry somewhere near and "serving" the eastern end of Great South Bay, and Moriches and Shinnecock Bays; birds of unknown origin are frequently seen there, although not in large numbers. Distance renders it unlikely that Jones Beach area heronries, or those on Robins, Gardiner's and Plum Islands, supply these birds.

Comment on Yellow-crowned Night Heron, in this study a species more remarkable for its absence than its numbers, is in order. As Table 5 indicates, the maximum recorded was 47 pairs in 1974 (erroneously given as 93 pairs in Buckley and Kane 1975: 133), dropping abruptly to 12 pairs in 1975 and never rising beyond 23 pairs (1978). While the reservations mentioned earlier certainly apply, it would seem the numbers in the areas we censused dropped precipitously after 1974. And although this species historically had been found in some numbers away from the south shore and its mixed-species heronries, many former colony sites have long since been destroyed by development. Whether or not the birds displaced moved to adjacent areas remains unknown. However, there is one bright spot—the largest group we found was 25 pairs along the Loop Causeway in 1974, a number previously exceeded only once—Tobay Pond, 30 pairs in 1956 (Bull, 1964)—and individual colony maxima of eight, eight, and nine pairs in 1975, 1976, and 1977 had also previously been exceeded by only two higher counts (of 10 and 15, once each), so perhaps Long Island Yellow-

TABLE 5

Summary of All Colonially Breeding Waterbirds in the Long Island Area from 1974-78, as Reported in This Study

All data are in pairs; other conventions are discussed in the text. GBH = Great Blue Heron; GE: Great Egret; SE: Snowy Egret; CE: Cattle Egret; LBH: Little Blue Heron; LAH: Louisiana Heron; BCNH: Black-crowned Night Heron; YCNH: Yellow-crowned Night Heron; GI: Glossy Ibis; GBBG: Great Black-backed Gull; HG: Herring Gull; LG: Laughing Gull; CT: Common Tern; RT: Roseate Tern; GBT: Gull-billed Tern; LT: Least Tern; BSK: Black Skimmer. Column totals exclude YCNH, GBH [the latter occurred only at Sandy Hook, N.J.]

	1974 pairs/ colonies	1975 pairs/ colonies	1976 pairs/ colonies	1977 pairs/ colonies	1978 pairs/ colonies	Means
GE	252/7	410/13	298/14	311/13	216/12	297
SE	730/9	932/17	1398/18	1401/15	1228/21	1138
CE	16/3	14/4	21/2	15/1	66/3	26
LBH	34/4	20/5	11/4	9/3	25/5	20
LAH	13/3	14/5	8/3	10/4	18/4	13
BCNH	455/11	516/16	430/18	509/19	760/23	534
[YCNH]	[47]/[4]	[12]/[2]	[17]/[4]	[21]/[6]	[20]/[10]	[23]
GI	465/11	644/14	741/16	892/17	574/18	663
GBBG	1838/21	1307/22	1243/24	1702/27	1503/36	1519
HG	16764/27	20768/28	15691/28	14428/35	10985/45	15727
LG				→	1/1	
CT	11128/34	12329/39	14972/40	13918/43	14005/54	13270
RT	1854/9	1694/11	979/9	924/8	618/7	1214
GBT	→	2/1	1/1	0/0	2/1	
LT	1719/31	2628/34	2491/38	2188/29	2237/47	2252
BSK	339/13	458/10	495/12	342/10	458/12	418
[GBH]	[14]/[1]	[8]/[1]	[4]/[1]	[4]/[1]	[0]/[0]	
Totals	35607	41736	38779	36649	32693	37094

→ = year of discovery

crowns are holding their own. Colony occurrence figures for the five years are four, two, four, six, and 10 pairs, so while Yellow-crowned Night Heron may not be the most numerous heron on Long Island, neither is it the least numerous. We have never seen a breeding population estimate for all of Long Island, but suggest that in the period of this study it is not likely to have been in excess of 50 pairs, and in some years might have been as low as 25 pairs.

A final word on herons concerns the colony establishment and abandonment (turnover) rates of heronries concentrated on the south shore of western Long Island (Figs. 11, 12, 13). While this will be the subject of a separate paper, a few points are pertinent here: (1) colony sites were abandoned and then reused with unexpected frequency; (2) site fidelity in the colonies beyond the southwestern shore was, by comparison, extraordinarily high, suggesting a greater shortage of suitable sites in those areas; (3) spoil islands or elevated spots in marshes, with shrubbery or preferably trees, seemed the preferred habitat, but some colonies were on the ground in *Phragmites;* (4) freedom from disturbance while winter and early spring roosts are established and maintained may be critical to colony use in the ensuing breeding season; (5) protection of a series of alternate colony sites may be more critical on southwestern Long Island than elsewhere.

2. *Gulls.* Gulls on Long Island appear to be more colonial than terns, with only a few pairs of Herring Gulls (Table 6) and even fewer of Great Black-backed Gulls (Table 7) not found in 11 major colony areas outlined in Fig. 3.

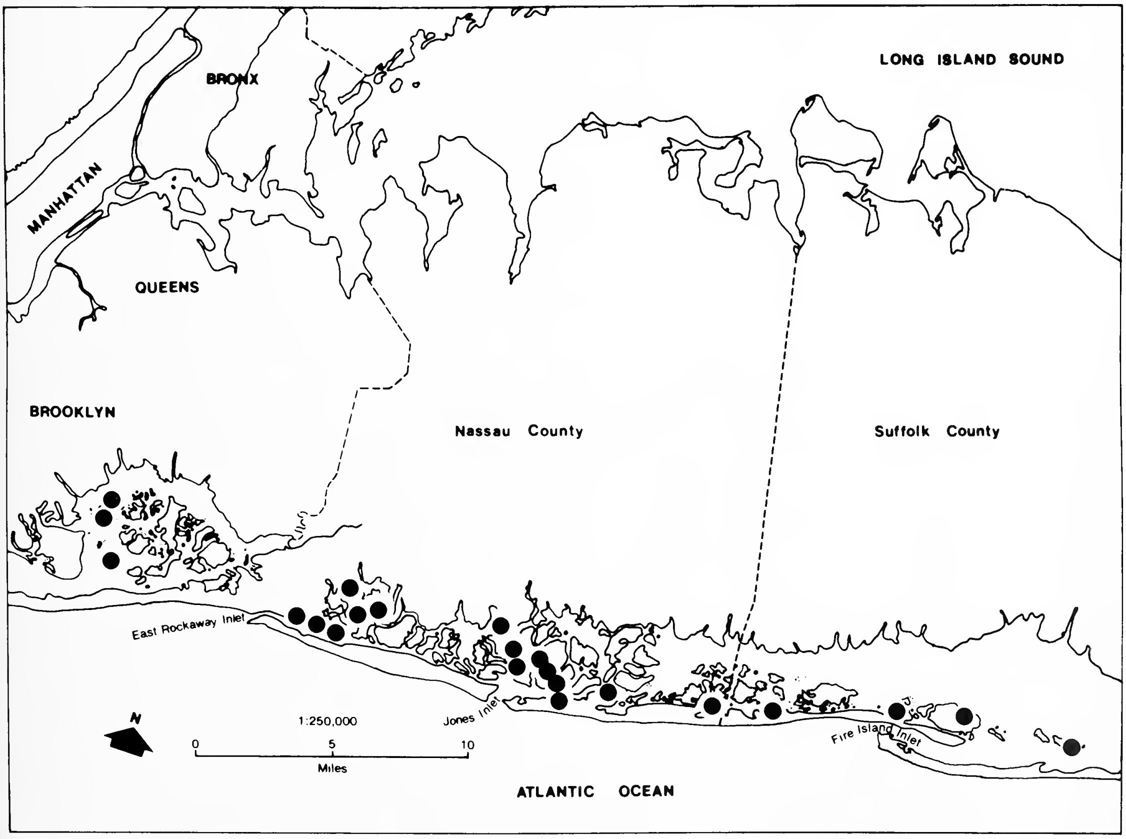

Figure 11. Sites of heronries in the marshes of southwestern Long Island in 1974–1978. Not all sites were used in all years.

Figure 12. Nascent heronry at East Fire Island, Great South Bay, in low bushes and vines on a former dredge spoil site. Photographed June 1978, looking west/southwest.

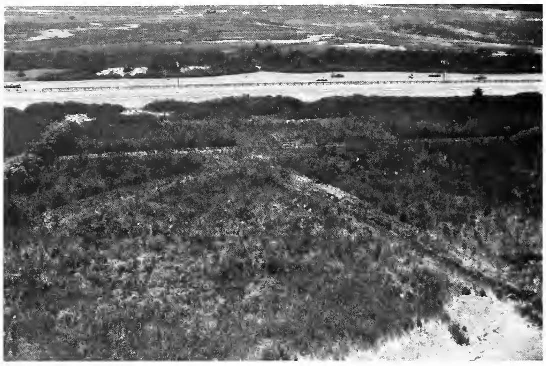

Figure 13. Snowy Egret-Glossy Ibis colony along the Meadowbrook Causeway, Jones Beach. On the ground in *Phragmites* and bayberry, this colony has moved over the years of the study. Photo looking west across Meadowbrook Parkway; Jones Beach is out of view to the left.

Two features of the distribution of these areas are noteworthy: there are no Herring/Great Black-backed Gull colonies anywhere in Peconic Bay, even on Robins Island, and we have only once found breeding Herring Gulls along the entire north shore of Long Island between Orient Point and the Bronx-Whitestone Bridge (five pairs at Stony Brook Harbor in 1978). While the absence of Herring Gulls in the two areas supporting between 50% and 70% of Long Island's Least Terns (see Section IV) is probably coincidental, the gullery apparently developing at Stony Brook Harbor bodes ill for the Common Tern colony there, and its eventual spread eastward to Port Jefferson Harbor and westward to Lloyd Neck seems certain. A final gull distribution note—Gardiner's Island is clearly the center of Long Island's Great Black-backed Gull population. This probably reflects, among other things, the Great Black-back's role as a littoral and offshore natural food scavenger/predator, as opposed to a littoral/mainland artifact scavenger such as Herring Gull.

3. *Terns.* The most noteworthy aspects of Long Island's Common Tern colonies emerging from our study were their ubiquity in marshes, and their unexpected stability. The former is discussed in Section IV, and the latter will be treated elsewhere.

IV. QUANTITATIVE RESULTS

A. *Colony numbers and population sizes.*

1. *Herons. Great Egret* (*Casmerodius albus*) appears to be holding its own on Long Island, occurring in 7–14 colonies each year, and while its lowest numbers were in 1978 (216 pairs), we do not feel this represents a downward trend. However, as about half the Long Island population (40%, 54%, 52%, 45%, and 51% for the five years) was in one colony near the Storehouse (Fishing Station) at Jones Beach (Figs. 14, 15), Great Egret may be more vulnerable than most herons to catastrophe. The maximum count for one heronry was 220 pairs in 1976 at the Storehouse colony, a significant increase over the 50 pairs reported for Jones Beach in 1973 by Bull (1974). Additional colony sites beyond those mentioned in Bull (1974) and outside the hatched area of Fig. 3 (where the species occurred in almost all colonies) were Plum Island, Stony Brook Harbor, and Huckleberry Island. (See Table 3 for number of years present in those colonies.)

Snowy Egret increased greatly in at least the first half of the 1970s, and between 1974 and 1976 almost doubled its Long Island breeding population (Fig. 16, Table 5). While the number of colonies in which it occurred between 1974 and 1975 also almost doubled, that growth has levelled off at about 17–21 colonies; we feel it is too early to say if the apparent slow-

TABLE 6

Numbers of Breeding Pairs of Herring Gull in the L.I. area in 1974-78
Numbers below "LI Totals" are those breeding outside the nine major colony clusters on this table. Areas reading down this table correspond to the first nine areas of Fig. 2.; n.a. = not applicable

	1974	1975	1976	1977	1978
Plum Island	996	1000	740	900	790
Gardiner's Island	6318	8093	5575	4481	3020
Shinnecock Inlet	557	538	520	475	375
Moriches Inlet	803	180	350	457	290
Fire Island Inlet	1843	2894	2728	1802	1523
Jones Inlet	1466	1810	1445	1636	1153
Lawrence Marsh	492	175	345	375	484
Jamaica Bay	3329	4568	2959	3448	2292
Lower N.Y. Bay	910	1500	1012	824	742
Totals:	16734	20758	15684	14398	10669
LI Totals:	16764	20768	15691	14428	10985
	30	10	7	30	n.a.

TABLE 7

Numbers of Breeding Pairs of Great Black-backed Gull in L.I. Area in 1974-78
Numbers below "LI Totals" are those breeding outside the nine major colony clusters on this table. Areas reading down this table correspond to the first nine areas of Fig. 2.; n.a. = not applicable

	1974	1975	1976	1977	1978
Plum Island	5	45	50	75	62
Gardiner's Island	1572	1085	910	1278	1172
Shinnecock Inlet	72	56	58	78	60
Moriches Inlet	48	10	33	23	20
Fire Island Inlet	54	44	50	61	57
Jones Inlet	22	6	30	25	24
Lawrence Marsh	3	0	17	7	13
Jamaica Bay	49	36	81	146	71
Lower N.Y. Bay	9	20	13	8	12
Totals	1834	1305	1242	1701	1491
LI Totals	1838	1307	1243	1702	1503
	4	2	1	1	n.a.
Gardiner's Island percent	86%	83%	73%	75%	78%

ing of the Snowy Egret's extraordinary population increase is real. Maxima of 150 nests at Canarsie Pol in 1965 and 180 nests at Lawrence Marsh in 1967 (Bull, 1974) were exceeded in every year of this study, with 250 pairs at Tobay Heading, 250 pairs at Pearsall's Hassock, 240 pairs at Ruffle Bar, and 225 pairs at the Storehouse in the 1976 peak year. Out-

Figure 14. Aerial view of Storehouse and West End area, Jones Beach State Park. Gullery occupies most of sandy area in center of picture, and a Great Egretry can be seen in the tall Japanese Black Pines marked with an arrow. Jones Inlet is marked JI; photo looking southwest, June 1976.

Figure 15. Close-up of Great Egret colony in Figure 14. Photo taken June 1976.

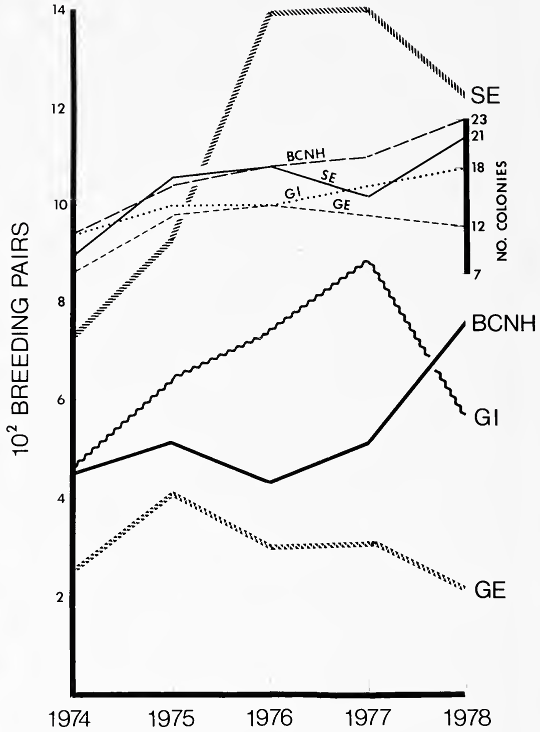

Figure 16. Selected heron-ibis population and colony trends for Long Island, 1974–1978. SE: Snowy Egret; BCNH: Black-crowned Night Heron; GI: Glossy Ibis; GE: Great Egret.

side of the hatched area of Fig. 3, where the bulk of the population breeds, Snowies nested in the following colonies beyond those reported in Bull (1974): Plum Island, Robins Island, Stony Brook Harbor, Huckleberry Island, and South Brother Island; see Table 3 for details.

Cattle Egret retains only a toehold as a breeder on Long Island. During this study it was found only at Zach's Bay (1974: two pairs); Storehouse (1975, 1976: one pair); Pearsall's Hassock (1974: 10 pairs; 1975: two pairs; 1978: eight pairs); Ruffle Bar (all five years: four, 10, 20, 15 and 28 pairs), Canarsie Pol (1975: one pair), and South Brother Island (1978: 30 pairs). It does not appear likely soon to become a dominant member of the Long Island waterbird avifauna.

Little Blue Heron also barely breeds on Long Island: the colony maximum of six pairs at Lawrence Marsh in 1961 (Bull 1974) has been exceeded, but not often. An estimated 20 pairs in the Seganus Thatch colony in 1973 (Buckley and Davis 1973: 848) reached 30 pairs in 1974, dropped to 11 in 1975, and never again came near those numbers. Ten at Tobay Heading in 1978 was the only count above 6 in one colony after 1975, and it has never occurred in more than 5 colonies in any one year. With 1973–77 totals of 27, 34, 20, 11, and 9 pairs, one might have prepared for Little Blue Heron's departure from Long Island's breeding avifauna, but 25 pairs nested in 1978, so the shaky situation presists. Outside of southwestern Long Island, we found this species only at Plum Island in 1974 (2 pairs) and 1975 (1 pair) but no nests were seen. It is most reliably found in the moving heronry complex involving sites at Tobay Heading/Gilgo/Seganus Thatch, and in lesser numbers at Pearsall's Hassock; we have never found it in the Jamaica Bay colonies.

Louisiana Heron's Long Island distribution follows that of Little Blue in many respects. Bull (1974) recorded only 4 "proven" nestings, of single pairs, but he did list 12 pairs in 1973 from the Jones Beach area. There were actually 13–14 pairs (Buckley and Davis 1973: 848), and total Long Island breeding pairs of Louisiana Heron in the period 1973–1978 were 13–14, 13, 14, 8, 10, and 18. Ten pairs each at Seganus Thatch in 1974 and at Tobay Heading in 1978 were colony maxima. Outside the hatched area of Fig. 3 we have recorded only single Louisiana Heron pairs at Plum Island (1976) and Stony Brook Harbor (1974); nests were not seen in either case. The Louisiana Heron is not well established on Long Island, and except for occasional pairs in Lawrence Marsh is virtually restricted to the Jones Beach area. We have recorded only one pair (1978) at Jamaica Bay, where the species first nested in New York State in 1955.

Black-crowned Night Heron is the "traditional" breeding heron of Long Island, although judging by counts during the 1930s, its present numbers and average colony size represent a drastic reduction. In 1935 Allen (1938) reported 3,400 pairs in 20 heronries, the largest of which contained an estimated 600 pairs. The average size of his heronries (188 pairs) was significantly larger than the average size (33 pairs) of the 23 heronries we censused in 1978 (t = 4.490, 41 df, $P < 0.001$). Strikingly, most of his colonies were inland, not along the south shore where most are today. In our five years of surveying, we were able to locate a Black-crown night heronry in only *one* of Allen's locations: Gardiner's Island. He reported three colonies and 750 pairs there, but we had one or two colonies with a combined maximum of only 104 pairs. And while we did find night herons in as many as 23 different colonies in one year (1978), our maximum count for all of Long Island was only 760 pairs (1978). Although we have possibly missed more night herons of both species than any other colonial waterbird during our five-year study, these would all have been small groups at "inland" locations, as larger groups would almost certainly have been reported by local bird clubs. One can only conclude that the Long Island Black-crown population has genuinely decreased over the last 40 years.

Erwin (1979), on the basis of empirical regression analyses of adults observed against known numbers of nests from Massachusetts colonies, feels that a conversion factor of × 4.0 is closer to reality for Black-crowns. Using this factor, the maximum for Long Island for 1978 would become 3,040 pairs, slightly less than the estimated population in 1935; the Gardiner's Island maximum count (the highest in our study anywhere on Long Island) would go to 416 pairs, closer to its earlier maximum of 750. and closer still to the 600-pair largest single colony in 1935, at Great Neck. This would all be most heartening *except* that Allen's data are all given as [estimated] pairs, not [counted] nests, with no additional details, so Erwin's 4.0 factor might equally apply to them. Nonetheless, Black-crown is still the ubiquitous heron on Long Island, having been found in all but two colonies. (Snowy Egret is a close second, not occurring with Black-crown in only five occasions.) Furthermore, the trend for breeding pairs and colonies of Black-crowns in the present study period seems clearly up (Fig. 16). We found new colonies apparently unrecorded in Bull (1974) at Robins Island, Huckleberry Island, South Brother Island, and possibly also Plum Island.

Glossy Ibis, like Snowy Egret, underwent a rapid population expansion during the period of this study, its numbers almost doubling between 1974 and 1977 (Table 5, Fig. 16). Concurrently, the number of colonies occupied each year rose uniformly from 11 to 18. In this study, outside the hatched area of Fig. 3 we have recorded ibis only in the colony on Plum Island and in both Gardiner's Island colonies, although never more than 10 pairs on the former and five in the latter. In 1972 there were 75–100 pairs estimated on Gardiner's Island (Buckley and Davis, 1973: 848), but these numbers were never approached again. That year between 500 and 1000 pairs were believed nesting on Long Island, with more than 500 along the Jones Beach strip (Buckley and Davis, 1973: 848)—numbers approached again only in 1977. While no systematic helicopter censusing was done in 1973, that year may have seen peak numbers of breeding Glossy Ibis across the entirety of Long Island. Between 1974–1978, colony maxima were almost split between Pearsall's Hassock and Ruffle Bar, with figures in the peak years of 1975, 1976, and 1977 as follows: Pearsall's Hassock 220, 200, 257; Ruffle Bar 105, 205, 312. Only one other count topped 100 pairs (122 at Zach's Bay in 1974), so the Glossy Ibis center of Long Island is clearly to the southwest.

2. *Gulls. Herring Gull* underwent a great population increase in the northeastern United States in the early part of this century, but its population across New England was stabilizing in the 1950s and 1960s (Drury and Kadlec, 1974). At the same time the species was extending its range south of New York, and in the 1970s it is viewed as "expanding rapidly" in the area from New Jersey to Virginia (Erwin, *ms.*). Long Island data have been equivocal, with island-wide censuses all but lacking. Bull (1974) did not indicate whether he thought the Long Island Herring Gull population was stable, increasing, or decreasing, but Drury (1973: 291) listed its "western Long Island Sound" and "Block Island Sound" populations as doubling between 1953 and 1973. Drury and Kadlec (1974) subsequently concluded that between 1965 and 1972 the population between New Jersey and New Brunswick had increased little, owing to a decrease in productivity, and that competition for scarce resources (most likely suitable nest sites) was probably the limiting factor. Those authors noted that gulls "at present" (1973) in colonies in southern New England and New York were "acting as if the colonies were fully occupied, although land area was still available," in contradistinction to their observation that "only a few years ago" the Nantucket and Block Island Sound populations were thriving.

Our data (Table 6) for the entire Long Island area reveal a peak population in 1975, with marked drops in 1976, 1977, and 1978. Discussion in Section IV will examine in more detail data from the nine major breeding areas over this period, but the decline is general and real. It is important to note that in 1976 we first noticed large empty areas which previously had been occupied portions of colonies, as well as great numbers of idle, adult-plumaged gulls, not in "bachelor groups" but standing in clusters of pairs within or near the colonies. These phenomena seemed to increase in 1977, and in 1978 were so prevalent that numbers of non-breeding "adults" were recorded in case the trend was more than short-term. That year the proportion of assumed non-breeders ranged from 19% in the Bostwick Point colony, through 57–73% in the four Jamaica Bay colonies, to 62% and 75% at Plum Island and North Brother Islands respectively. A similar phenomenon was noted in New England, where between 1962 and 1965 Drury and Kadlec (1974) found that about 20% of the adults were not breeding, and while they had no data to indicate that the percentage of non-breeders had increased subsequent to 1965, they stated that "rapid replacement of adults that were removed from breeding colonies in recent years suggests that competition for territories is intense." Data for Long Island should be collected again as soon as possible. It will be interesting to see if and when the "wave" of non-breeding reaches the now-exploding New Jersey population (Buckley, 1977, 1979; Burger, 1977; Kane and Farrar, 1976, 1977).

Herring Gull colonies on Long Island were concentrated in 11 areas (Fig. 2), and in a population ranging between almost 11,000 and almost 21,000 pairs, no more than 72 pairs were found outside those areas in any given year. The largest colony cluster was on Gardiner's Island, the second largest at Jamaica Bay, and the third at Fire Island Inlet (Table 6). Those at Gardiner's Island and at Fire Island Inlet (Fig. 17) appeared to obtain little of their food from garbage dumps, while those at Jamaica Bay probably obtained most of their food at dumps, producing a chicken-bone substrate in the Canarsie Pol colony. The largest aggregation was 8,100 pairs on Gardiner's Island in 1975, although this had dropped to 3,000 pairs three years later.

New colony areas unreported by Bull (1974) included Lawrence Marsh, North and South Brother Islands, Huckleberry Island, and Stony Brook Harbor. Numerous new actual colony sites within the other numbered areas of Fig. 2 will be detailed elsewhere. A trend of increasing colony sites each year (Table 5) is puzzling in view of the species' decline in numbers (see Part B).

Great Black-backed Gull distribution is strikingly different from that of Herring Gull. Each year between 73% and 86% of its population was in the Gardiner's Island colonies, the next three largest clusters being an order of magnitude smaller at Shinnecock and Fire Island Inlets, and Jamaica Bay (Table 7). As will be discussed in Part B below, Great Black-back seem to be holding its own on Long Island, and the size of the Gardiner's Island population between 1974–1978 (910–1572 pairs) makes it one of the largest on the eastern coast of the United States. (Drury [1973: 296] lists only *80 pairs* for all of Long Island as recently as 1972, a figure clearly in error.) As with Herring Gulls, the steady increase in the number of colonies in which Black-backs occur can not be related with any confidence to the size of Long Island's breeding population. Major new colony areas (Fig. 2) unknown to Bull (1974) include Lawrence Marsh, Hoffman and Swinburn Islands (Figs. 18, 19), North and South Brother Islands, and Huckleberry Island.

3. *Terns.* Nisbet (1973) synthesized the first estimate known to us of the *Common Tern* population of Long Island, arriving at 11,000–12,000 pairs annually between 1968–1972, although the total was a composite of data from different years. In our study period we censused between 11,100 and 15,000

Figure 17. Fire Island Inlet (crossed by bridge on left) and Captree State Park (in center and foreground). A large Herring Gull colony occupies the sandy and vegetated areas between the road connecting the Fire Island Inlet bridge with the mainland out of the picture to the right, even filling the traffic cloverleafs. Photo taken June 1978, looking southwest.

Figure 18. Herring and Great Black-backed Gull colony on Hoffman Island, Lower New York Bay. Verrazano Bridge at top right, and Staten Island on the left. Photo looking northwest, taken June 1979.

Figure 19. Herring and Great Black-backed Gull colony on Swinburn Island, Lower New York Bay. Hoffman Island is just visible at upper left; see Figure 18. Photo looking north, taken June 1979.

pairs each year. As significant portions of the population in 1974–1978 were marsh-nesting (*ca.* 20% each year; see Part B below), Nisbet's earlier estimate might have been low, and thus the Long Island population might have actually declined in the period 1968–1978 if the same percentage were marsh-nesting in each year between 1968 and 1978. We unfortunately do not know what percentage of terns was marsh nesting in 1968–72, so we cannot answer that question firmly. However, we do believe our data show either a slight Common Tern increase or at least no decline in the period 1974–1978, *contra* Nisbet's (1973) conclusion for New England.

In a mixed-method ground census of Common Terns on the eastern half of Long Island (east from Lloyd Neck on the north shore, and east from mid Fire Island on the south shore), Duffy (1977) found 5659 pairs in 13 colonies in 1972, and 6063 pairs in 20 colonies in 1975. Our census of that same area for 1974–78 is given in Table 8. Unfortunately, 1975 was the only year we overlapped Duffy, but comparison of results is still interesting. In 1975 we found about 7800 pairs in 26 colonies,* and we believe the additional 1700 pairs and 6 colonies we found was due to our being able (1) to overcome the re-nester movement problem by effectively simultaneous coverage, and (2) to cover all areas, however remote, by helicopter. Our population and colony figures are quite uniform across the five years, supporting this contention. It is difficult to say that our 1975 figure is more "accurate" than his, as he may well have detected re-nesters as well as late first nesters we could have missed. We do believe our method yields results that are more readily comparable from year to year, and we feel sure that we missed very few terns when we surveyed—which was each year at the optimal time on Long Island for nesting Common Terns.

At present it would seem that Long Island's Common Tern population is among the most stable on the east coast, and that distribution among many colonies (*cf.* Table 9) across a wide variety of habitats (Buckley and Buckley *in prep.*) is cause for guarded optimism. This is balanced somewhat by the fact that between 1974 and 1978, six colonies (Great Gull Island, Port of Egypt, Lane's Island, Moriches Inlet West Island [Fig. 20], Cedar Beach, and West End) accounted for 66–84% of Long Island's breeding population (Table 10), thus concentrating the population in only a few locations.

TABLE 8

Comparison of Data Obtained by a Mixed-method Ground Census of Common Terns on L.I. Sound and "Eastern L.I." as Defined by Duffy (1977), with Aerial Census Figures from the Present Study

For purposes of this comparison, Duffy's population and site numbers have been amended to bring his study area into conformity with ours by elimination of all Conn. shore and Fisher's I. data and we have counted even isolated single pairs of terns as "colonies."

	This Paper		Duffy	
	pairs /	sites	pairs /	sites
1972	—	—	5659	13
1973	—	—	—	—
1974	6556	27	—	—
1975	7796	26	6063	20
1976	8028	29	—	—
1977	6292	27	—	—
1978	7452	32	—	—

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*For purposes of this comparison only, we counted even solitary pairs as "colonies," and we modified Duffy's study area to exclude Fisher's Island and the Connecticut shore, thereby allowing comparison of both data sets.

TABLE 9

Maximum and Minimum Counts of Common Tern (CT), Roseate Tern (RT), and Black Skimmer (B Sk) at the Eight Major Colonies of Fig. 3 and Table 1

Numbers in brackets are the years out of five each species was present in each colony; dashes indicate non-occurrence at any time in 1974-78.

	CT	RT	B Sk
T^1	2000-2500 [5]	475-1100 [5]	—
T^2	496-1058 [5]	1,4 [2]	11-33 [5]
T^3	536-1175 [5]	6-561 [4]	18-31 [5]
T^4	1160-1550 [5]	1-124 [5]	32-83 [5]
T^5	2200-3300 [5]	24-55 [4]	78-162 [5]
T^6	1562-2500 [5]	—	31-166 [5]
T^7	412-1138 [4]	—	—
T^8	224-843 [4]	—	—

Studies by Gochfeld (pers. comm.) indicate that Great Gull Island, Cedar Beach, and West End fall clearly into the category of "seed colonies" (*sensu* Buckley and Buckley, 1976) and may be thus the most important of all Long Island tern colonies. The steady increase in the number of occupied colonies between 1974–1978 (Fig. 21) is probably beneficial to the Long Island Common Tern population, since the resulting dispersion minimizes impact from such catastrophic events as hurricanes and rat predation. Thus the even decline in size of the six main colonies (Table 10) is both reassuring and vaguely alarming.

It is clear that the largest colonies known from Long Island were found in days past (*cf.* Bull, 1974), although the present study's maximum (3,300 pairs, Cedar Beach, 1977) has apparently been exceeded only three times—4,000 pairs at Gull Island in 1886, and 6,000 pairs each at Orient in 1930 and at Moriches Inlet in 1963. Complete data on the numbers and locations of colonies historically occupied

Figure 20. West Inlet Island, Moriches Inlet. Site of major Common Tern and Herring Gull colonies in 1974–78. Dome-like structures at foreground and back center are sites of dredge spoil deposition. Looking east/southeast in June 1978; Moriches Inlet opening to ocean is just out of view to the upper right.

TABLE 10

Common Tern Population in the Six Largest Terneries on L.I., 1974-78

All data in pairs.

	1974	1975	1976	1977	1978
Gull I.*	2500	2500	2000	2000	2223
Port-of-Egypt	496	406	1058	820	828
Lane's I.	1175	920	828	536	675
Moriches Inlet West Island	1160	1495	1404	1214	1550
Cedar Beach**	2200	2550	2650	3300	2330
West End**	1800	2100	2500	1900	1562
Annual Totals:	9331	10071	10440	9770	9168
L.I. Totals:	11128	12329	14972	13918	14002
% in Main Colonies:	84%	82%	70%	70%	66%

*combination of Gull I. Project figures and our own aerial estimates

**combination of actual [new] nest counts and our own aerial estimates are apparently unavailable, so enumeration of sites first found in this study is not possible.

Roseate Tern was the only species this study showed to be declining dangerously on Long Island. Always only locally abundant on Long Island, which is paradoxically part of its historical center of abundance in the western North Atlantic (Cape Cod and eastern Long Island), the absolute Long Island population declined from almost 1,900 pairs in 1974 to about 600 in 1978, as did the number of colonies in which it occurred—a maximum of 11 in 1975 and a minimum of seven in 1977 and 1978 (Fig. 21). The only colonies in which Roseates occurred in all five years were Great Gull Island, Hicks Island, and Moriches Inlet West Island, although they nested somewhere on the Gardiner's Island/Cartwright Island complex in each of the five years. Thus, except for Moriches Inlet, all five-year sites were in the Block Island Sound/Gardiner's Bay area. Moriches Inlet is now the western-most locale where one can expect to find breeding Roseates, although its numbers for 1974–1978 fluctuated wildly (1, 124, 30, 26, and 51 pairs).

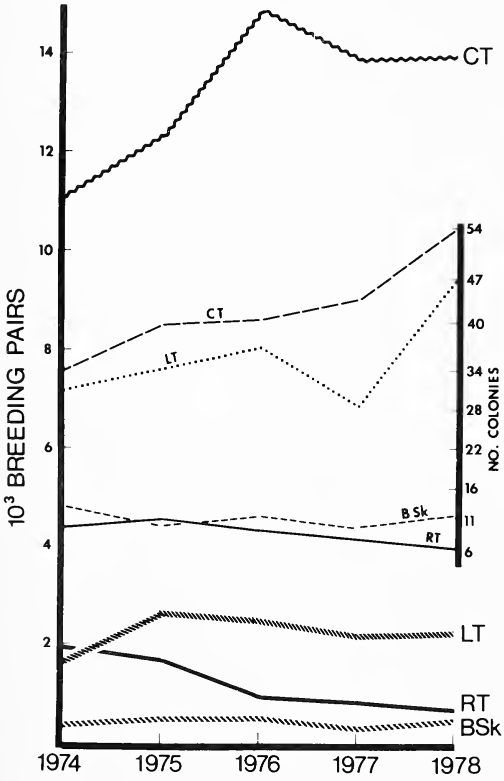

Figure 21. Population and colony trends for Long Island terns and skimmer, 1974–1978. CT: Common Tern; LT: Least Tern; BSk: Black Skimmer; RT: Roseate Tern.

Aside from Great Gull Island, where numbers for the five years were 1,100, 900, 800, 800, and 475 pairs, the Gardiner's Bay area, and the Lane's Island colony where rats were extirpating the Roseates (561, 276, 28, 6, and no pairs), no single colony between 1974–78 ever had more than the 62 pairs at New Made Island in 1975 or the 55 pairs at Cedar Beach in 1976. In sum, Roseate Terns on Long Island are being restricted more and more to the Gardiner's Bay/Block Island Sound area, and everywhere—even there—are declining in absolute numbers and in number of colonies in which they occur. Known reasons are several—rat predation, scarcity and defoliation of their preferred goldenrod and tall-grass habitat, and tidal flooding. However, these do not explain why the population is declining even on Great Gull Island, and why its range on Long Island is shrinking eastward. Roseate Tern is clearly the most threatened colonial waterbird on Long Island, and may merit formal classification as a United States Threatened Species.

Least Tern, on the other hand, may never have been more numerous on Long Island than it is today, where until this study its distribution had not been understood. As Table 5 and Fig. 21 indicate, Least Tern numbers were fairly constant for the five years, ranging between 1,700 and 2,600 pairs. Their number of occupied sites (discussed in more detail in Part B) varied enormously, from 29 in 1977 to 47 in 1978—years with almost identical numbers of breeding pairs. Colony size and turnover rate also varied widely, which is expected in a species with a fugitive breeding strategy using almost vegetation-free, pebble- and shell-strewn sand. This is a short-lived habitat where vegetative succession occurs rapidly, is subject to more frequent human disturbances than probably any other habitat used by Long Island waterbirds, and is created and then destroyed by man's construction and land-filling activities. In the New York Bight Least Tern so far has not been found even attempting to nest on salt marshes when displaced from its usual beachfront habitat. Roof-nesting, which is known from Florida (Fisk, 1978) and elsewhere, seems never to have been noted in our area; flat, pebble-covered shopping center roofs along the north shore of Great South Bay and other bays in Nassau and western Suffolk Counties might be profitably investigated.

Bull (1974) records maximum Least Tern colonies of 120 (once), and 200 (three times) pairs. Yet in 1973 a colony at Eaton's Neck was estimated to contain 600+ pairs (S. Ruppert *in* Buckley and Davis, 1973: 850), and in subsequent years it had 475 pairs (1975), 851 pairs (1976), 702 pairs (1977), and 506 pairs (1978). The importance of north-shore Least Terns is discussed in Part B. Numerous other colonies in the 100–400+-pair range were found in this study, on the north shore, on Peconic Bay, and along the south shore from Mecox Bay as far west as Breezy Point. No new sites were found in this study beyond the major concentrations along the north shore and on Peconic Bay (see Fig. 2). Despite extraordinary pressure from people, Least Tern appears to be holding its own on Long Island, the same conclusion reached for Cape Cod by Blodget (1978), who also concluded that its present numbers may represent a population maximum—popular sentiment to the contrary.

Black Skimmer is essentially at the northern edge of its range on Long Island, although each year a handful of pairs nest in southeastern Massachusetts. Its population has apparently been more or less stable for the past 25 years, and in the period reported here its numbers and the number of colonies in which it occurred varied little (Fig. 21, Table 5). Colony growth and interactions between Cedar Beach and West End were discussed in detail by Buckley, Gochfeld, and Buckley (1978), and these two areas had the highest populations during this study—162 and 160 pairs in 1976, with 166 pairs at West End in 1978. The apparent drop in maximum colony size from those reported by Bull (1964, 1974) may or may not indicate a slight decrease in the Long Island population recently, but not enough data are available to determine this. Black Skimmer has always been rare away from the major inlets (and their large Common Tern colonies) on the south shore of Long Island, and during this study we never found breeding skimmers away from Commons, although one pair of each on John Boyle Island in 1976 came close. Bull (1974) noted only three breeding attempts on the North Shore proper, and only a few pairs sporadically on Peconic Bay, except for a group varying between 11 and 33 pairs (increasing each year) at Port of Egypt, Southold. The still, shallow waters they require for feeding are apparently scarce away from south shore bays.

Noteworthy were marsh-nesting skimmers in three Long Island locations, apparently the first found there. At Lane's Island between 18 and 31 pairs nested with Common and Roseate Terns for the five years, most nest scoops being in tiny patches of bare sand among the tidal wrack, although a few nests were actually placed atop wrack composed of dead *Spartina alterniflora* culms or eelgrass (Fig. 26), and on nearby Tiana Island one pair nested with Commons on *Spartina* wrack in 1974. In the Black Banks Island Common Tern colony where Gull-bills were found breeding in 1975, skimmers nested with Commons in an essentially marsh situation: the area was subsiding, was being rapidly colonized by *S. alterniflora,* and was entirely flooded during spring and storm tides. In 1975, 15 pairs, and in 1976 21 pairs, nested here, but none subsequently despite persistence and growth of the tern colony, still present in late June 1979. In the five years we found skimmers in a total of 18 colonies, details of which will be published elsewhere.

B. *Detailed population and colony analyses of selected species.*

1. *Herring and Great Black-backed Gulls.* Tables 6 and 7 record the numbers of breeding pairs of each species in the nine major areas for which five years of data are available. Are the populations in the nine major areas behaving independently each year?, or, across the years, is there a general pattern to which all colonies seem to be adhering? The analytical approach used to answer these questions was to assign a rank to each colony area across the five years,

ranking the largest population for each year 1, and so on down to the lowest population for each year, ranked 5. Friedman's 2-way ANOVA (*cf.* Siegel, 1956) sets the null hypothesis as no difference between summed ranks for each column (the years); for Herring Gull the test yields $Xr^2 = 14.40$, 4 df, P ⅓ 0.01. For Great Black-backed Gulls, $Xr^2 = 9.87$, 4 df, P ⅓ 0.05. These results—that the summed columns differ significantly among one another—are interpreted to mean that (a) Herring Gull colony numbers were uniformly declining in 1976–1978, following uniform peaking in 1974–1975; (b) Great Black-backed Gull colonies were also behaving similarly, but the conformity was much weaker although still statistically significant; (c) as noted in Table 11, the *relative* tendencies are rather different, the Black-backs peaking in 1977, Herrings in 1975, and Black-backs evidencing no great decline.

Similar analysis using the parametric two-way ANOVA without replications yielded for Herring Gull an F of 33.63, 8 df, $P < 0.001$ for area counts, and an F of 3.44, 4 df, $P < 0.015$ for year counts; thus the average colony size difference is very highly significant (expected) and the inter-year difference is highly significant, to about the same level determined by the non-parametric Friedman test. For Great Black-backed Gull, the area F was 108.42, 8 df, $P < 0.001$, and the year F was 1.01, 4 df, n.s. This suggests that, aside from the obviously significant area numbers difference, the years were not significantly different from one another across all colonies; that is, they were not behaving similarly in terms of their population fluctuations. It may be an arguable mathematical question whether data distributions are rendering dubious the results of the Black-back parametric analysis, but probably not an arguable biological question—the parametric test found no significance, the nonparametric one just barely demonstrated significance. The point is that Black-backs are certainly behaving differently from Herring Gulls on Long Island (aside from their obvious distributional differences) and that they are weakly or not at all "coordinated" between and among colonies. That is to say, each colony is more or less responding to different resource pressures determining its population growth tendencies, which is quite different from the pan-colony response that seems to be occurring in Herring Gulls.

The decline in Herring Gulls in the Long Island area, first detected in 1976, has been marked not only by its occurrence in virtual lock-step across all nine major areas, but also by its precipitous nature—suggesting exponential decay, of which radioactive decay is a familiar example (*cf.* Batschelet, 1971). A least-squares exponential equation-fitting program was tried, using data for all nine areas for the four years from 1975 (peak) to 1978 (trough). The resulting equation ($y=24821e^{-0.20x}$) had an R^2 of 0.964, indicating an excellent fit for exponential decay. (See Fowler and Bigelow [1979] for possible problems with R^2 increasing as a function of slope as well as goodness-of-fit, apparently not a problem in this case.) While future population projections usually have little biological reality because many factors are constantly affecting population dynamics, it is indicative of the magnitude of "decay" that this equation predicts extirpation

TABLE 11

Upper Half: The Respective Ranks Each Year for the Entire L.I. Population of Herring and Great Black-backed Gulls; Lower Half: Summary of Friedman Two-way ANOVA-by-Ranks Analysis of Data in Tables 6 and 7

	1975	1975	1976	1977	1978
Herring Gull	2	1	4	3	5
Great Black-backed Gull	4	5	2	1	3
	Friedman Two-way Analysis of Variance by Ranks:				
Herring Gull	$X_r^2 = 14.40$, 4 df, $p < 0.01$				
Great Black-backed Gull	$X_r^2 = 9.87$, 4 df, $p < 0.05$				

of the Long Island Herring Gull population in about 50 years should the present rate of decline remain unchanged.

Possible reasons for such a rapid decline are not at hand, although Drury (1974) opined that intraspecific nest site competition was becoming intense (for unknown reasons), and suggestions have also been advanced that competition with the more aggressive Great Black-back for nest sites and possibly for food has increased. The recent and somewhat precipitous closure of large numbers of outfalls discharging raw or only primarily treated sewage, and of open garbage dumps (now replaced by "sanitary landfills") are doubtless contributing factors, as may be reductions in commercial fish catches and processing plants/fishing fleets. The full answer is likely complex, and might even involve pesticides, poisons, or pathogens—always suspected in precipitous population declines. A sudden increase in a parasite of some sort has been reported in Herring Gulls at the Fire Island Inlet area (D. B. Ford, pers. comm.), but details are not available.

2. *Common Terns.* Prior to this study, marsh-nesting Common Terns were believed extremely rare. But in fact, as Buckley (1977, 1979) pointed out, they were well known to Alexander Wilson in New Jersey in 1830, a fact that has escaped almost all subsequent authors, including Bent. Consequently, we too were quite unprepared for the large numbers we found nesting in Long Island marshes in 1974, and especially for the immense marsh colony at Lane's Island in Shinnecock Bay (Figs. 22, 25–27). It soon became apparent that marsh nesting was anything but uncommon on Long Island and as Table 12 shows, each year about 20% of the 11,000–15,000 pairs of Long Island Common Terns were nesting in marshes, apparently successfully to judge from colony stability. Table 13 presents Common and Roseate Tern data from some 12 marsh colonies from 1974–78, but statistical analyses will not be done here. The gross significance of the numbers in Table 13 is that (a) marsh colonies may be remarkably stable from year to year; (b) they may fluctuate wildly from year to year; and (c) they may desert and then reestablish at the same sites in unpredictable numbers. The

Figure 22. Lane's Island, Shinnecock Bay, site of the largest salt marsh Common/Roseate Tern colony on Long Island. Photo taken June 1978, looking southwest.

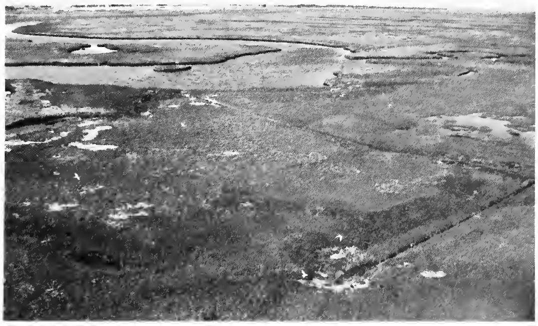

Figure 23. Close-up of Marsh colony north of Gilgo Beach, Jones Beach strip. Photo taken June 1977, looking south.

Figure 24. Aerial view of salt marshes in Great South Bay north of Cedar Beach, Jones Beach strip. Arrows indicate patches of high-tide-deposited drift atop which terns nest. Photo looking north in June 1978.

Figure 25. Close-up of marsh-nesting Common Terns and Black Skimmers at Lane's Island, Shinnecock Bay. Photo taken June 1977.

Figure 26. Black Skimmer nest on drift at Lane's Island, Shinnecock Bay. Photo taken June 1977.

braces indicate colony clusters at (proceeding down the Table) Shinnecock Bay, Hempstead Bay, and Jamaica Bay.

While Common Tern seems reasonably successful nesting in marshes, Roseate is far less so. Table 14 presents Roseate Tern data in a manner comparable to the Common Tern figures in Table 12. And although Roseate is generally declining on Long Island, it is faring especially poorly in marshes. It is not at all clear whether their overall decline is being mirrored in their marsh numbers, or whether their manifest lack of success in marsh nesting has been responsible for their decline. After all, in 1974 31% of Long Island's Roseate population was in marshes, and according to the late LeRoy Wilcox (pers. comm.), the Lane's Island colony had been especially non-productive. More likely their overall decline is a function of both these factors.

Although the number of marsh-nesting Common Terns on Long Island hovers around 20% each year, there are subtle differences in number that suggest a relationship between the total annual Long Island tern population and the fraction of that population nesting in marshes each year. To test this assumption, the data of Table 12 were analyzed by regression analysis, and although the sample size was only five, a highly significant linear relationship is indicated ($R^2=0.96$). The most parsimonious explanation for this effect—that is, that the percentage of marsh-nesting Common Terns increases as the total Long Island Common Tern population increases—is that suitable non-marsh nesting habitat is in short supply, forcing increasing numbers to the marshes each time the breeding population expands.

Figure 27. Nest (arrow) of Common Tern on tidal drift among *Spartina patens* at Lane's Island, Shinnecock Bay, Long Island. Photo taken June 1978.

TABLE 12

Percent of Common Terns Nesting in Salt Marshes on L.I. Each Year from 1974-78

	1974	1975	1976	1977	1978
# Colonies in marshes	10	17	20	24	33
# Pairs	1907	2138	3599	2941	3113
Fraction of Total LI Population	17.1%	17.3%	24.0%	21.1%	22.2%

TABLE 13

Pairs of Common Terns Nesting in Selected L.I. Salt Marsh Tern Colonies in the Period 1974-78

Braces connect colonies we believe form consistently interbreeding populations.
See text for additional discussion.

	1974	1975	1976	1977	1978
Lane's Island	1175	920	828	536	675
Tiana Island	25	75	56	64	17
Triton Lane Marsh	—	—	32	70	23
New Made Island	—	315	613	421	414
Jonas Creek Island	20	25	14	29	20
Goose Island	—	253	16	—	—
Cinder Island	268	3	—	124	31
North Cinder Island	—	—	20	35	—
Garrett's Marsh	5	13	22	28	15
Joco Marsh	—	89	425	432	406
Silver Hole Marsh	—	323	345	240	138
East High Meadow	—	—	368	322	193

TABLE 14

Percent of Roseate Terns Nesting in Salt Marshes on L.I. Each Year from 1974-78

	1974	1975	1976	1977	1978
# Colonies in Marshes	2	2	2	2	0
# Pairs	561	338	46	8	0
Fraction of Total LI Population	30.3%	20.0%	4.7%	0.9%	0%

Conventional wisdom points an accusing finger at Herring Gulls, but we believe them to be the culprits in only a few Long Island locations (Houde, 1977a, b). We suspect breeding habitat scarcity is more likely tied to development of coastal areas, human disturbance, and the increasingly unnatural condition of our barrier beaches, especially at inlets, where the low dune-hummock topography especially prized by Common Terns is almost gone on Long Island (see Buckley and Buckley [1977] for additional discussion).

Yet another aspect of marsh colonies impressed us during our censusing, *viz.* their generally smaller size when compared to non-marsh colonies. Data on colony size from a complete census of the ocean coast of New Jersey in 1977 were contrasted with those from Long Island that same year. The major points emerging were (a) New Jersey is so developed that there were not enough Common Terneries away from marsh locations to allow comparison with Long Island; (b) the mean size of Long Island and New Jersey salt marsh terneries was not significantly different, but (c) both Long Island and New Jersey salt marsh colonies were significantly smaller than Long Island non-marsh colonies (Table 15). Reasons for the small and unexpectedly similar sizes of New Jersey and Long Island marsh colonies are unclear, but may be a function of the area available on salt marsh islands for dead *S. alterniflora* culms to collect in large enough windrows (Figs. 23–26), and of the available patches of *S. patens,* (Fig. 27) both of these being favored locales for marsh colony establishment. Burger and Lesser (1978) attempted to identify those features common to all Common Tern colonies in their New Jersey study area, but did not comment on colony size limitations imposed by salt marsh features; the matter deserves investigation.

The large average size of non-marsh colonies on Long Island is significantly determined by the size of colonies located at or near the bay/ocean inlets along the south shore east of urban Rockaway and East Rockaway Inlets. Analysis of our data from colonies in the vicinity of those underdeveloped inlets (Jones, Fire Island, Moriches, and Shinnecock) suggested a fairly constant difference in the number of breeding terns associated with each inlet for each of the five years (Table 16). Inlets are well-known as concentration points for marine and shore birds, usually ascribed to the oxygenation achieved by ebb and flood of confined, rapidly racing inlet waters, which in turn leads to increased primary and secondary productivity of inlet waters. The small fishes fed on by Long Island Common Terns (*Ammodytes, Menidia, Fundulus, Cyprinodon*) are especially abundant and accessible at inlets and their attendant mudflats.

We thus hypothesized that the occurrence of large colonies at suitable, development-free inlets was directly related to the prey-fish productivity of each inlet. However, as quantitative data on non-game fish populations at these inlets are nonexistent, we were forced to look for some other, less direct, measure of possible inlet fish productivity. The most convenient variable was the tidal prism for each inlet, *i.e.*, the amount of water flowing through the inlet throat during each tidal cycle. Such data were obtained for the four inlets in question, and regression analysis was used to address the question of a possibly quantifiable relationship between inlet tidal prism and the number of pairs of Common Terns breeding at each of them for five years. (For such an analysis, the independent variable (X) is assumed to be measured without error for the more normal Model I regression analysis. Tidal prism data are extraordinarily difficult and expensive to obtain, and are constantly changing with inlet morphology, so in fact there may have been some measurement error, but we have ignored it. The consequences are generally not deemed critical unless statistical significance is marginal.) We obtained our inlet data from Dr. H. Lee Butler, Waterways Experiment Station, U.S. Army Corps of Engineers, who is a recognized authority on inlet tidal dynamics.

Figure 28 displays the line and equation resulting from the combined five years of data

TABLE 15

Comparison of Mean Colony Sizes for Marsh and Non-marsh Common Tern Colonies on L.I. and in New Jersey in 1977 Only

*** = significantly different at 0.001 level; NS = not significantly different.

Common Terns	Mean Colony Size in Birds [N]		
Long Island Non-marsh	600.6 [19]		***
Long Island Marsh	94.5 [24]	NS	
New Jersey Marsh	115.8 [47]		

TABLE 16

Numbers of Pairs of Common and Roseate Terns Nesting at Colonies in the Immediate Vicinity of the Four Major Undeveloped Oceanic Inlets on the South Shore of L.I.

Inlet	1974	1975	1976	1977	1978
Shinnecock	2170	1321	1466	972	933
Moriches	1282	1934	2061	1664	2452
Fire Island	2224	2590	2705	3358	2477
Jones	2034	2100	2504	1900	1562

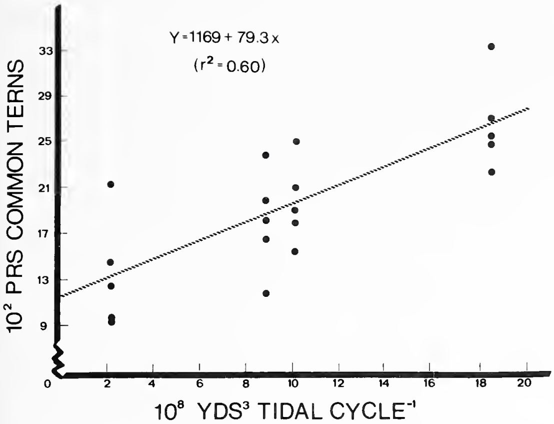

Figure 28. Linear regression of number of pairs of Common and Roseate Terns nesting in vicinity of the four major inlets on the south shore of Long Island, on the tidal prism of each of the inlets which are, reading from left to right: Shinnecock, Moriches, Jones and Fire Island. Individual data points over each inlet's tidal prism represent census figures for years 1974–1978. See text for additional discussion.

points. While there is some spread about the line and the R^2 is only 0.60, the line is very highly significant ($P<0.001$). We thus assume that inlet tidal prism, and in turn the fish population supported by that volume of water, was a major factor determining colony size at these four inlets. If we look at the data for each of the five years separately, we find that for 1975, 1976, and 1977 the relationship was even stronger, with R^2s of 0.97, 0.86, and 0.98. In 1974 and 1978 no statistically significant regression lines could be fitted to the data. We believe that the unexplained variance in the 1974 and 1978 data (all) and the combined five year set (40%) is likely due to variation in fish population, human and predator disturbance at colonies, and weather. For example, 1978 was the first year in the Cedar Beach colony following construction of the Southwest Sewer District pipeline cut, which removed a significant part of that colony; and 1974 saw the (abnormally?) highest population in the Lane's Island marsh colony, which subsequently was reduced to 43% of its 1974 size (by failure to obtain adequate food?). In sum, despite the inherent shortcomings of this technique, it would appear to have demonstrated the direct dependence of colony sizes on inlet tidal prisms and hence on the fish-food supply provided by those inlets. It deserves confirmation for other areas where similar multi-year data exist for colonies at discrete tidal inlets of known prism. Unfortunately, it is not applicable to such important locations as Great Gull Island, which, although located in fish-rich areas, cannot be associated with inlets.

A last observation on Common Tern populations is provided by the westernmost cluster on Long Island, at the apex of the New York Bright. Historically, a large colony has been located in the general area of Breezy Point and Jamaica Bay (New York) and Sandy Hook (New Jersey). In 1971 the major colony had been at Breezy Point, but fires set by vandals that year obliterated the entire colony. It seems that none nested successfully in 1972, 1973, or 1974. In 1975 we also found none, but 15 pairs had arrived by late June. At the same time, fluctuations were taking place in numbers nesting at Sandy Hook, and in a major saltmarsh colony in eastern Jamaica Bay present for the first time (in our survey) in 1975. Table 17 compares the breeding populations for the three areas, which we believe form one breeding population, a contention supported by the fact that even though a total of only 20 adults was banded at Silver Hole Marsh in 1976, one was recaptured at Breezy Point in 1978 (Post and Gochfeld, 1979). We do not mean to imply that these birds constitute a gene pool apart from those east and south of this general area, but rather that they form a deme more intracon-

TABLE 17

Number of Pairs of Common Terns Nesting at the Westernmost L.I. Sites plus Sandy Hook, N.J.

See text for discussion.

	1974	1975	1976	1977	1978
Jamaica Bay Marshes	0	412	1138	994	737
Breezy Point	0	0	224	843	782
Sandy Hook	5	253	222	0	0
	5	665	1584	1837	1519

nected than to others to the east or south. Perhaps the most intriguing implication of this interpretation is that Common Terns move from marsh to beach and back, from year to year, which would buffer them very well indeed against the vagaries of habitat availability in the Long Island area. Recent data from Breezy Point (Gochfeld, pers. comm.) extend the beach-marsh interchange to colonies as far away from Breezy Point as Barnegat Bay, New Jersey.

3. *Least Terns.* This species has been the source of much recent concern, possibly uncalled for as far as Long Island populations are concerned. The most surprising Least Tern discovery we made in the five years was the magnitude of the Peconic Bay and Long Island north shore populations, labelled respectively A and B in Fig. 2. Table 18 indicates that these two areas together accounted for between 55% and 70% of the entire Long Island population each year; and that there were significantly more occupied sites in the Peconic Bay area than on the north shore, where the impression was of aggregation into fewer but larger colonies. Analysis of numbers of each *site* (thus including single pairs) confirmed that in 1974, 1975, and 1978 Peconic Bay did have significantly smaller "colonies" than the north shore, where dispersal was generally less. (Test results were: 1974, t=3.235, 18df, P<0.01; 1975, t=2.392, 24df, P≃0.025; 1976, t=1.753, 22df, n.s.; 1977, t=1.259, 16df, n.s.; 1978, t=2.662,

TABLE 18

1974-78 Population and Breeding Site Data for L.I. Least Terns in Areas A (North Shore) and B (Peconic Bay) of Fig. 2

All population data are in pairs. Symbols: S = number of sites; # = breeding population; % = percent of total L.I. breeding population that year; M = mean population at each site; ** = mean population at each site in two areas that year very significantly different at 0.025 level or less; ns = mean population at each site in two years that year *not* significantly different.

	S	#	%	M
1974				
North Shore	8	878	51%	109.7
Peconic Bay	12	323	19%	26.9**
		1201	70%	
1975				
North Shore	10	1439	55%	143.9
Peconic Bay	16	403	15%	25.2**
		1842	70%	
1976				
North Shore	6	1004	40%	167.3
Peconic Bay	18	550	22%	30.6 ns
		1554	62%	
1977				
North Shore	6	823	38%	137.2
Peconic Bay	12	378	17%	31.5 ns
		1201	55%	
1978				
North Shore	7	942	42%	134.6
Peconic Bay	12	400	18%	22.2**
		1342	60%	

23df, $P<0.015$; all years pooled, $t=4.534$, 112df, $P<0.001$.) Thus the tendency is generally true, although in individual years it might be blurred by the birds' reactions to local events.

V. CONCLUDING REMARKS

We believe the results presented here amply demonstrate the value of "simultaneous" helicopter censuses of all of Long Island. Aside from short-term, greatly reduced disturbance of breeding birds, the use of helicopters provides insight into population changes, colony shifts, and other large-scale effects not always visible to the on-ground, in-colony worker—whose data on production are nonetheless important to interpretation of aerially taken census figures. (See Buckley, Gochfeld and Buckley [1978] for a Long Island example of the interaction of the two kinds of data.) We hope that others will duplicate elsewhere the kind of multiple-year helicopter survey census we have begun on Long Island.

We are now analyzing our Long Island data from another point of view: how often should aerial censusing be done, and what losses of information result from census intervals greater than one year? At present we can only reiterate that the analyses presented here would for the most part not have been possible without *annual* censusing (optimally by the same observers); this echoes the conclusions reached by Diamond and May (1977) that accuracy of estimation of insular species-turnover rates is improved by an order of magnitude when the censusing is annual rather than decennial. While the cost of multi-person helicopter use is *absolutely* high, its *relative* cost is not, and if the data thus obtained allow prompt action that could result in preventing a local extirpation (Roseate Tern is a good example), few would oppose the outlay.

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COMMENTS

Nisbet: I have some concern about helicopters. In Massachusetts almost all of our colonial waterbird colonies are in places where either public or private landowners vigorously object to the landing of helicopters. Some of them even vigorously object to low flights. We had an incident in which the landing of a helicopter on a private island made the owner so angry that we almost lost our access rights. Are you able to get permission to land in all of your places, or have you not had this problem at all?

P. Buckley: Virtually all the places where we landed were publicly owned. We obtained prior permission to land on Gardiner's Island, and it and most of the other privately owned islands we were interested in were isolated. If privately owned islands were occupied, we simply didn't land there. So we didn't have that problem. I think, however, in the congested Northeast where there are FAA minimum ceilings on fixed-wing planes, helicopters, which have no such ceilings, provide an extraordinarily valuable tool. We should make every effort not to abuse the privilege.

Gochfeld: Some years ago the Fish and Wildlife Service conducted a heronry survey by fixed-wing aircraft in the same area that these helicopter surveys were done. Can you comment on the comparison of the number of colonies found and on their composition using these two methods?

P. Buckley: In 1976, a fixed-wing craft did a survey and a census of heronries on Long Island. They found three heronries, while that year, we found 21. In addition to the fact that they were flying fixed-wing aircraft with ceiling problems, they also didn't know the area. It isn't very difficult to quarter over a section of marsh with a helicopter, but you don't do that with a fixed-wing plane. We consistently sought out all possible colony sites and checked them out. Moreover, Long Island supports a significant number of colonies comprised largely of dark waders—Black-crowned Night Herons and Glossy Ibis. You will not see these from the air unless you are literally beating the bushes: we actually used the helicopter to flush out the birds, and they responded very well. There are astonishing differences between what you can locate from a helicopter and what you can find from a fixed-wing plane.

Simpson: I was just wondering, are the birds on Long Island given some kind of protection? I noticed in one of your photographs that there were tire tracks on the beach, and obviously there are lots of people around the colonies. Are they fenced off or do people just stay away from there?

P. Buckley: We are trying to keep all colonies within National Park Service areas posted and protected, but most colonies are unprotected. Most heronries are reasonably safe, being out on the salt marshes, and so are the terns, but they are subject to occasional disturbance.

J. Keith: From your Herring Gull figures, it seems that the drop since the peak of breeding population is much faster than adult mortality would normally be. Do you have any idea where those birds are going? Are they staying in the area and not breeding, or are they moving out altogether?

P. Buckley: In 1976, we saw significant numbers of adults standing around at the edges of colonies, obviously not territorial—so much so, that in 1978 we started to record those data. We had not seen the phenomenon previously. Secondly, Darrell Ford tells me that in the Captree State Park gullery a number of eggs are failing to hatch, and chicks are dying after hatching. Whatever is hitting the Herring Gulls is hitting them very hard, and apparently in all areas.

Keith: As well as breeding pairs, do you then have total numbers of adult Herring Gulls?

P. Buckley: After 1977, we do. Prior to that we simply assumed every bird or pair spaced out inside a colony was territorial, and breeding. We didn't count club birds. After 1977, we have broken them down.

Davis: Paul, your aerial shots of the East River gull flocks showed a remarkable lack of feeding habitat. Do you have any idea where the birds feed?

P. Buckley: Probably on garbage dumps.

Davis: How far do they go?

P. Buckley: As the Herring Gull flies, over to the beautiful Hackensack meadows, about 10 mi. straight across Manhattan and the Hudson River.

Austin: I am very jealous of your methods today compared to what we had half a century ago. We couldn't fly over the colonies, we had to make our guesses of the size of each Cape Cod colony by walking through and by the numbers of birds we could band. In those days we had no gulls. I remember the first gulls coming in to breed on Cape Cod. How are we going to get rid of these darn Herring Gulls that come in? The first ones were on Bird Island in Marion, and I remember my father angrily picking up the eggs and throwing them into the water because they were interfering with the terns, and saying, "Let's get rid of this bird now." If we had only had the methods of today back 40 to 50 years ago, I think we'd see quite some changes which would be interesting, and Ian has certainly done a grand job of assessing what we tried to do, and comparing our reports to what he has found in recent years.

COASTAL SURVEYS—NORTHEAST AND NORTHWEST

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Abstract

The function of coastal surveys is to gather data upon which one can base comparisons. In order for the comparisons to be valid, the accuracy of the censuses must be well within the limits of the changes to be detected. Seabirds, waders, and waterfowl have inherent advantages for the study of numbers because they gather in discrete habitats or along shorelines. Our work in the northeastern U.S. indicated that data of low inherent "rigor" were valuable to confirm population trends if the counts were made consistently, at intervals of several decades, and if important changes in numbers occurred. We have concluded that repeated counts at short intervals and attempts to achieve high levels of rigor may be misleading, because there are large changes in numbers of birds at their breeding sites within the day, between days, and from month to month. There are, furthermore, surges of numbers over several years. Our studies of the biology of seabirds in Alaska tend to support our intuitive conclusion that one cannot safely accept implications about changes in numbers until the biological reasons for the normal fluctuations are known. At some time in the process, it is necessary to ask what information is needed from a survey and how the data collected will be used to answer specific questions. One must know this before one can decide how precise the data must be, but it may not be advisable to decide this ahead of time. We believe that different levels of rigor will satisfy different sorts of questions and that resorting to absolute standards of rigor may distract attention from gathering the information that is really helpful.

Introduction

The purpose of coastal surveys is to record population sizes, to compare them, and to interpret differences. This meeting of students of waterbirds, celebrating the centenary of the Linnaean Society of New York, provides a focus for examining the interactions between biology and mathematics which comprise such a study. The hosts, the American Museum of Natural History, have an admirable record of maintaining high standards of scholarship. However, this paper will seem to question the degree to which absolute standards are justified or valuable under field conditions and under the constraints of "cost effectiveness."

Perspectives

1) *Attitudes.* Ideally we should gather data which are accurate and draw conclusions which are right. We would like to be precise in the counts of heronries, gulleries, or seabird cliffs, and in our measurements of breeding success. We would like to test each observation and conclusion. But it is also obvious that levels of precision are only obtainable at a cost, and it may be necessary to double the cost in order to raise the level of precision 10 percent. Does the greater precision contribute to increased validity of results or to self-gratification?

Statistical techniques have helped field biologists in many highly important ways during the last 30 years. They have made a number of analyses possible and reinforced the whole intellectual structure, but there is a danger of "*Deus ex machina*." Unfortunately a number of quantitative or statistical techniques are now so generally accepted that they are used as a reflex action without considering whether they help to clarify biology, confuse the situation, or are simply irrelevant. Konrad Lorenz (1958) said: "The current overrating of quantification as a source of knowledge has very serious epistemological consequences. The first and worst is that it leads to contempt of observation pure and simple, which is the basis of all inductive science. The depreciation of observation has gone so far that the term 'naturalistic' as applied to scientific work has assumed with some behavioristic psychologists a definitely derogatory connotation." I think that the chief use of mathematics is to encourage people to think in new or unaccustomed ways. Mathematics is one of many ways of doing that.

During the 1960s, we sought the advice of statistical theorists on the application of statistics to our work on gulls. Their advice was: A) the purpose of statistics is to ensure consistency in measurement, and to qualify "common sense;" B) the use of sampling techniques or statistics will not solve *ipso facto* biological problems. In contrast, they commented, the way to solve sampling problems is to understand the biology of the organisms to be sampled. Hence, we were advised that we should not develop a program for formal sampling of New England's population of gulls because we already knew that the gulls were clumped along the coast. We should plan systematic observations at places where gulls gathered.

2) *Experience*. At the start of the 20th century, few people made systematic counts or estimates of marine birds, but those available in New England provide a basis for comparisons (Drury, 1973, 1974; Drury and Kadlec, 1974; Nisbet, 1973). The estimates made in the first half of this century were made by people concerned either for endangered species or for pest species. The surveys were not so much to answer questions as to demonstrate what many people already knew. Dutcher (1901, 1902, 1903, 1904, 1905), Norton (1907, 1923, 1924a, 1924b, 1925a, 1925b), and to a smaller degree Knight (1900), Pearson (1910, 1911), and Townsend (1923) surveyed the coast of Maine to document the disappearance of seabirds in the wake of the plumage trade. They were systematic, but their precision was low and they made no use of statistics.

A quarter century later Gross (1935, 1944a, 1944b, 1945a, 1945b, 1951a, 1951b), addressing the problems of the Herring Gull (*Larus argentatus*) and Double-crested Cormorant (*Phalacrocorax auritus*) as pest species, again made systematic surveys. Gross related the number of eggs found in nests to the numbers of pairs of gulls on each island and gave an estimate of the "non-breeders" on the island. About the same time, Lewis (*e.g.* 1942) in eastern Canada and Southern (1939, 1951), Southern and Reeve (1941), Fisher and Vevers (1943, 1944, 1951), and Fisher and Waterston (1941) in Britain counted other seabird populations. Still, little use was made of formal statistics.

However, clear conclusions can be drawn from the data because the data were gathered in a systematic way, were gathered over a period of decades, and reflect evident changes in numbers. We can follow the changes in populations of Herring Gulls on the coast of New England as in a great surge they extended their nesting range from eastern Maine southwest to the coast of New York during 35 years (Drury, 1973, Fig. 2). Similar changes were taking place with Common Eiders (*Somateria mollissima*), Double-crested Cormorants, Great Black-backed Gulls (*Larus marinus*), Laughing Gulls (*L. atricilla*), and Black Guillemots (*Cepphus grylle*) as shown on a logarithmic plot of numbers against time in decades (Drury, 1973, Figs. 2, 3, and 4). During the same decades spectacular changes occurred in the populations of Great Egrets (*Egretta alba*), Snowy Egrets (*E. thula*), and Little Blue Herons (*Florida caerulea*). We are no less sure of these changes just because they are not documented decade by decade.

3) *Location*. The work that will be reported has been done in New England and in northwestern Alaska. In both regions political constraints have limited us to half of a natural geographical or biological unit. We have omitted the Canadian shore of the Gulf of Maine and the Siberian shore of the northern Bering Sea. The two areas are of roughly the same geographical size, but are vastly different in the numbers of evident vertebrates. The northern Bering Sea and the Bering Strait support about four million breeding seabirds, which is about twice the number breeding in all the Atlantic coast between central Labrador and Cape Hatteras. The continental shelves of the North Atlantic are visited in summer by hundreds of thousands of Northern Fulmars (*Fulmarus glacialis*), Greater and Sooty Shearwaters,

(*Puffinus gravis* and *P. griseus*), and Wilson's Storm-Petrels (*Oceanites oceanicus*), and, of course, small remnants of once larger numbers of marine mammals. On the other hand, hundreds of thousands of Short-tailed Shearwaters (*Puffinus tenuirostris*) visit the northern Bering Sea in addition to about 20,000 Gray Whales and 120,000 Walrus, four species of seals, Bowhead Whales, Porpoises, Finback and Minke Whales, Belugas, and more.

The productivity of the inner Gulf of Maine apparently depends on the circulation of water which enters the Bay of Fundy from the Nova Scotia current. As this water rises up the slope at the entrance to the Bay, the upwelling turbulence creates conditions favorable for high primary productivity. Apparently the products of this growth "settle out" as the water continues to flow westward along the coast of Maine.

The productivity of the northern Bering Sea results from shearing and mixing of several water masses and the turbulence associated with the confinement of the flow as the water passes through the narrows west of St. Lawrence Island and the Bering Strait. Nutrient-rich deep waters flow northward from the Aleutian or Bering Sea Basin north of the Aleutian Islands. They rise over the edge of the continental shelf, continue through the Strait of Anadyr, and mingle with shelf and coastal waters enriched by outflow of the Yukon, Kuskokwim, and Anadyr Rivers. The Bering Strait, especially the shallow water west of Big Diomede (Ratmanova), has primary productivity comparable to the lower limits of that of the major upwelling systems of the world.

PURPOSES OF THE WORK

1. In New England our work was on contract with the U. S. Fish & Wildlife Service, part of it with the Branch of Animal Depredations Control Research, to establish why large gulls are attracted to urban airports and why their populations have been increasing. A) We surveyed breeding islands of gulls from aircraft and boats, and in the course of this work we counted the "other vertebrates" in order to assess the possible impact of measures which might be recommended for controlling reproduction of or killing the large gulls. We censused breeding islands from the air between Grand Manan and Delaware Bay. We censused from the surface between Grand Manan and Stonington, Connecticut. B) We made a winter air survey of the coast from northern Mexico to Prince Edward Island for numbers and age groups of large gulls. C) Another part of our work in New England was to survey the herons nesting on the coasts of Rhode Island, Massachusetts, New Hampshire, and Maine. This contract was with the U. S. Fish & Wildlife Service to investigate the possibilities of using wading birds as indicators of levels of environmental pollution (Custer and Osborn, 1977).

2. In Norton Sound and the Bering Strait, Alaska, our work has been on contract with the National Oceanic and Atmospheric Administration. The project is an environmental assessment of the Outer Continental Shelf, preliminary to leasing areas for exploration and development of oil reserves. The objectives of our work are: A) To locate the principal areas where waterfowl and shorebirds gather; B) To locate the breeding areas of seabirds and to study their breeding biology; C) To identify the food used and establish where the birds feed at sea, and, if possible, to relate the feeding grounds to characteristics of the water masses.

METHODS

Waterbirds are suited to our studies because they assemble in discrete habitats or gather along a linear seacoast. Most seabirds nest in a few concentrated, and often conspicuous, places. They are large, for the most part nest in the open, and are therefore convenient to census, in contrast to the subjects studied by upland biologists, whose major problems, when counting mammals or birds, may be finding their subjects in the first place.

During the last decade several observers in different parts of the world have developed techniques for estimating large and changing numbers of seabirds on their breeding grounds or at sea. Most agree as to the problems but differ in solutions according to local conditions, purposes, and their own backgrounds.

Guidelines have been prepared, on behalf of "Operation Seafarer" in Britain, and of the Canadian Wildlife Service in Canada (Nettleship, 1976). The purpose of the instructions is to guarantee that counts are made in consistent, comparable ways. These instructions include directions for using mapped sample plots to measure populations of birds which nest underground in burrows or piles of rocks. Directions for techniques to be used for birds which nest in the open and therefore can be counted directly include the making of a permanent record, and the calibration of results from different techniques. It is to be recognized that differences may exist among observers and among repeated estimates made from the air, from the ground, or from photographs.

Nettleship (1976), Nelson (1978), and others, including the "pioneers" Fisher and Southern, have used cameras to record birds on a cliff. Cameras with large negatives and long lenses have been used in the work in the Canadian Arctic to take pictures from aircraft. Photographs can be used as direct evidence, but I think that they need as much interpretation and calibration as do estimates made from the air or counts made from the sea. We took photographs of the cliffs at Bluff and Sledge Island in Alaska in 1975 and found that the differences between counts made from the photographs and those made from the water several days later were so extreme as to make the counts unusable as a basis for calibration of our direct counts until we understood daily movements.

The major concern of all these techniques is to avoid boggling the mind of the observer.

In both New England and northwestern Alaska we have concentrated on conspicuous species, and made estimates by the most convenient method is order to gather samples over the entire area as soon as possible. Then we have gone to some effort to relate these techniques to the results of detailed counts at sites where the number of breeding birds was known with some precision. Evidently others have used similar methods for extrapolating results. Blok and Roos (1977) reported that they started their censuses in the Netherlands with samples of some well-known heronries. Then they applied their techniques to less well-known or accesible heronries.

1. In New England our surveys were designed a) to locate and estimate the size of breeding aggregations of seabirds and herons and b) to count wintering gulls and estimate the proportion of each of three age classes so as to prepare a life table.

In New England a) we estimated virtually all of the gulleries several times from the air. We compared estimates made from a plane flying at about 400 ft. to counts made of photographs taken at the same time, to counts made from a boat circling the island, and to counts of nests made on the ground (Kadlec and Drury, 1968a). The counts made from the surface were usually made some weeks before or after the counts from the air.

We tested the accuracy of counting nests on the ground by making systematic transects of an entire nesting area and marking nests as we counted. When we had completed the search of the area, we ran a "capture-recapture" test to find the proportion of marked to unmarked nests by walking other transects across the area already counted. We found an accuracy of about 90 percent in our counts of nests made on the ground (Kadlec and Drury, 1968a).

On the East Coast b) we also surveyed the wintering population of large gulls to prepare life tables for them. The fact that each of four year-classes of Herring Gulls are distinguishable quickly from the air allowed us to count these elements of the population. We established the relative proportions of three age groups: first-year birds as one category (uniformly brown), second- and third-year birds together (intermediate plumages with patches of brown, gray, and white), and adults or all older birds as a third category (uniformly gray and white). To do this we flew along coastal beaches and over lagoons, turning to fly the perimeters of small and large towns and cities, looking for smoke over dumps and all the places where our experience told us gulls gather. As we passed over each group of gulls we estimated the larger of the three age categories and counted the smaller. Two observers were involved, one on each side of the plane. Estimates were recorded (Kadlec and Drury, 1968b) on a small scale chart used for navigating.

2. In Alaska the purpose of our survey included: a) locating concentrations of waterfowl; b) locating and measuring the size of seabird cities and the nesting sites of dispersed breeders such as cormorants (*Phalacrocorax*), puffins (*Fratercula*), and Glaucous Gulls (*Larus hyperboreus*); c) preparing a life table for Glaucous Gulls.

In Alaska, a) we established the distribution of the concentrations of waterfowl by flights over the lowland parts of the southern Seward Peninsula at the beginning, middle, and toward the end of the ice-free period. We flew a zigzag pattern over the rivers, shoreline, tundra, and lakes. The details of which lakes or what parts of the flats we flew over were decided as we flew, primarily by the pilots, who kept a sharp lookout for waterfowl. In other words we were locating major concentrations and making gross, not detailed comparisons.

In Alaska, b) we used aircraft to locate and estimate the numbers of breeding seabirds between St. Lawrence Island on the south and Cape Lisburne on the north by flying the coastline and estimating the size of breeding populations of Pelagic Cormorants (*P. pelagicus*), Glaucous Gulls, Black-legged Kittiwakes (*Rissa tridactyla*), murres (*Uria* spp.), Horned Puffins (*Fratercula cornuta*), Tufted Puffins (*Lunda cirrhata*), and Pigeon Guillemots (*Cepphus columba*). This technique is not suitable for estimating the populations of auklets because they nest underground in cobbles and boulders. At a sample of seven cliffs, we compared the estimates made from the air with counts made from a small boat moving slowly past the foot of the cliffs in order to establish whether our air estimates fell within the normal variation of counts made from the water. They did.

In the counts made from a boat directly in front of the cliffs, we "calibrated" differences among observers by having two or three observers make counts of the same species on the same sections of the cliff at the same time. Some people counted by "twos," others by "tens." Some were consistently higher than others, some ranged from low to high, but generally observers are consistent as to which they do. When two observers were close in their estimates they tended to alternate having higher estimates (Table 1). These problems are familar to those who survey waterfowl for the U. S. Fish & Wildlife Service.

Once an observer's counts are calibrated with those of other counters or to the actual numbers on a cliff face, he can apply a correction after each exercise. There is no point in trying to "adjust" each estimate as it is made. Data gathered by several observers can also be combined once a figure for calibration is found.

TABLE 1
Counts of Common Murres Made by Two Observers at the Same Time at the Bird Cliffs at Bluff, Alaska in 1978.

(Note that in one case the higher count is made alternately by the observers. In the other case Observer 1 is consistently higher than Observer 2. Observer 1 is the same person in each example. Observer 2 is different in each case.

Section of Cliff	Observer 1 No. Murres	Observer 2 No. Murres
A	710*	590
A to C	1820	2500*
C to D	2220	3230*
D to E	830*	800
E to F	1270	1330*
F to G	440	520*
G to H	605*	555
H to I	760*	650
I to J	12	34*
Cliff Total	8667	10209

Section of Cliff	Observer 1 No. Murres	Observer 2 No. Murres
A	550	750*
A to C	4000*	3450
C to D	10300*	5650
D to E	3170*	2170
E to F	3910*	3520
F to G	2010*	1310
G to H	1600*	1280
H to I	2380*	2020
I to J	360*	270
Cliff Total	28280	20420

We made several air estimates of the numbers of birds on the cliffs at Bluff and compared them to counts made from the water. We did the same at Egg Island, Cape Denbigh, Sledge Island (Ayak), King Island (Ukivok), and Little Diomede Island (Ignalook). These comparisons gave us correcting factors which we applied to the numbers that we estimated only from the air at the cliffs on St. Lawrence Island near Savoonga, Gambel, and the southwest Capes. We also compared air estimates at Cape Thompson and at Cape Lisburne with surface counts made by Springer and Roseneau in 1976-78, and by Swartz (1966) in 1959-61. It is important for the observers making estimates at strange cliffs to be adept at shifting the units of estimates up and down from 50's to 100's, to 250's, to 500's, to 1000's, to 5000's.

The estimates one gets from an airplane at 120 knots are obviously less precise than those one would get sitting on the ground counting through a telescope or binoculars. Aerial surveys, however, may be much easier and cheaper and, in many cases, may provide the only information one has the opportunity to collect.

In order to understand the causes of variation, or confusion, in our counts, we mapped areas on the cliffs and measured hourly and daily variation in numbers of birds. We discuss these observations in the next section.

The Biological Meaning of Changes in Numbers

Lloyd (1975) suggested that at least five counts need to be made at a nesting cliff in order to include expectable variation in the numbers of Razorbills (*Alca torda*), Common Murres (*Uria aalge*), and Atlantic Puffins (*Fratercula arctica*). Similar short-term changes in numbers of Herring Gulls were discussed in the previous section (see also Kadlec and Drury, 1968a; Drury, 1974). The effects of the birds' comings and goings can be smoothed out by calculating means, which provide a sort of consistency; but for the consistency to be valuable the reasons for the changes must be understood. One of the first things to learn is what different elements of the birds are doing. Not all birds at nesting islands and cliffs are breeding; for example, we know the number of eggs produced is much smaller than half the maximum total number of birds present.

Black-legged Kittiwakes have many conspicuous advantages for this study. They segregate into discrete territories which they defend daily, and they build conspicuous nests. However, many kittiwakes occupy ledges or sites which are not suitable for nests; yet pairs are seen repeatedly at some of these sites. Some birds may occupy their roosts every day all summer but are not joined by a consort. Some birds pair and bring in nesting material; the nests may fall off, or the nests may persist and the birds not lay eggs.

Nelson (1978) describes similar experience with North Atlantic Gannets (*Morus bassanus*): "The main difficulty in interpreting gannet counts is to know what has been counted. Many investigators, including those doyens, Fisher and Vevers, did not count what they say they did. Early counts were sometimes expressed as the number of individuals, but in the main they have been given as 'pairs' and frequently as 'breeding pairs,' or 'nests.' Actually, they are site-owning individuals: *many* were breeding; *most* had nests; and the *great majority* had mates and thus did represent pairs. It is impossible in a single count, or even a few, to distinguish pairs that have a nest from those that have merely a site, for there is every gradation from a bare site to a large pedestal. Also, a good nest can be demolished in half an hour. Similarly, it is often impossible to distinguish non-breeders from failed breeders, and since the latter are nevertheless 'breeders,' impossible to get a direct figure for breeders. So gannet counters, whether direct or from photographs, are in fact counting individual birds, each of which represents at least an occupied site (this assumes that a pair present on the site together, is counted as one site, but see below) . . ."

We assume that similar levels of motivation or breeding activity are found in murres and puffins, as in kittiwakes and gannets. Unfortunately, the details are obscure on first glance at murres and puffins.

We will discuss what we have learned about Common Murres at Bluff Cliffs in some detail and compare our interpretations with those of British and Scandinavian students working on the same species. We have made counts of the Common Murres at the bird cliffs at Bluff that vary from 7,000 to 90,000 birds. Most counts cluster between 20,000 and 50,000, which in itself is an impressive "error" (Table 2). We can show in this case that the actual *error* in each count is less than 10 percent; we can show that equally large changes in numbers may be recorded during a single 24-hour period. The birds really do come and go; one should be surprised if they didn't.

We know that more birds are at the cliffs at certain times of the year. Maximum numbers are often present during late May and June, when birds first gather on the cliffs and on the water below the cliffs. However, minimum numbers may be present in the same period within a few days of a maximum count. Birkhead (1978) shows the same pattern among Common Murres at Skomer Island west of Wales. He recorded a tide of attendance running over several days when the birds first came. He also recorded a flux that runs its course during a 24-hour period. The tide may obscure the flux and the fluxes may be out of phase between two cliffs not very far apart, as is shown by our data from Bluff and from Square Rock in June of 1977 (Fig. 1).

Once eggs are laid, a certain number of birds settle down and are present consistently. Additional birds come in during the day and leave late at night or early in the morning. The numbers reach a maximum late in the evening. There is less coming and going during days of strong winds and choppy seas, as Birkhead (1976) reported, but the birds start to leave the cliffs anyway after several days of bad weather. There is a general exodus as soon as the sea calms, except for the most highly motivated "incubators."

The extra birds, above the "incubators," are of two sorts. One sort has relatively little attachment, as is shown by their readily flying off when an observer or airplane is still at some distance. This number, "fliers," has been larger during those years when reproductive success is low, *e.g.* 1976, than it is when reproductive success is moderate (1975 and 1977) or when it was high (1978) (Table 2). The second sort of "extra" birds, although they do not have eggs or chicks, are reluctant to fly. These two categories on average account for just under half of the birds on the cliffs at Bluff in the middle of a day during incubation in July and early August.

Chicks begin to fledge after the first week of August and, after that, birds leave the cliff in patches as the chicks have jumped. Some patches persist around groups of unfledged chicks into September.

In the first half of August, there are at times large numbers of birds at the cliffs; apparently they are subadults visiting the ledges to prospect for nest sites. Occasionally, throughout the period of incubation, high counts occur, for reasons which are not clear. It may be that waves of non-breeders and failed breeders return to the cliffs responding to their own motivation and to favorable conditions at sea. These waves may coincide and reinforce each other.

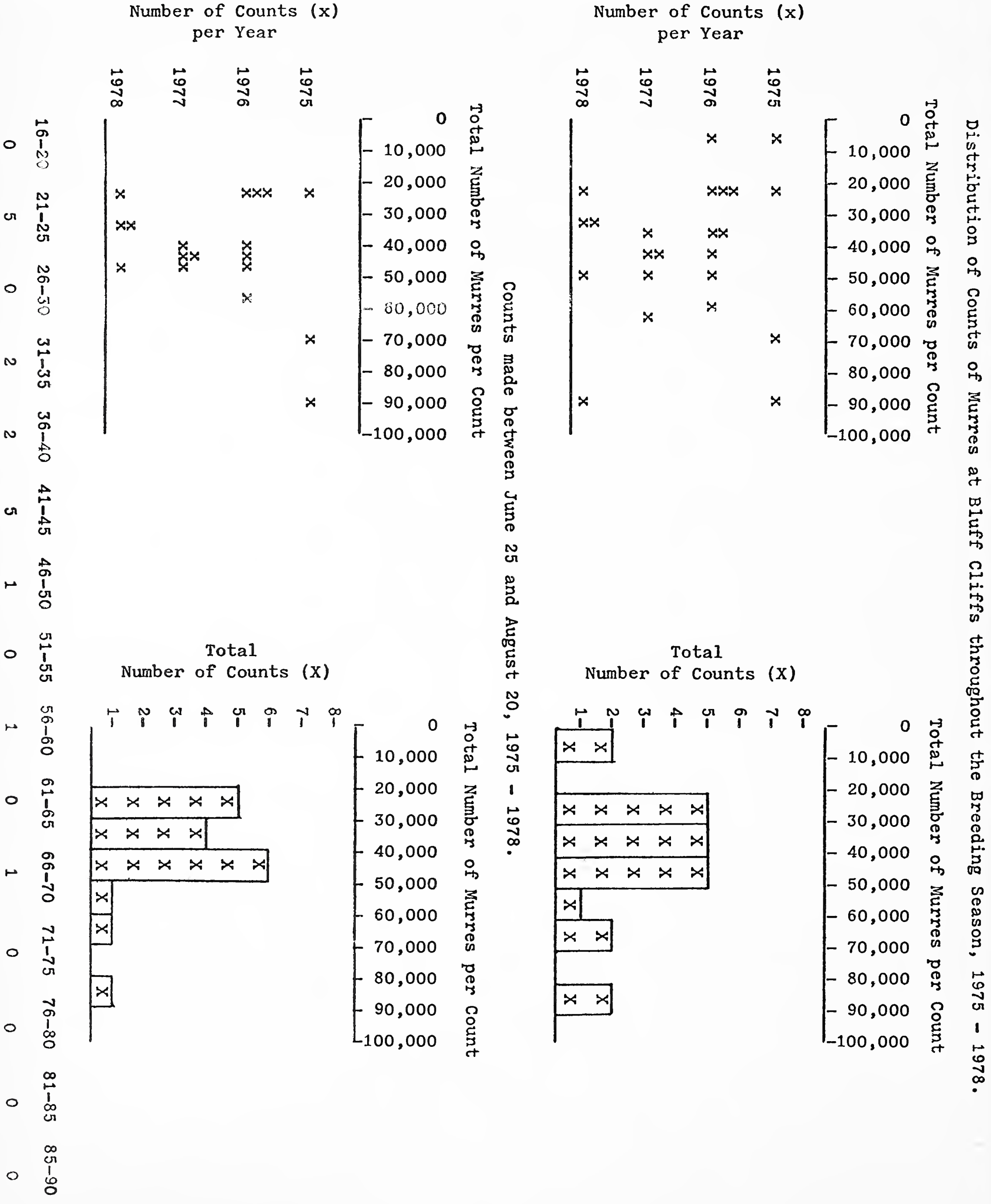
We need to relate the numbers which we count to the number of breeding pairs in order to know what are the productive elements of the population. We would like to have the sort of precise information which Dyck and Meltofte (1978) gathered at the Faroe Islands. They made a census of a cliff face called Høvdin on June 7, watching through a telescope as Faeroese fowlers worked the entire face, and counted the eggs as the murres left with the progress of the eggers. The overall percentage of eggs to birds was 51.1; but using the size of the embryos, the authors calculated the proportion of eggs not yet laid and arrived at a figure of .67 for the ratio of pairs to total birds on the cliff. In 1978, we got the figure .56 in the course of a study of individual birds occupying mapped "breeding sites". At each site we recorded whether an egg and/or chick appeared in the course of July and August by visiting the study area for several hours every other day and recording the actions of every bird. Southern, Carrick, and Potter (1965) and Tuck (1960) used the figure of .6, which seems to be a good average figure to apply to averaged counts (described below) where detailed information is not available.

We soon noticed that some birds assumed characteristic postures and that many, although

TABLE 2

Counts of Murres at Bluff Cliffs Throughout the Season and During the Incubation-brooding Periods.

(A large spread exists in these counts. Most of the variation was found when the birds did not have close attachment to the nesting ledges. One could establish a mean for these figures and give a 95% confidence limit, but that would be misleading. There are really two peaks, five counts between 20,000 and 25,000 and five counts between 40,000 and 45,000.)



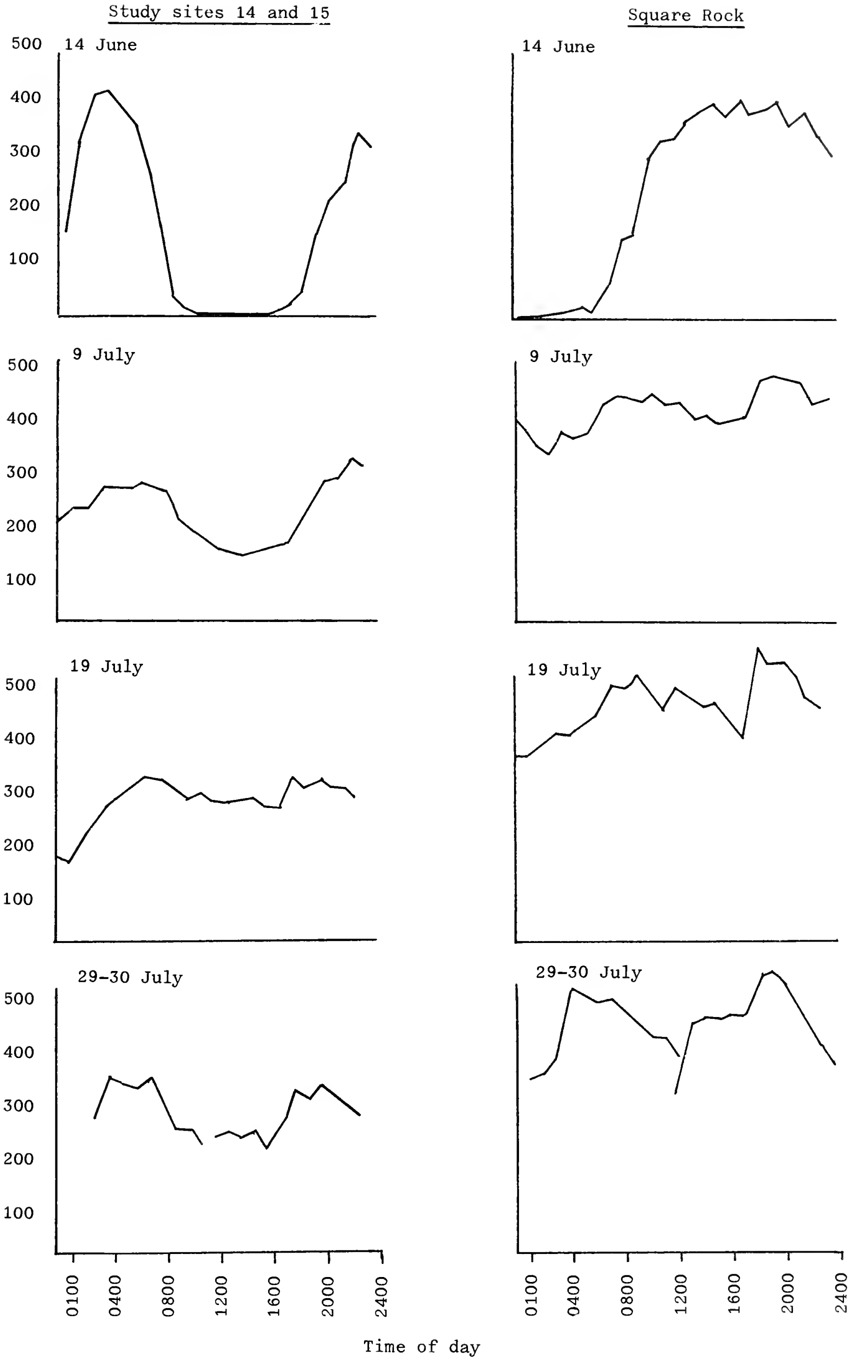


Figure 1. Changes in daily attendance in the course of the season at Bluff Cliffs and Square Rock. The large fluctuations in numbers in the course of 24 hours is evident when the birds first come back in spring. The fluctuations are damped as soon as eggs are laid. Note that the fluctuations are out of phase between these two nesting cliffs only two kilometers apart.

not all, of these were sheltering an egg or brooding a young one. The special postures which murres assume when incubating an egg include facing the cliff face, lowering the breast (thus bending their back), and often raising their bill to rest it against the back wall of the ledge. The special postures of birds which are brooding young include lowering one wing and bending their backs. Both "incubators" and "brooders" are often marked with excrement that has splattered on them during the hours they have held their posture.

Our observations of the locations of hundreds of murres over many hours have established that many murres "incubate" or "brood" over bare ledge, while many foster an egg or chick without assuming any recognizable posture. If, however, one can clear one's mind of this "bias introduced by reality" and simply count the total number of birds in an incubating or brooding posture, one can compare the results with the real numbers established by the laborious process of indentifying individual eggs and chicks. We found very close correspondence over the several years of our study, whatever the cause of the correspondence. This technique, though perhaps anathema to a precise scientific mind, provides a way to get a quick estimate of the level of reproductive effort on any section of cliffs. Our tests indicate that the difference between "incubators" and the actual number of eggs or chicks is within the limits of variation in different parts of one set of cliffs.

What figure should be used to multiply by .6 or .67 in order to arrive at a figure for "breeding birds?" For a single figure one might choose the average of counts made during the incubation period. It is important to identify the date and time at which counts were made and to associate the count with the stage in the daily cycle of coming and going at the cliff counted. One can minimize variation by counting at certain times of the day. In 1976, a poor year, we have seven counts which average 20,000. In 1977, a good year, we have three counts which average 36,200. In 1978, a good year, we have three counts which average 30,000. These counts, eliminating the poor year, give us a spread of 20,000 to 25,000 "breeding pairs" which is the same spread which we had arrived at in the course of detailed counts and corrections for the cliffs, face by face. If "fliers" are added, 1976's average of all birds becomes 35,000; 1978's average becomes 32,500; and 1977's average becomes 42,000. Thus, if one includes fliers, one decreases the differences between years.

The central breeding element varies much less than the maximum and minimum counts, and their numbers can be assessed in the northern Bering Sea by making 5 to 10 counts in the middle of the day during mid and late July. The number of birds which probably have eggs can be further assessed by counting 1) the "fliers" (birds which probably do not have eggs that year) as the census is made, and 2) the proportion of incubators and brooders to total adults from fixed study sites.

DISCUSSION OF VARIABILITY IN NUMBERS AMONG CENSUSES

A fixed figure may be misleading in any of the numbers counted during the breeding season because variability is a norm, and this certainly applies to the numbers of birds estimated to be at the cliffs between years. One had to be careful about how one applied corrections, too; for example, the estimates of murres on the cliffs of Storra Karlsö in the Baltic in the 1950s was 35,000 to 40,000, but Hedgren (1975) concluded that, because of differences in methods, his detailed estimate of 6,400 pairs (12,800 birds) should *not* be used to conclude a change in populations. Dyck and Meltofte (1975) considered their estimate of 9,650 pairs on one cliff in the Faroes to correspond to an estimate of Nørrevang (1958) of 15,000 pairs; they supported their conclusion by quoting the field counts: 14,500 by Dyck and Meltofte and 14,750 by Nørrevang.

Large changes in the size of murre populations have been reported during the last two decades. Some of these changes can be demonstrated, such as those on the cliffs in the Barents Sea, at the cliffs on the Faroes, or in West Greenland. We should probably question some others, and until we know more about normal tides and surges in numbers, it will be hard to explain even these well-documented changes. Southern, Carrick, and Potter (1965) suggested that flooding of some bird cliffs by newcomers who have moved over a substantial number of degrees of latitude might explain some changes. The decreases in the numbers of murres breeding on the cliffs in Greenland may be a response to heavy shooting pressure, but until the source is known for the murres responsible for the remarkable increase in numbers breeding on Funk Island, between Newfoundland and Greenland (20,000 in 1936 and 1,000,000 in 1958, Tuck, 1960), it will not be clear whether the decrease in Greenland reflects mortality or reproductive failure, or simply emigration.

Southern, Carrick, and Potter (1965) studied several bird cliffs in northern Scotland, comparing counts of bridled individuals of Common Murres to non-bridled birds. The bridled form is limited to the Atlantic, is distinguished by a white ring around the eye and a white line running from the ring back to the nape, and ranges from 1% of Common Murres in the south to over 5% in the north (Iceland and Bear Island).

At Hafnaberg (Iceland) at a cliff of 2,000 birds, the bridled birds made up 28.8% in 1939 and 18.1% in 1949. At St. Kilda at cliffs of 30,000 birds, bridled birds made up 16.5% in 1939 and 10.5% in 1948. At Hermaness in the Orkneys, bridled birds changed from 23.7% to 16.9% in the same years. During the subsequent decade, the changes were almost precisely reversed.

The speed of these changes is remarkable in a long-lived species (86-88% annual survival rate at the cliffs in northern Scotland), with a slow turnover of the population. If one suggests differential mortality or reproduction, the selection coefficients required are unrealistically large (.5-.7, Southern, Carrick, and Potter, 1965). These authors suggested movements of large numbers of birds over long distances, flooding cliffs with newcomers.

We must consider the possibility of surges of large numbers of birds when we explain large changes in numbers of murres at some Alaskan cliffs, although estimates made in previous decades seem to be uniformly higher than those made during the 1970s. Fay and Cade (1959) made general estimates of the numbers of birds on St. Lawrence Island, and Kenyon and Brooks (1960) made estimates of the numbers of birds on Little Diomede Island in the 1950s. Staff of the U. S. Fish & Wildlife Service estimated numbers on many of the bird cliffs in the early 1970s.

The authors of these estimates agree that we should not use the earlier estimates for detailed comparisons. Most estimates were made at a great distance and under circumstances which did not allow systematic treatment. The clearest explanation was offered by Kenyon (pers. comm.), who said that his lower estimates are the totals of his data, and the higher figures were numbers which he considered to be the upper limit possible. Our data from Little Diomede Island agree with his lower estimates (Fig. 2).

The circumstances are more complicated, however, in making comparisons between Swartz's estimates at Cape Thompson, 1959-61, and those of Murphy, Roseneau, and Springer (1976, 1977). The latter authors have used Swartz's original notebooks to arrange to make counts at the same places and on the same dates as Swartz; they have found what seems to be a large decline in numbers. They are continuing their studies and will test stratified sets of samples both at Cape Thompson and at Bluff.

No matter how accurate each system of counting may be, the changes in numbers of birds at the cliffs which occur hour to hour, day to day, month to month, and the "surges" from year to year, make intermediate levels of precision misleading.

SURVEYS OF THE AGE STRUCTURE OF GLAUCOUS GULLS AND HERRING GULLS

The fact that each of four year-classes of Herring Gulls is distinguishable quickly from the air allowed us to count the elements of the population along the Atlantic Coast and to construct a life table. Glaucous Gulls similarly have four readily recognizable plumage and age categories. As we said above, we used only three categories: birds of the year, subadults,

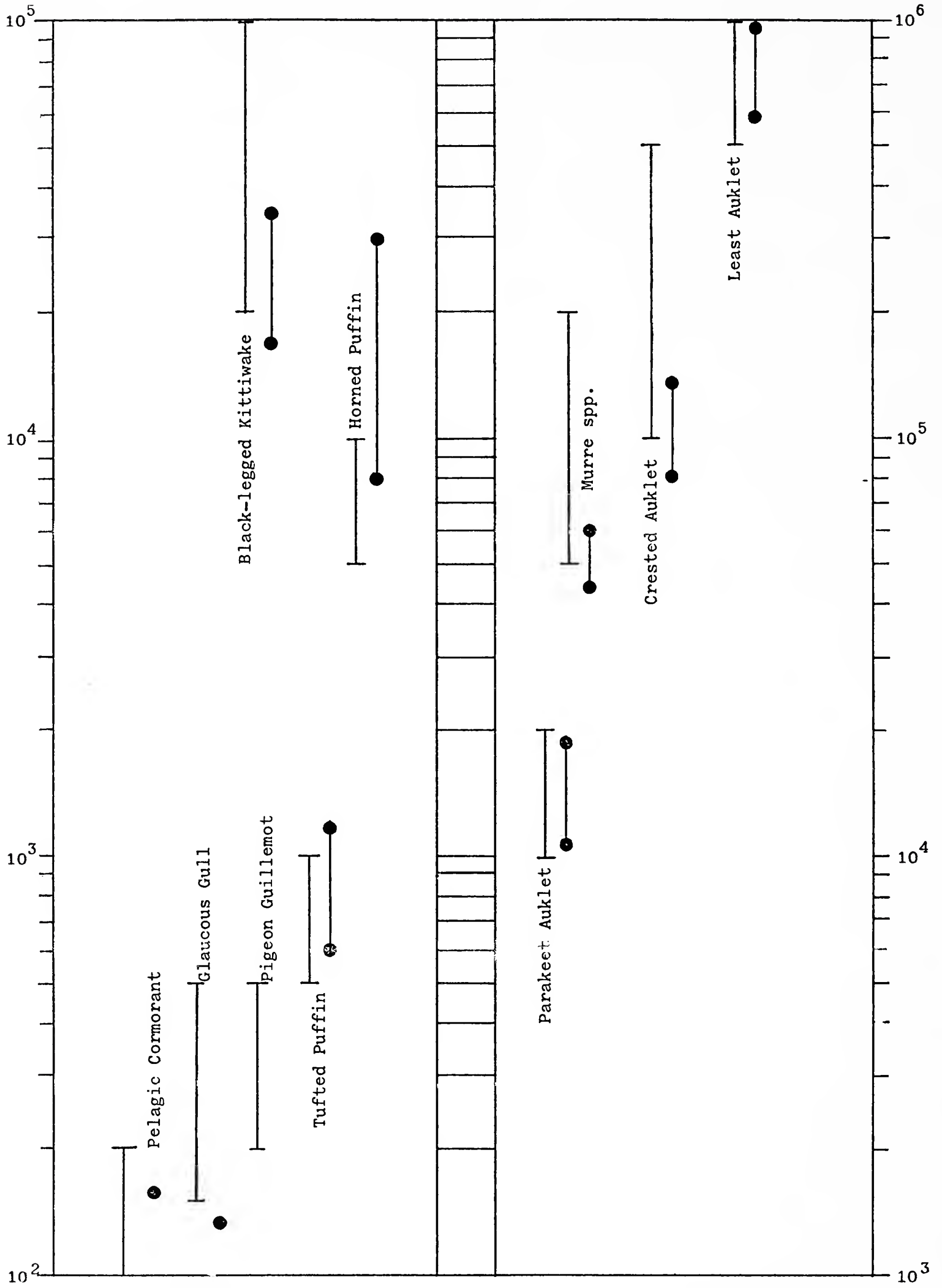


Figure 2. Numbers of seabirds at Little Diomede (Ignalook) in 1954 and 1958, and in 1977.

The numbers represented by the lines with perpendicular ends are from Kenyon and Brooks. The lines with circles at the ends are our data. Kenyon reported that the lower estimates are the results of his tallies; the higher are possible expansions of the estimates. The differences in our estimates reflect differences between two ways of estimating the area of the sides of the island. Note that Kenyon and Brooks were not on the island in July and August when the subadult Horned Puffins prospect the cliffs.

and adults. The category of subadults includes birds that are either one year or two years old with plumage intermediate between the uniformly tan birds-of-the-year and the uniformly gray and white adults.

The Glaucous Gull population, like the Herring Gull population, occurs primarily along the beaches. In Alaska, sand or shingle beaches extend almost uninterrupted from the delta of the Yukon to Point Barrow. Many Glaucous Gulls gather near fish camps where people set gill nets for migrating salmon. Others gather near villages, and many follow salmon upriver to the spawning grounds. Gulls gather in large flocks at the mouths of rivers and congregate in regions where human populations are more dense.

Subadult Glaucous Gulls gradually move into the northern part of the breeding range during the course of the summer and join small flocks near inlets or villages. Young of the year begin to fledge in mid-August. A survey made in late July will show most of the subadults, and will escape the practical difficulty of trying to estimate numbers of three different age groups at the same time.

We made our censuses by flying along the beach at about 100 ft. altitude using a small tape recorder to enter data. We estimated the size of each flock and counted the numbers of subadults or chicks.

We can treat these samples as a unit, or we can use them as part of a larger sample which includes the data gathered by observers at sea. Preliminary examination of the data collected at sea gathered by Divoky (pers. comm.), by the observers of the Coastal Ecosystems Study group of the Fish & Wildlife Service, and by observers of the Manomet Bird Observatory off New England, suggests that a majority of the birds at sea are subadults. The subadults are freest to follow food sources.

We can use the data we have for Glaucous Gulls in Alaska to compare with the age structure of the Herring Gull population on the East Coast. A suggestive bulge appears in the life table indicating a large population of subadults. We can therefore predict that in the future Glaucous Gulls should be increasing in Alaska as they have along the East Coast. The data are imprecise and the samples sparse. Does that mean the prediction should not be made?

CONCLUSIONS AND COMMENTS

Conclusion 1: On the one hand, I believe that one *should not* draw conclusions based on data gathered in the course of scattered surveys made over a few years, no matter how precise and thorough the counting of each sample.

On the other hand, I believe that one *can* draw informative conclusions from counts or estimates in spite of differences in sampling techniques and precision, provided: a) estimates were made in a systematic way; b) overall changes in numbers have been considerable; and c) the biological reasons are understood for the changes that occur daily and weekly.

Comment: I disagree with the conclusion of many scientists that numbers which show large variability, hence a large "standard deviation" or "standard error," are unreliable and that the narrower the normal curve the greater the rigor. In fact, in the numbers we get from counts at seabird cliffs, the variation is large but the error is small. We can measure variation by calibrating among counters, and calibrating among techniques, times of day, and parts of the breeding season. If the patterns are regular and understandable in biological terms, hence predictable, they are contributions to biological knowledge and not error.

We concluded from the exercises in estimating the numbers of birds at gulleries that there were both real variations in numbers — a biological feature — and error — a feature of our techniques. I believe these two are often confused and that it is important to keep them separate. We found that error was introduced in the data collected from the air, primarily by light conditions. We found that error was introduced into the counts made from the water because parts of the nesting area were obscured. In practice during our air surveys two observers made estimates at the same time, and we found that the higher estimate or count consistently proved more reliable. We also found that counts and estimates varied from hour to hour and day to day, often more than the variation between observers. We found that we could make the air estimates more consistent with the ground counts by totalling the estimates bay by bay (Kadlec and Drury, 1968a).

We found that the counts of nests on each island varied considerably between years, more than we expected when we started (Table 3, below, from Drury and Nisbet, 1972). Evidently there were large annual variations in the numbers of nests even on islands which were in the densest part of the breeding range, near centers of the human population. Our other studies suggest that not only were about 20% of the birds occupying territories and not laying eggs, but that in addition, there were about 20-30% of the adults in the region living around the towns and cities and not attached to an island. We presume that any of these birds could breed unless they were excluded from the breeding islands by social pressure. In other words, the variation in numbers between years is again not "error."

We have become convinced that there is no single number which can be used to represent the size of a seabird city. If a range of numbers is used, that may be as misleading as a single figure. Our experience censusing Herring Gulls and Great Black-backed Gulls, or Black-crowned Night Herons (*Nycticorax nycticorax*), Great Blue Herons (*Ardea herodias*), and egrets in coastal New England convinced us of this, but we did not have the data to confirm the impression. Our work on Common Murres at the seabird cliffs in northwestern Alaska does document the conclusion.

Numbers should be regarded as a series of approximations for the important biological information. One should consider percentage differences, not absolute differences, and one should use logarithmic series until shown that it is preferable to do otherwise. For example, we have found that the numbers of murres which we estimate at cliffs fall into "sets": 2000-5000; 10,000-15,000; 25,000-50,000; 60,000-90,000; 150,000-200,000. We have no difficulty distinguishing among these "sets." Note that the percentage "error decreases as the numbers increase. We believe that the limits to these sets is fixed by the area of cliffs and that the techniques which we have are adequate to establish real differences.

Unfortunately, by acknowledging the variability of numbers of seabirds we leave the data from censuses vulnerable to misuse. Cynical individuals will be able to manipulate data to their own ends and fool some people, as was done with winter censuses of Robins (*Turdus migratorius*) during the squabbles about pesticides in the 1960s. It is doubtful that much can be done about this as long as the great majority of biologists insist upon applying to active vertebrates the standards of uniformity of behavior conceived in studies of cells and molecules. As J. A. Keith first pointed out to me, there is a fundamental break in patterns of be-

TABLE 3

Numbers of Breeding Pairs of Gulls at Some Massachusetts Gulleries, 1961–69.

(These counts were made by groups of observers systematically searching islands and marking each nest found. Note that there is a lot of variation despite the fact that these islands are in the area of most concentrated population of gulls. There are many pairs of gulls which settle on the islands but cannot establish territories and there are many (20%) adult gulls in the area which are apparently excluded from the breeding islands.)

NUMBERS OF BREEDING PAIRS OF GULLS AT SOME MASSACHUSETTS GULLERIES

Year	1961	1962	1963	1964	1965	1966	1967	1968	1969
Gullery									
North Gooseberry Island		200	225	262	234	*	*	162	134
Island South of Cat Island			275	290	294	279	289	297	278
Marblehead Rock			315	296	312	304	259	287	247
Egg Rock	510	530	470	450	525	530			
Green Island	305	260	258	227	320	*	*	*	
Little Calf Island			231	207	243	310	300	280	265
Norman's Woe					530	508	484	478	462

*Colony disturbed by introduced predators havior at the level of the individual. Chemical, physical, and physiological processes may tend toward equilibria and regularity, but in processes that involve populations each individual is to some degree in competition with every other individual. Thus adaptations tend to be centrifugal, not centripetal (see also Svärdson, 1942). It is not in the interests of individual plants and animals to conform to patterns consistent with normal curves. Unfortunately, this aspect of the Darwinian intellectual revolution does not yet have very wide acceptance.

Conclusion 2: I believe that waterbirds and seabirds have many advantages for the purposes of estimating and studying numbers, in contrast to species which are dispersed through their habitats.

Comment: As I have indicated, the data that we have gathered on the distribution of waterfowl in Alaska are subject to large variations and are not suitable for statistical comparisons. Yet they allow us to collect a lot of information on where the birds are actually concentrated and provide a basis for establishing fixed transect lines for comparative measurements in the future. Fig. 3 presents the results of surveys made in 1977, and shows that differences are obvious in spite of lack of suitability for statistical tests. It would have cost us almost as much again to set up fixed transects to establish our results statistically after we knew where to look.

Recently, the managers of the Outer Continental Shelf Environmental Assessment Program decided that seabirds are not useful as environmental indicators because their numbers vary widely. I presume that this decision was based on arguments such as I gave in the last section, and assumptions that the numbers of other organisms vary less or more predictably. I believe that this is a mistake. Actually, we can see and document the changes in seabird numbers, whereas changes in the numbers of less conspicuous wildlife go undetected or misunderstood. In estimating populations of dispersed or cryptic animals, one must depend upon mathematically designed techniques of sampling, such as line transects, grab samples, or net tows, and, as a result, additional real error is introduced that may mask real biological changes. Waterbirds and seabirds gather regularly at their breeding grounds, are distributed along a linear shore, or gather in discrete wetlands. Consequently, it is often possible to examine an entire population.

Some of the results coming from studies which have examined a population directly and demonstrated the "wild" oscillations in the population have disillusioned some of us about the classical generalization known as the Lotka-Volterra equation and its corollary, the tendency to reach equilibrium at carrying capacity. If a species exists whose population is saturated and stable at carrying capacity, it would be ideal to use for monitoring environmental insults. But in a world of mathematical abstractions, one does not have to worry about industrial chemicals.

Conclusion 3: I believe that the search for a high degree of scientific rigor such as provided by scientific experiment can be more of a hindrance than a help in gathering data needed for decisions on environmental problems when the subject is populations of large vertebrates. Use of comparative techniques and circumstantial evidence is more effective.

Comment: The classical procedures in scientific research involve choice of a cleanly circumscribable problem for which one can achieve an unequivocal and quantitative answer. One tests results by experiment and writes a report. However, this approach seldom can be used to deal with socially important problems, especially with a limited budget. Most of the work I have done was undertaken because someone identified a problem important enough to them to pay for an answer. I have needed to establish in my own mind what question is at the heart of the problem. What biological knowledge should be sought? What data can be gathered? To what uses will the data be put? What levels of precision and rigor are required? What will be the cost of achieving a higher level of precision or rigor?

I suggest that there is a hierarchy of rigor

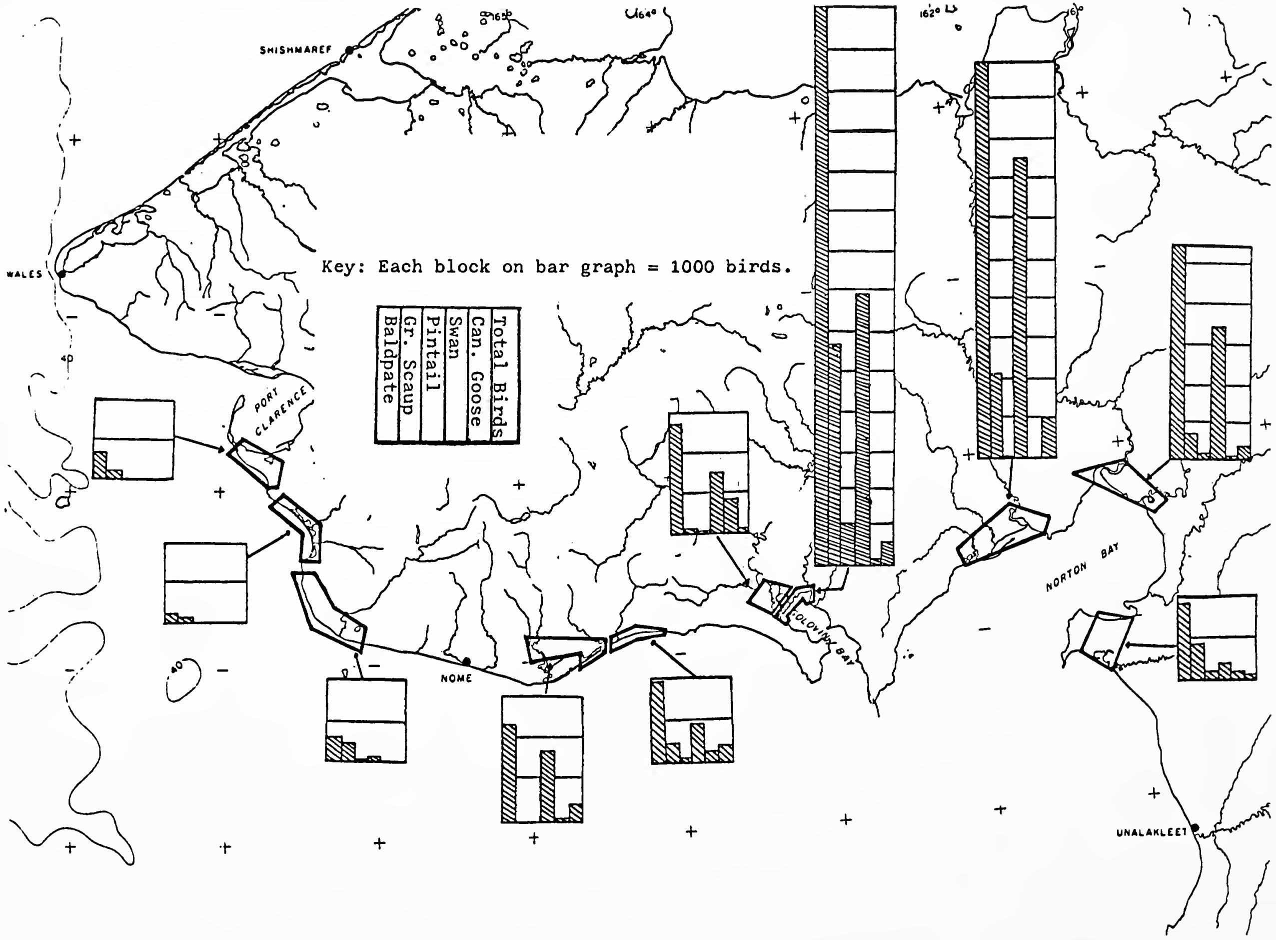


Figure 3. Numbers of waterfowl in major habitats on the south shore of the Seward Peninsula, Alaska. Major differences in the concentrations of waterfowl are evident, although the methods of gathering the data prevent us from performing standard statistical tests for "significance."

according to the uses to which data will be put: a) the lowest level is that sufficient to give an attentive biologist an idea; b) next, that needed to convince an open-minded fellow biologist that the idea is worth pursuing; that needed to give reliable advice to a "decision-maker;"c) that needed to publish a paper in a formal journal; d) that needed to count as evidence in court or publish a paper which is contrary to current biological consensus; e) that needed in a political controversy. After a few months' study in 1962, I was convinced that expectable levels of sanitation at sanitary landfills would not keep gulls from feeding. Yet, in 1980, after this conclusion has been confirmed in numerous places in all parts of the world, the E.P.A. is unwilling to accept the conclusion because it is not consistent with their official policy. In 1950, I read evidence which convinced me that I should give up smoking, but in 1979 an important number of those who sold cigarettes refused to accept evidence from the U. S. Surgeon General's Report which was many orders of magnitude more rigorous.

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Many people have contributed generously of their time to this work and as a consequence can no longer look over a harbor without counting the boats. I want especially to thank my sons Bill, Peter, and John, who have played major parts. It is important in any work like this to have someone who is very intelligent and very lazy and who regards the work from a detached point of view. I also want to thank J. Biderman, M. Drury, J. B. French, Jr., J. A. Kadlec, I. C. T. Nisbet, C. Ramsdell, B. G. Steele, and A. Watson, who have discussed the data and ideas at length in many places and in many helpful ways.

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COMMENTS

Simpson: You mentioned at the beginning of your talk that you thought that aerial estimates were more accurate than photographic estimates?

Drury: It seems to me that they have different functions. We tested photographs against aerial estimates of the same section. The problem with photographs is that often the light is such that they don't show the birds that you can see with your eye.

CENSUSING WATERBIRD COLONIES: SOME SAMPLING EXPERIMENTS

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Abstract

The results of several small-scale ("within-colony") and large-scale ("among-colonies") sampling procedures in colonial waterbird colonies are examined. In general, strip transect methods (20% sample) appeared to be superior to point-centered quarter or quadrat sampling methods both in the field and using an artificial population model. Further, the strip transect is equally effective under three spatial regimes (random, clumped, uniform) while the quarter method is suggested only when nests are randomly distributed. Regression analyses of (aerial) adult estimates *vs.* selected nest counts revealed high variability both among species and "among censuses" for a given species. Observer differences in estimation ability probably account for much of the variance. Large differences in the adult/nest ratio were found among species because of differences in nesting vegetation density, plumage color, colony attendance, behavior, etc. Three statistical treatments of the data used in the least squares regression analyses revealed that, as a safeguard, census data should be log transformed before further statistics are applied.

Introduction

Determining the number of animals per unit habitat is usually a prerequisite to conducting studies of population processes in the field. This necessary first step, however, may often prove to be the most arduous due to the elusive or cryptic nature of the organisms, habitat structure, timing, non-uniformity of sampling methods, etc. [see Overton (1971) and Caughley (1977) for reviews].

Waterbird population estimation has been the subject of a number of papers (Belopol'skii, 1957; Kartaschew, 1963; Kadlec and Drury, 1968a, 1968b; Nisbet, 1973; Drury, 1973–4; Nettleship, 1976; Buckley and Buckley, 1976; Erwin, 1979). Because most waterbird species are relatively large and diurnal and nest in discrete, compact colonies, censusing might be expected, *a priori,* to be relatively straightforward. Nonetheless, dense vegetation (wading birds especially), asynchronous breeding schedules, immense colony sizes, and the propensity for as many as 10–15 species to nest together in mixed colonies present particular problems to the field investigator. Further, immigration into the colony, renesting, and nest desertion throughout the nesting period create a dynamic flux which defies any *precise* count of the breeding population for the entire season (Drury, 1973–4).

In this paper, I present some results of sampling schemes and estimation procedures tested during 1976 and 1977 in waterbird colonies along the northeastern U.S. coast (Erwin, 1979). Two scales of estimation are used: (1) "within-colony," where the intensity of effort is directed at estimating nest numbers at each of a small number of colonies, and (2) "among-colony" or regional, where populations from a large number of colonies are estimated by combining adult estimates with nest counts from a few colonies. The results are used to make recommendations for future waterbird inventories.

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METHODS

"Within colony" sampling

Total counts

"Total" nest counts provide the best absolute measure of the breeding population at a given time. However, a once-through nest count in a colony may not provide an accurate census. We examined error rates in the "once-through" method by sampling a number of plots in seven Massachusetts gull colonies in 1976 and 1977. In rectangular plots ranging in size from 0.06 to 1.10 ha, teams of 3–6 workers systematically walked through the colony, marking active nests with spray paint. A second total nest search was conducted, with marked and unmarked nests recorded. A Lincoln index (mark-recapture) was then applied to calculate "true totals" in the sample plots (Overton, 1971).

Field sampling methods

One plot sampling method—the strip transect—and one plotless (distance) method—the point-centered quarter—were used to test their relative efficacy in both gulleries (n = 6) and heronries (n = 3) in Rhode Island and Massachusetts. Initially, total active nest counts were made in the colony (or sample plot). Then, samples of 10% and/or 20% were taken using the strip transect method. From 8–15 points were sampled at fixed intervals along an arbitrarily delineated transect line for the point-centered quarter method (for details, see Appendix A, Erwin, 1979). Sampling estimates were then extrapolated and compared to the total nest count. Qualitative assessment of vegetation density and nest distribution was made at each colony.

Artificial population sampler

In the laboratory, I applied both of the above sampling methods and the quadrat method to three artificial populations of colored discs (Artificial Population Sampler, Schultz Developments, Walnut Creek, Cal.) distributed either randomly, uniformly, or patchily. Ten% and 20% samples (approximately) were used for all three methods. Sampling points were determined using a random numbers table.

"Among colony" sampling

In early June, visual estimates of adults were made at colonies by several experienced investigators using helicopters. Within 10 days of the aerial census, nest counts were made at selected colonies in six states to provide "ground truth." No colonies were included in which nest disruption had occurred between censuses due to storms, *etc*. The species included in the study are: Common, Roseate, Arctic, and Least Terns (*Sterna hirundo, S. dougallii, S. paradisaea, S. albifrons*); Great Black-backed and Herring Gulls (*Larus marinus, L. argentatus*); and Black-crowned Night Herons (*Nycticorax nycticorax*). Additional data on Great Egrets (*Casmerodius albus*) were provided from a fixed-wing survey conducted in 1978 in Louisiana by J. Portnoy. In this case, "ground truth" was provided by comparing black and white photographic counts with visual estimates.

The different surveys allowed for testing the effects of differences in observers, regions (states), and habitat as well as species.

RESULTS

"Within colony"

Total counts

The error rates within sampling plots based on "one-search" efforts varied from 4–22% (Table 1). Vegetation density appeared to account for much of the variation, with sparsely vegetated plots having lower errors (4%, 7%, and 9%) than the moderate-densely vegetated plots ($\bar{x}$ = 15%). The relatively high frequency of "missing" nests in one-search efforts is surprising considering the small sample plot sizes and spatial uniformity of habitat.

Field sampling

Applying the strip transect and point-centered quarter methods yielded highly variable results (Table 2). The quarter method seemed effective only when vegetation was sparse and nests were relatively uniform in distribution. The strip transect method yielded superior results in five of the seven colonies where both methods were employed.

Artificial population

In general, even the best sampling method rarely provides an estimate more accurate than ±10% of the true population parameter (Table 3). Taking a 20% sample using the strip transect method provides a fair amount of precision as well as accuracy, regardless of the spatial distribution. Both the quarter and quadrat methods provide poor estimates when "nests" are clumped (which is probably the usual condition). The quarter method appears to provide reasonable estimates only when the distribution

TABLE 1
Assessment of a One-Search Total Nest Count Method for Determining Census Accuracy in Selected Massachusetts Gull Colonies
(Marked sample plots used in all colonies.)

Colony	Vegetation Density	Nest Dispersion	Sample Plot Size (hectares)	No. Marked-1st Search	"True"[a] Total	% Error
1976						
1	light	uniform	0.45	25	27	7
2	medium	uniform	0.06	52	56	7
3	medium	uniform	0.14	25	29	14
4	medium	uniform	0.14	39	50	22
1977						
5	medium	uniform	0.55	82	93	12
6	light	uniform	0.73	183	190	4
7	dense	medium	1.10	343	442	22
8	light	medium	0.53	180	198	9

[a] Based on Lincoln Index, where $\frac{X_t}{N_m} = \frac{N_t}{N_{m'}}$, X_t = total no. nests
N_m = no. nests marked at 1st search
N_t = total nests found at 2nd search
$N_{m'}$ = total nests found at 2nd search that are marked

TABLE 2
Assessment of Sampling Method Accuracy in Selected Gull and Heron Colonies in Massachusetts and Rhode Island (based on Nest Counts)

			Sampling Method			
			Point-centered Quarter (plotless)		Strip Transect (area)	
Colony	Vegetation Density	Nest Dispersion	Estimate/Actual	% Error	Estimate/Actual	% Error
Gulls						
1	light	uniform	192/198	3	250/198	26
2	dense	medium clumped	3675/1873	98	1667/1082 (south only)	54
3 a Vegetation	medium	medium clumped	690/852	19	947/852	11
b Rock		uniform	2075/1828	14	1626/1828	11
4	light	uniform	867/213	400	—	
5	dense		—		534/221	142
6	light	uniform	97/92	5	82/92	11
Herons						
1	dense	medium uniform	80/115	30	—	
2	dense	medium uniform	122/223	45	256/223	10
3	dense	highly clumped	15/76	80	78/76	3

is random (Grieg-Smith, 1964), while the quadrat method is unreliable under all spatial conditions.

"Among colony"

The best estimates of adults were compared to total nest counts (or photo counts) at selected colonies using least squares regression methods (Table 4). Results varied greatly both 'among' and 'within' species. In general, standard errors were relatively low (except for gulls in New England). For a given "group" (gulls, small terns), however, large differences in the ratios of adults to nests were found among regions and censuses, in accord with Kadlec and Drury (1968b).

Such differences led to a consideration of the "noise" factors in the estimation process. Because of the logistics of the gull census in New England, it was possible to compare one observer's estimates in two regions with those of two other observers. Thus, both between-state and between-observer differences could be examined. The results (Figs. 1 and 2) indicate that there is little difference between the Maine and Massachusetts colonies in their "censusability" (Observer 2: b = 0.30 *vs.* 0.35), but major differences occur between observers. Observer 1 tended to overestimate the larger (>1,500 nests) colonies while observers 2 and 3 consistently underestimated them. A plot of the raw adult estimate-nest count data from observers 2 and 3 reveals the high variability in the estimation (Fig. 3).

Recognizing this variability, I made two transformations of the data in an attempt to improve the fit (raise the r^2) of the regression model, natural logarithmic and a weighted measure. This second transformation is commonly applied where the standard deviation increases proportionally to the X data (Johnston, 1972), probably a trademark of animal censusing. Data are treated as follows:

$$
\begin{array}{ll}
Yi/Xi = \alpha + 1/Xi\beta + Ui/Xi; & Ui = \text{error term} \\
 & i\alpha = \text{y-intercept} \\
 & \beta \;\; = \text{slope}
\end{array}
$$

In effect, then, less weight is given to larger Y values which presumably are more variable.

When applied to the gull data, neither transformation significantly improved the fit of the data, with the weighted transformation actually achieving a worse fit (Table 5). Using the raw data in statistical analysis may be appropriate,

TABLE 3

Relative Accuracy of 3 Sampling Methods Under 3 Spatial Regimes, Clumped, Random, and Uniform Distribution. Data are % Errors (estimated/actual)

Overestimate = +
Underestimate = −

Method	Random R[a] = 1.02 Density = 142/m²	Uniform R = 2.33 D = 68/m²	Clumped R = 0.40 D = 153/m²
Strip Transect[b]			
(1 cm wide)			
10% sample	83+/30−/44−	62+/3+/18+	8−/37+/37+
20% sample	6+/16+/6+	10+/3+/10+	8+/12−/11+
Point-Centered			
Quarter			
ca. 10% sample	13 −	15 −	50 −
ca. 20% sample	8 +	41 +	70 −
Quadrat			
1 plot = 5% area			
2 plots (10%)	34 +	12 −	50 +
4 plots (20%)	5 −	19 −	15 −

[a] Clark and Evans (1954) R values [b] Results of three replicates given.

TABLE 4
Regression Analysis of Aerial Estimates of Adults Versus Nest Counts in Selected Waterbird Colonies

Species	Location	N (colonies)	b (regression coefficient)	S.E.	R^2
Terns					
Common, Roseate, Arctic	Maine, Mass., R.I.	17	1.49	0.14	0.88
Common	Conn.	6	0.90	0.13	0.93
Least	Mass.	7	0.93	0.02	0.99
Gulls					
Herring-Gr. Black-backed	Mass.	11	0.45	0.05	0.93
Herring-Gr. Black-backed	Maine	9	1.70	0.08	0.99
Herring-Gr. Black-backed	New England	29	1.03	0.23	0.76
Herons					
Black-crowned Night	Mass., Md., Va.	10	0.24	0.02	0.93
Great Egret[a]	La.	12	0.86 0.70	0.09 0.08	0.89 (J.P.) 0.89 (B.N.)

[a] Regression based on photographic counts of adults (X data); results shown for two observers, J.P. and B.N.

TABLE 5
Results of Least Squares Regression Analysis (Aerial Adult Estimate *vs.* Ground Count)

(in 20 Massachusetts gulleries and 12 Great Egret colonies in Louisiana. Independent variables are nest counts and photographic counts, respectively. Gull estimates are combined counts of 2 observers.)

Data Treatment	b (regression coefficient)	S.E.[a]	r^2
Gulls			
Untransformed	0.39	0.035 (9%)	0.81
ln transformed	0.77	0.070 (9%)	0.81
Weighted[b]	0.54	0.090 (17%)	0.46
Egrets			
Untransformed	0.70	0.078 (11%)	0.89
ln transformed	0.83	0.068 (8%)	0.94
Weighted[b]	0.82	0.070 (9%)	0.23

[a] Standard error and percent of mean b (in parentheses)
[b] See text for formula

then, unless assumptions about normality are violated. Probably logarithmically transformed data are the best to use.

Habitat differences among gull colonies in southern New England allowed me to compare estimates in sparsely vegetated colonies with those in dense vegetation. Based on the raw data in 11 "sparse" and seven "dense" colonies, least squares regression yielded a higher adult/nest ratio ($b = 0.67$) in "sparse" colonies than in "dense" ones ($b = 0.53$). In other words, about 25% more gulls are "seen" in the former case. The large number of densely vegetated gull colonies in Massachusetts no doubt explains the small slopes (Figs. 1 and 2) in the regressions. Where vegetation does not obscure the observer's view, a slope of ≥ 1.0 is expected since, during incubation, at least one adult should be in attendance at the nest at all times.

DISCUSSION

Using sampling methods in colonies does not provide highly reliable results. Even with 20% samples, only the strip transect method shows promise of achieving reasonable accuracy. One source of bias using the point-cen-

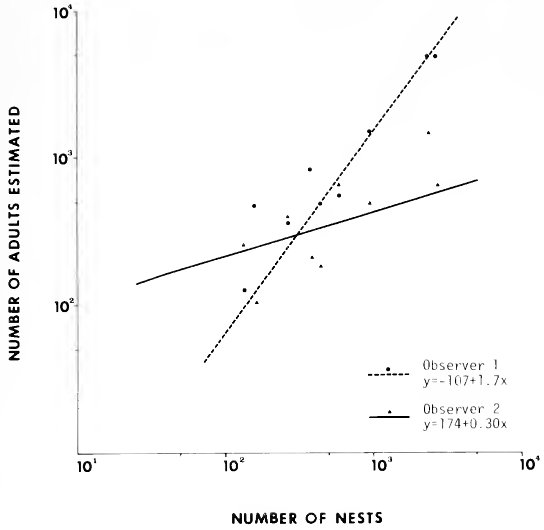

Figure 1. Observer differences in aerial estimation of gulls at 9 Maine colonies, May 31, 1977. Least square regression equations are given.

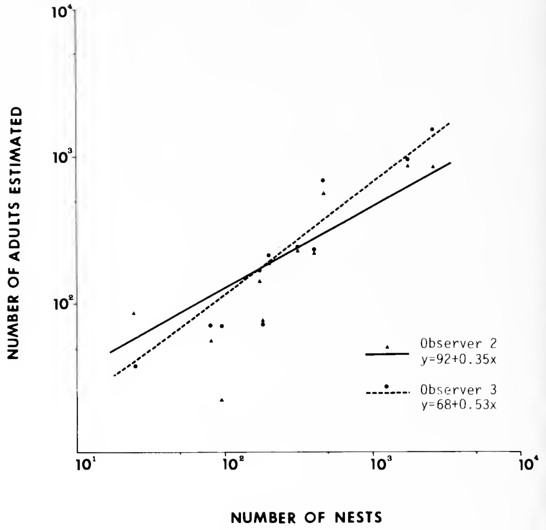

Figure 2. Observer differences in aerial estimation of gulls at 11 Massachusetts gull colonies, June 1, 1977. Least squares regression equations are given.

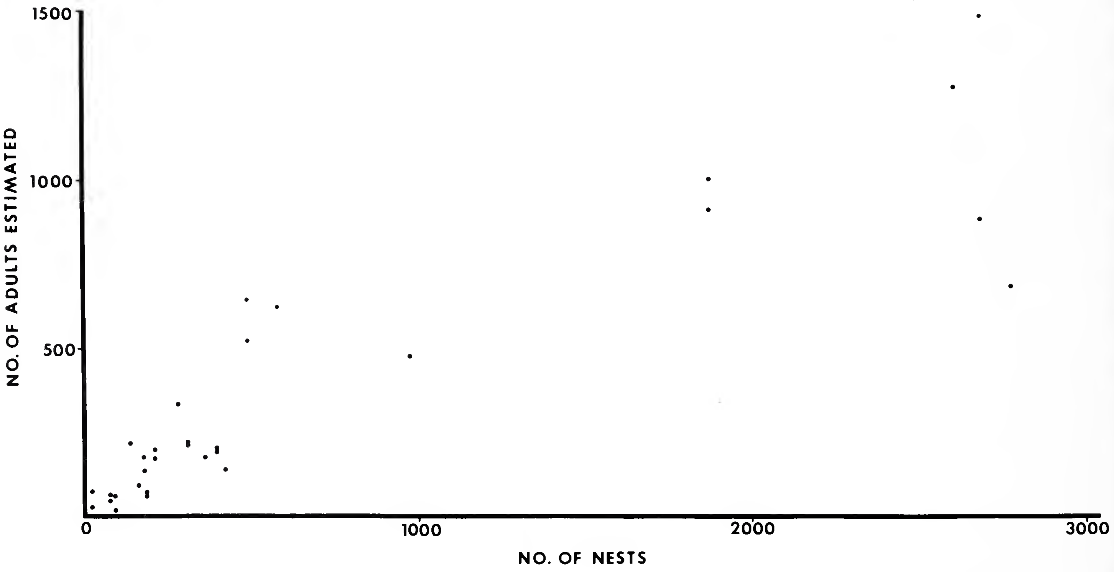

Figure 3. Adult estimates by observers 2 and 3 at 20 gull colonies in Massachusetts, 1976–1977. Single points indicate where only one observer made an estimate.

tered quarter method in the field arose from our selection of the transect line. In most cases, for the sake of expediency, diagonals within the sampling rectangle were followed, not randomly selected lines. However, even in the artificial population model when lines were randomly selected, only one of six tests yielded a result within 10% of the true total. Interestingly, the strip transect method appears to be equally reliable regardless of the spatial distribution. Plant ecologists recommend only the quarter method, however, when a random distribution is assumed (Greig-Smith, 1964). If the assumption is met, the quarter method is, in most respects, superior to the other distance methods (Cottam and Curtis, 1956).

Comparing aerial estimates of adults with nest counts at selected colonies yielded some interesting results. Least Terns seem to be the most predictable (lowest relative standard error, highest r^2) species, while the larger terns are more variable. Nisbet (1973) found that adult/nest ratios for Common Terns averaged 1.1 during the day, 1.9 in late evening. Buckley *et al.* (1977) also reported that a conversion of about 1.1 could be applied to arrive at the number of breeding pairs in a colony with "about a ±20% error." The composite ratio of 1.03 (adults/nest) for New England gulls is almost identical to that reported by Kadlec and Drury (1968b). Part of the discrepancy between observers 1 and 2 in Maine was believed to be definition of the census area. On most of the New England islands, gulls nest both on the rocky perimeter and in the interior vegetation. However, large numbers of non-breeding adults and immatures also loaf on the perimeter and, if these are included in the count, overestimation will result. Conversely, concentrating on the vegetated areas will cause an underestimate. Thus, the perception of colony limits could profoundly affect census accuracy.

The extremely low visibility (ratio 0.24 adults/nest) of Black-crowned Night Herons during aerial censusing only serves to confirm the suspicions of field investigators. The extremely dense vegetation, coupled with the propensity for herons to remain tenaciously on nests, renders them highly inconspicuous. The large, white Great Egret, in contrast, nests on the tops of vegetation and is much more amenable to censusing (ratios of 0.70 and 0.86). Much more empirical work remains before meaningful species "correction factors" can be applied for large-scale inventories of waterbird colonies.

As illustrated by these results (and those of others before), any breeding census of waterbirds, whether at the single-colony or regional level, will yield only an *approximation* of the total number actually nesting throughout the season. Setting a goal of high census accuracy is not only unrealistic, then, but may be counterproductive because of the disturbance induced. The most important factor in obtaining systematic sampling results is probably observer consistency. A given observer's estimate may be quite inaccurate but as long as he is consistent (high precision), his "bias" can be calculated and corrections made accordingly. Using the same observers repeatedly allows comparisons among years with the emphasis on the relative, rather than absolute, numerical changes.

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COMMENTS

Gochfeld: I wanted to make two comments and ask a question. As you mentioned with the Common Terns the ratio of 1.1 birds per nest is a pretty good one, showing variability with time of day and season. I have also found, by using ground counts of the birds where there are known numbers of nests, that on any given day there are real differences in different parts of the colony at the same time. Weather seems to be an important factor, and in skimmers, tide seems to be quite important as well. And again, we can really refine this by knowing the birds well. But it may not be that important whether the correction factor is 1.1 or 1.15.

For those people who are interested in the helicopter, there is a real price difference between the bubble at about $150 an hour, and the Ranger at about $240 or $280 an hour. This cancels out if you are going to cover an area of more than 200 miles, and then it may sometimes be cheaper to use the Ranger, which goes about 1.7 times as fast. It is also a much more powerful craft and pilots can maneuver it around heronries without the risk of ending up upside down on the ground. I think the safety of the Ranger is better, but I use a bubble all the time. You can photograph better from the bubble.

Plant ecologists have known for a long time that choice of quadrat size is crucial in sampling for both colony estimates and clustering, and it depends not only on the size of the creature you are examining and the size of the colony, but sometimes on very subtle factors which aren't always well elucidated. Now my question is—on your simulated maps, did you ever use different size quadrats, and did that make a difference?

Erwin: I just arbitrarily selected a quadrat size that was 5% of the total area, which is probably unrealistically high. Then to get the 10% and 20% I used two quadrats and four quadrats, respectively.

I'm so glad you made the point about the helicopter. Except for those of us who are working with mega-bucks, the rest of you are sitting there thinking, "Who is going to have the money to afford any kind of aircraft?" Since there is a continuing effort by several of the Federal agencies in censusing colonial waterbirds, there presumably will be sufficient funds for a lot of aerial work, at least in selected areas along the coast.

P. Buckley: We have received a lot of requests for information on the comparative costs and efficiencies of helicopters. Francine and I are preparing a manuscript looking at the technique of aerial censusing by helicopter, and contrasting the five-passenger Bell Jet Ranger with the two-passenger piston-driven "bubble."

Parkes: I would like to suggest an experiment—send a good censusing team on foot into a colony of conspicuous birds like terns or gulls rather than the inconspicuous herons, and, using the best possible ground census method, come up with figures. Then a helicopter team—different people—should census the same area. Following this, the ground census team returns to count the nests again. As a control, have the ground census team go through a colony, census the birds, and then without the helicopter disturbance in between, census the birds again and see if there is any difference at all between the figures.

This comparison between the colonies censused both on foot and by helicopter and those censused on foot only might give some insight not only as to the relative accuracy of the methods, but also to the relative *disturbance* caused by helicopter and foot censuses, a matter that has concerned many of us since the helicopter censuses began.

Erwin: That is a good suggestion, Ken, and it brings to mind the question of timing also. It is nice to try to do simultaneous counts, and apply all methods at the same time. I was aware that you do run into this "repeated sample" bias problem. That is why we had the ground counts and nest counts made after the aerial estimates, rather than the other way around.

Duffy: Would you elaborate on the future of Federal funding or plans for censusing?

Erwin: In three weeks I am going to be starting at Patuxent in the Migratory Bird and Habitat Research Laboratory, where I have been designated their colonial waterbird specialist. One of my four or five immediate goals is to look at population monitoring methods, recommendations and efficiency, etc. In addition, Marshall Howe will be studying the shorebirds. These are both permanent positions so there will be continued interest in both breeding colony populations and winter and migratory distributions over a long period of time. The National Park Service is also taking a more active research role in this. Paul Buckley seems to have been able to generate lots of funds over the past five or six years from Park Service sources to cover most of Long Island.

Schreiber: I would like to make two points, Mike. First of all, in my census work with pelicans and gulls we have found that, over an 8- or 10-week period through the nesting season, the adult-to-nest ratio will change dramatically. In pelicans, from very early in the season it will go from 22 to 25 adults per nest, down 8 weeks later to 0.2 adults per nest. So the timing of your census is absolutely critical to coming up with a reasonable kind of figure. Second, and perhaps more important, and I don't mean this as a criticism at all, is that it is very nice to have figures or census data for the numbers of nests, but if in collecting the census data you are in fact wiping out the nesting attempts, the figures for the number of attempts don't mean anything because you are ruining reproduction. I think that we have to be very careful in carrying out these censuses so that we are in fact not destroying the nesting colonies.

Erwin: That is a good point, and I am sure we will hear more about it later when people talk about human disturbance factors. It is a good thing that you mentioned the timing. We tried to time it so that we were censusing at mid to late incubation, recognizing that there can be a large amount of spread among colonies; but that seemed to be a good time that everyone agreed on.

Duffy: I was wondering if any efforts had been made to determine the proportion of nonbreeding birds in a population? Do you know of any census efforts in this area?

Erwin: It is too bad you raised that problem. I think the reason for the major difference between the two observers doing Maine is that the fellow who had the 1.7 adult-nest ratio was overestimating by including non-nesting birds in the rocks surrounding the colony. In Maine, you have a situation where you get dense vegetation in the interior of the island surrounded by big rocks. The birds nest both in the rocks and in the vegetation. You have to stratify your counts, as Bill Drury can confirm, and assume that individuals on the outside part of the rocks are probably loafing birds, with a high percentage of immatures and probably a high percentage of non-nesting adults among them. All birds on the interior parts of the rocks are probably nesting. Again, know your species and know their behavior before you go out and count everything under the sun.

THE EFFECTS OF TIMING OF BREEDING, DISPERSION OF NESTS, AND HABITAT SELECTION ON NESTING SUCCESS OF COLONIAL WATERBIRDS

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Introduction

This paper examines the effects of three major factors on reproductive success in colonially nesting waterbirds. Although most of the research focuses on the family Laridae, appropriate information regarding other families will be cited as well.

The definition of nesting success depends upon the focus of the investigator, but usually it includes some measure of fecundity, *e.g.* the size and numbers of eggs in a clutch, and production rate, *e.g.* hatching, fledging, or post-fledging success. Often several different measures of success are used, sometimes concurrently, making comparisons between studies as well as determination of the contribution of any particular variable on relative reproductive fitness difficult.

We often treat biological problems as if they were univariate, whereas in most settings a number of variables often operate simultaneously. Teasing them apart requires either relatively sophisticated statistical techniques, controlled experiments, or both. Furthermore, while we seek cause-and-effect relationships, identifying causes may be impossible. Explanations are often no more than extended descriptions. Attempting to discern ultimate causes by focusing on primary levels (Krebs, 1978) may lead to contradictory conclusions. For example, predation and food distribution are often used to explain various aspects of social organization, but Patterson (1965) and Krebs (1971) used predation to explain both colonial and dispersed nesting schemes.

The selection of a methodological approach to problem solving poses its own difficulties. The comparative approach can generate a large amount of data as well as ideas and hypotheses, but it does not necessarily explain relationships among variables. Few comparative studies offer "controlled" observations. Connell (1975) discusses "natural experiments" in which systematic observations may substitute for controls, but data from most comparative studies are correlational rather than empirical and of a limited heuristic value. Further, the use of taxonomic units for comparisons raises the question of the independence of observation among closely related groups, as well as the validity of conclusions based upon comparisons between units whose taxonomic and hence biological relationships are matters of debate.

On the other hand, the experimental approach attacks functional problems in a more straightforward way, but it can end up being relatively artificial as well as limited when results are extrapolated to the natural setting. Further, the increasingly serious question of the experimenter's own manipulations interfering with and possibly biasing interpretation of the reproductive phenomenon under investigation (*e.g.* Gillett *et al.*, 1975, Robert and Ralph, 1975) must be adequately addressed.

Timing of Breeding

Lack (1968) suggested that patterns of nesting dispersal are adaptations, evolved through natural selection, that enable species to raise the greatest number of young. Social stimulation, food, and predation are all factors that may influence the timing of breeding. Since Darling (1938) suggested that stimuli from nearby courting and nesting individuals enhance reproductive synchrony of mated pairs as well as the entire colony, the survival value of colonial nesting and the significance of breeding synchrony have received considerable attention. Darling hypothesized that in large colonies of gulls, and perhaps of other birds, laying started earlier and birds completed their clutches more quickly than in small colonies.

Darling also found that predators such as Great Black-backed Gulls (*Larus marinus*) and Gray Herons (*Ardea cinerea*) took a steady toll of young Herring Gull (*L. argentatus*) chicks. He suggested that the shorter the nestling period, the less the resultant mortality due to predation. Given a constant low rate of predation, birds that begin breeding during the peak period would be less likely to lose their nests and young than birds that nest earlier or later. The probability will be less for individuals breeding in highly synchronized colonies than for individuals nesting in less synchronized colonies.

MacRoberts and MacRoberts (1972) summarized the impact of Darling's hypothesis on subsequent research and readdressed the question: Is there a correlation between the degree of synchrony and the amount of stimulation received from conspecifics engaged in reproductive displays? They maintain that the results of much research have been equivocal.

For example, according to MacRoberts and MacRoberts, both Coulson and White (1960) and Horn (1970) found that the onset of breeding in the Black-legged Kittiwake (*Rissa tridactyla*) and Brewer's Blackbird (*Euphagus cyanocephalus*) was correlated with density. This was interpreted as partly the effect of social stimulation. However, Orians (1961) for the Red-winged and Tricolored Blackbird (*Agelaius phoeniceus* and *A. tricolor*), as well as Vermeer (1963) and Widemann (1956) for Black-headed and Glaucous-winged Gulls (*L. ridibundus* and *L. glaucescens*), found no evidence for density-correlated synchrony. Furthermore, as colony size or density increases the spread of laying has been found to be unrelated, or to increase rather than decrease (Coulson and White, 1960; Vermeer, 1963; Robertson, 1973; MacRoberts and MacRoberts 1972). Moreover, Coulson and White (1956, 1958, 1960) and Coulson (1968) argue that the differences in the onset of breeding in the kittiwake are attributable, at least in part, to differences in age, breeding experience, and physical conditions.

Parsons (1975) noted that most published studies report a decline in nesting success as a function of time of season. Such declines have been observed in the Herring Gull (Paynter, 1949; Paludan, 1952; Kadlec and Drury, 1968; Erwin, 1971; Morris and Haymes, 1977); the Glaucous-winged Gull, the California Gull (*L. californicus*), and the Ring-billed Gull (*L. delawarensis*) (Vermeer, 1963, 1970); the Razorbill (*Alca torda*) (Plumb, 1965); the Shag (*Phalacrocorax aristotelis*) (Snow, 1960); the Black Noddy (*Anous tenuirostris*) (Ashmole 1962); and the Sooty Tern (*Sterna fuscata*) (Ashmole, 1963).

Other studies have documented other patterns, reaffirming the conception that multiple variables may operate simultaneously to determine nesting success. For example, Brown (1967) found that Herring Gulls and Lesser Black-backed Gulls (*L. fuscus*) breeding in midseason were the most successful. Similar results were generally found by Kadlec *et al.* (1969) and Erwin (1971) for Herring Gulls in the northeastern U.S., as well by Kruuk (1964) and Patterson (1965) for Black-headed Gulls in England. In a limited number of instances, moreover, late-breeding birds are found to have greater success. Such results have been reported by Harris (1969) for European Oystercatchers (*Haematopus ostralegus*) and Erwin (1971) for Great Black-backed Gulls. Occasionally some studies fail to document any differences in nesting success as a function of season, as for example the studies of Nelson (1966) for the Gannet (*Morus bassanus*) and Harris (1970) for the Swallow-tailed Gull (*Creagrus furcatus*).

Parsons (1975) extended the breeding season of Herring Gulls by large-scale egg removal, which resulted in many re-layings. He concluded that clutch size diminution as a function of time was the most important factor contributing to lowered production of chicks during the season.

While various studies have shown a decline in nesting success with laying date, date of hatching as related to post-fledging survival is less well documented (Parsons *et al.*, 1976). A high rate of mortality occurs just after fledging in many bird species, but such deaths often take place during post-breeding dispersal and migration; investigation of such mortality requires extensive banding.

Nisbet and Drury (1972) obtained evidence that early-hatching Herring Gull chicks have markedly lower post-hatching mortality. Similar survival patterns were reported for Franklin's Gulls (*L. pipixcan*) by Burger (1972). Harris (1969) found no such correlation in the European Oystercatcher, although Perrins (1966) noted that the late-hatching Manx Shearwaters (*Puffinus puffinus*) were less likely to return to the natal colony in subsequent years. Fretwell (1969) suggested that any survival advantage may be due to dominance of older young over later-hatching birds, possibly in the winter season. Conversely, Parsons *et al.* (1976) found that in Scottish Herring Gulls late hatching was no disadvantage.

For many species most nestling mortality occurs in the first few days following hatching (Nisbet and Drury, 1972; others). Some of this early mortality may be related to the size and possibly the quality of eggs, as well as certain qualitative differences among adults. Ryder (1975) examined the effects of time of egg-laying and egg size in relation to age of adult Ring-billed Gulls. Previously, studies had shown that older birds laid larger eggs than younger birds; *e.g.*, in Shags (Coulson *et al.*, 1969), Black-legged Kittiwakes (Coulson, 1963), Gannets (Nelson, 1966), and Short-tailed Shearwaters (*Puffinus tenuirostris*) (Serventy, 1967). In Ring-billed Gulls, Ryder (1975) found seasonal variation in laying date and a reduction in average clutch size among pairs to be a function of age and experience. Pairs composed of two mature birds started clutches earlier and laid larger eggs. Furthermore, eggs laid by mature birds had much higher hatching success than those laid by pairs in which at least one bird was less than fully mature.

Food availability may influence timing of breeding (Baker, 1938) and subsequent reproductive success. Perrins (1970) suggested that for some species of birds, the timing of laying is the result of an interaction between the evolutionary advantage of early breeding and the physiological state of the female. There is strong selection for early breeding, but a minimum threshold of food abundance must be exceeded for egg production. In such cases, the availability of food acts as a proximate factor (Hilden, 1965), delaying the commencement of breeding until the female is physiologically ready.

A fluctuating food supply could affect not only the timing of nest initiation, but certain aspects of chick survival as well. For example, Nisbet and Cohen (1975), for Common and Roseate Terns (*Sterna hirundo* and *S. dougallii*), suggest that synchronous hatching is an important factor affecting the survival prospects of younger chicks within a brood. Hatching intervals tend to lengthen during the season because adults start incubating the first egg in a clutch progressively earlier as the season advances. If food supplies dwindle late in the breeding season, the prospects for raising two or more young may decrease; lengthening of hatching intervals permits larger (*i.e.* first hatched) chicks within a brood to compete more successfully for food, an extension of Lack's (1966, 1968) explanation for asynchronous hatching.

Predation also affects timing of nest initiation and chick survival. Robertson (1973) found that early-nesting Red-winged Blackbirds were consistently more successful than late-nesting ones; predation pressure increased as the season advanced. Nisbet (1975) suggested that in circumstances where food requirements of a predator are relatively constant, a larger fraction of available prey might be taken when few of them are present as, for example, at either the beginning or the end of the breeding season. Such an effect had already been demonstrated by Ashmole (1963) for predation by feral cats on Sooty Terns, by Patterson (1965) for predation by Carrion Crows (*Corvus corone*) on eggs and chicks of Black-headed Gulls, and by Parsons (1971) for intraspecific predation (cannibalism) by Herring Gulls on chicks. Further, predators specializing on chicks might inflict the most damage at the beginning of the season, when earliest-hatched birds are small and more are needed to satiate the predator. Nisbet (1975) argues that this is the case in one Common Tern colony; in this instance, predation selected against very early-breeding birds.

Intraspecific predation may equal interspecific predation in importance as a determinant of temporal differences in nesting success. For Herring Gulls (Paynter, 1949) and for Ring-billed and California Gulls (Vermeer, 1970), greatest nesting success was found among early nesters where killing of chicks by conspecifics was at least equal to the mortality caused by other predators. For Lesser Black-backed Gulls, Davis and Dunn (1976) observed a marked decline in nesting success as the season advanced where the main cause of egg and chick loss was intraspecific predation.

To elucidate the determinants of success, at least at high densities, Hunt and Hunt (1976) modeled the optimal timing of hatching for chick survival by minimizing the probability of chick loss to neighbors and predators (Fig. 1). Adult aggressiveness and defense of territory increases at the time of hatching, so the probability of chick loss to neighbors is low early in the season when few pairs have young. The risk to chicks increases rapidly as hatching commences, and remains high for the remainder of the season. On the other hand, the highest rate of loss of chicks to predation is found early in the season, and decreases as hatching advances. Hunt and Hunt predict an optimal breeding time when $[1-(1-N)(1-P)]$ is at minimum, where N is the probability of being eaten by a neighbor and P is the probability of being taken by a predator.

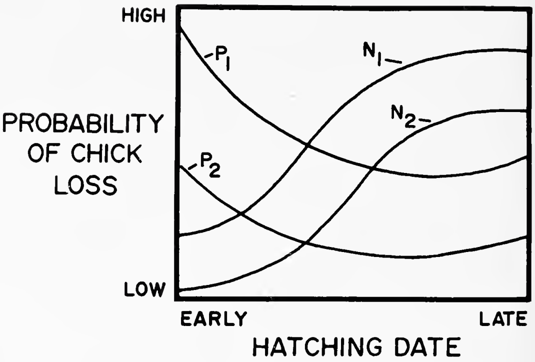

Figure 1. A model of optimal hatching date in which timing for maximum chick survival is predicted by probability of chick loss to predators and to neighbors. P_1 = loss due to heavy predation pressure; P_2 = loss due to light predation pressure; N_1 = loss due to very dangerous neighbors; N_2 = loss due to moderately dangerous neighbors. (From Hunt and Hunt 1976, © 1976, Ecological Society of America.)

Dispersion of Nests

Dispersion refers to nest placement within the colony, which, in turn, relates to associations between a nest occupant and its neighbors as well as to the density of nests within the colony. Nest density relates in one way or another to territory size.

In 1952, Darling hypothesized that an important function of territory is the provision of periphery, an edge where there is another bird of the same species also occupying a territory. Noting the work of Williamson (1949) on the Great Skua (*Catharacta skua*), Darling suggested a need for a minimal level of mutual stimulation among nesting pairs, not obtainable by solitary or widely scattered nesting birds.

Tinbergen (1952, 1956), writing on the significance of territory in gulls, suggested and later demonstrated (Tinbergen *et al.*, 1967) that spacing of nests is a corollary of procryptic coloration. Territorial fighting is a means of promoting the dispersal of cryptically colored nests. The actual location of nests in a colony depends on a balance between the advantages of dispersal and the advantages of clustering (Cullen, 1957; Kruuk, 1964). Clustering allows the possibility of mobbing a predator, although there may be a lower limit for colony size enabling effective mobbing (Burger, 1974b).

That breeding success is a function of

colony size has been demonstrated in Black-headed Gulls (Patterson, 1965) and Northern Fulmars (*Fulmarus glacialis*) (Fisher, 1952), Gannets (Fisher and Vevers, 1944; Nelson, 1966), Herring Gulls (Darling, 1938, but see Haartman, 1945), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus)* (Fautin, 1941), Red-winged Blackbirds (Robertson, 1973), and Tricolored Blackbirds (Orians 1961, Payne 1969). Hoogland and Sherman (1976) state that, within Black-headed Gull colonies (Patterson, 1965) and Red-winged Blackbird colonies (Robertson, 1973) at least, much of the increased breeding success in larger colonies results from decreased predation per nest. Nisbet (1975) discussed evidence leading to the same conclusion in tern colonies.

Tenaza (1971) suggested that the average number of young produced per breeding pair should vary as a function of colony size; in Adélie Penguins (*Pygoscelis adeliae*) peripheral nesters seemed to raise fewer young compared with central nesters. He maintained that the increased probability of predation for peripheral nesters, occurring as a function of their relative proportion to the number of central nesters in small versus large colonies, is a simple alternative to the Darling effect for explaining the relatively lower breeding success of small colonies of seabirds as compared with large ones.

A number of studies have reviewed particular effects of nest location on breeding success. Burger (1974a) reviewed the literature and found that most studies show optimal breeding success for gulls, at central locations within the colony. Hoogland and Sherman (1976) reviewed evidence that central nests experience less predation than peripheral nests. Among the species for which such differential success was found to hold were: Adélie Penguins (Eklund, 1961; Taylor, 1962; Reid, 1964; Penny, 1968), Black-headed Gulls (Kruuk, 1964; Patterson, 1965), Pinyon Jays (*Gymnorhinus cyanocephalus*) (Balda and Bateman, 1972) and White Pelicans (*Pelecanus erythrorhynchos*) (Schaller, 1964). That central nests are more successful than peripheral nests in ways at least indirectly related to decreased predation has been demonstrated in Brewer's Blackbirds (Horn, 1968), Cattle Egrets (*Ardeola ibis*) (Siegfried, 1972), Cliff Swallows (*Petrochelidon pyrrhonota*) (Emlen, 1952), and Bank Swallows (*Riparia riparia*) (Emlen, 1971).

Fit and less fit individuals may not be randomly distributed within breeding colonies. In Black-legged Kittiwakes, Coulson (1968) noted larger clutch size, higher hatching success, and more young fledged per pair in the center of the colony as compared to the edge. The differences in reproductive rate between the center and the edge seemed to be the direct result of variation in the quality of breeding birds. Central males lived longer, were recruited at a slightly heavier weight, and were more productive on an annual basis (Coulson, 1971). Age may have been responsible for some of these differences. Tenaza (1971), for the Adélie Penguin, noted that the mean number of eggs produced per nest decreased from central to peripheral to isolated nests. Further, central nests were of superior quality in terms of nest structure. In Franklin's Gulls (Burger, 1974a) center and edge were less definable, and reproductive success was better on the edge than in the center of the colony. Burger speculated that this seeming inconsistency with other studies was the result of better accessibility of nest sites and display areas at edge locations, which in turn provided greater social stimulation.

Differences in the quality of adults might be expected to result in qualitative differences in eggs or young (Coulson *et al.*, 1969). Ryder *et al.* (1977) noted that Ring-billed Gull eggs hatched more frequently in the center than at the periphery of the colony, but when the authors tested eggs from such areas in regard to relative nutrient and energy content, no differences in regard to quantities of proteins, carbohydrates, and lipids (at least in the yolks) were found. Similarly, Ryder and Somppi (1977) found no significant differences between central and peripheral nests in Ring-billed Gull embryonic development and size.

The effects of nest density on reproductive timing has been the association most often studied, although the distinction between colony size and density of breeding birds has not always been clearly maintained. Goethe

(1937) and Paynter (1949) were among the first to observe that eggs tend to hatch earlier in more densely populated portions of gull colonies. Coulson and White (1956, 1958) found that Black-legged Kittiwakes returned earlier to colonies in which breeding occurred early and that individuals returning to colonies early also usually bred early. In 1960 they showed there was a correlation between nest density and time of return to a colony; birds returned earlier to those areas where nest density was high.

Darling (1938) suggested that the greater the number of birds in the colony, the greater the synchronization of birds breeding within the colony. Thus breeding should be both earlier and of shorter duration in larger colonies. Conversely, Coulson and White (1960) showed that for kittiwakes the spread of breeding time was greatest in dense colonies. Similarly, MacRoberts and MacRoberts (1972), looking at social stimulation as a factor in the reproduction of Lesser Black-backed and Herring Gulls, were unable to support the Darling hypothesis. Social stimulation of reproductive events leading to breeding synchrony was not observed, nor was the timing of laying found to be correlated with nesting density. Also, no difference was found between spacing patterns of pairs nesting early versus late in the season.

Colony density has been suggested to influence not only colony synchrony but also reproductive success. Harris (1964) maintained that in the Black-legged Kittiwake there was no reason to suppose that size of the colony over an initial threshold value should bear any relationship to the productivity of the colony. Further, he noted that although a connection between mortality and breeding density is theoretically possible, it is very difficult to measure breeding density in cliff-nesting gulls.

In a landmark study of the Black-headed Gull, Patterson (1965) noted that an apparent correlation between density and success disappeared when partial correlation analysis removed the effect of year of investigation. Hence, there was no substantive relationship between nest density and breeding success. Although predation was the most important cause of egg and chick losses, Patterson noted that the spacing of nests differed from that expected on the basis of Tinbergen's (1952, 1956) hypothesis of dispersion among cryptic prey in order to minimize the formation of specific search images among predators. As the eggs of Black-headed Gulls are somewhat cryptic, Patterson had expected greater spacing of nests. Tinbergen *et al.* (1967) later suggested that Black-headed Gulls may profit from crowding through more effective attacks on predators. Brown (1967) also suggested that for Herring and Lesser Black-backed Gulls, increased density may contribute to earlier and possibly more efficient breeding through reduced losses of late eggs and chicks.

Interspecific interactions are associated with characteristics of nest spacing and location and may affect nesting success. For example, Erwin (1971) and McGill (1977) have documented a decrease in overall nesting success of Herring Gulls when nesting in close proximity to Great Black-backed Gulls as compared to nesting near conspecifics. McGill showed that in areas where the two species were nesting neighbors, Great Black-backed Gulls had fewer young survive to fledging than did Herring Gulls. Similar interactions have been noted among herons. Burger (1978) presented evidence that in New Jersey, Snowy Egrets (*Egretta thula*) suffer poorer success when breeding near Cattle Egrets than when they nest alone. Similar negative associations among Cattle Egrets and Little Blue Herons (*Florida caerulea*) were reported by Dusi (1968) and Werschkul (1977).

Christian and Davis (1964) suggested that for some mammals, crowding results in the advent of behavioral pathologies, including cannibalism. Intra-colony killing of eggs or young has been observed in many birds, *e.g.* Herring Gulls (Paludan, 1952; Brown, 1967), Glaucous-winged Gulls (Vermeer, 1963), and Black-headed Gulls (Weidmann, 1956). In some cases, the amount of mortality specifically attributed to cannibalism can be striking; Parsons (1971) reported that cannibalism accounted for approximately 23% of mortality of young in one colony of Herring Gulls.

General intraspecific aggression, quite apart from cannibalism, may also affect success. Buckley and Buckley (1972) noted that although high density was probably an anti-predator device for Royal Terns (*Sterna maxima*), eggs in unsuccessful nests failed because the parents were too often involved in bickering with close neighbors. Their results were compatible with those of Ansingh *et al.* (1960) and Dircksen (1932), who demonstrated that unhatched eggs in Royal Terns were significantly closer to other eggs than those that hatched.

Hunt and Hunt (1975) found Western Gull (*L. occidentalis*) chick survival was negatively correlated with the distance to the nearest neighbors' nests. There was no correlation between survival and either territory size or time of hatching. In a later study, Hunt and Hunt (1976) found that survival of chicks was significantly associated with territory size, but only for those years in which food availability was limited.

In neither year did inter-nest distance relate to chick survival, possibly because nests in large territories were frequently close to the territory boundary rather than the center, or because chicks left their nests shortly after hatching and thereafter used most of their territory. In years of low food availability, chicks that hatched early in the season on large territories had better survival rates than chicks hatched late in the season on small territories. In the year of high food availability, timing of breeding and territory size had little effect on survival.

Parsons (1976) compared nesting density and breeding success in the Herring Gull. The relationship between clutch size and nesting density was unclear in his study, but pairs nesting at the modal colony density had the greatest hatching and fledging success and reared the most chicks per pair of fledging. In addition, birds that spaced their nests the most uniformly were the most successful, possibly as a consequence of territorial behavior.

Birkhead (1977) studied the relationship of breeding success with nest density in Common Murres (*Uria aalge*). Breeding success—the number of pairs raising a chick to fledging—was greatest in dense groups within the colony and also appeared to be associated with spread of laying within groups. Birkhead maintained that dense groups nested over a shorter period of time and thus were less vulnerable to predation. Furthermore, birds in dense groups spent more time sleeping and less time in alarm-related behaviors compared with birds nesting in sparse groups. The increased nervousness as well as less tenacious incubation in sparse groups may have facilitated attacks by predators, *i.e.* gulls. In dense groups, murres could deter gulls by lunging at them, but not so in sparse groups. Krebs (1978) reiterated that failure of communal mobbing accounts for greater vulnerability of less protected nests.

Hunt and Hunt (1976) suggested that past attempts to relate gull chick survival either to inter-nest distance (Fordham, 1970) or to average nest density (*e.g.* Vermeer, 1963; Patterson, 1965; Fordham, 1970; Parsons, 1971; Dexheimer and Southern, 1974) have failed to show consistent and significant relationships because most such studies inadequately measure actual territory size (which also may change as a function of time of season) and thus further poorly differentiate the quality of individual territories. For example, in areas with the same density of nests, it is possible to have very different distributions of territory size. It may be necessary to examine territory size directly to understand the role of spacing within gull colonies.

Hunt and Hunt attempted to model optimal territory size (Fig. 2), given the potentially conflicting requirements of providing sufficient room for chicks to avoid being molested by neighbors and sufficient clumping for effective group defense against predators. Chick loss to aggressive neighbors was predicted to be greatest on small territories and to decrease as area increases up to an asymptote, beyond which further increase in territory size will not affect chick loss. The position of the asymptote will vary with terrain, availability of hiding places, aggressiveness of neighboring adults, and the tendency of chicks to move away from their nests as well as how well and how often the chicks are fed (Hunt and McCloon, 1975). When nests are clumped, defense of chicks either by mobbing or swamping of predators should be most effective. However, protection derived from coloration should be more effective if nests and chicks are widely spaced. The optimal chick territory size was predicted when

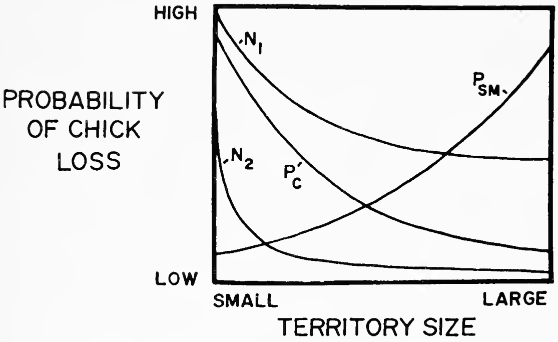

Figure 2. A model for optimal territory size in which territory size for highest chick survival is predicted by probability of chick loss to predators and to neighbors. N_1 = loss due to very dangerous neighbors; N_2 = loss due to relatively harmless neighbors; P_c = loss to predators due to failure of cryptic components of defense; P_{sm} = loss to predators due to failure of swamping or mobbing strategies of defense. (From Hunt and Hunt 1976, © 1976, Ecological Society of America.)

$[1-(1-N)(1-P_{sm})(1-P_c)]$ is at a minimum value, where P_{sm} is probability of loss to predation due to the failure of swamping or mobbing, P_c is the probability of loss of chicks due to the failure of cryptic components of defense, and N is the probability of loss of chicks to neighbors.

The Effect of Habitat

Colony and nest sites are selected on the basis of both ultimate and proximate environmental characteristics. Ultimate factors include food, breeding site requirements imposed by structural and functional characteristics of the species, and shelter against weather and enemies. Proximate features comprise the more immediate stimuli of landscape and vegetation; terrain; areas for nesting, feeding, and drinking; and other animals (Hilden, 1965).

The influence of other birds, either conspecific or heterospecific, can be either positive or negative, as cited earlier in this paper. Interspecific competition for colony and nest site resources is generally found to result in increased specialization and reduced overlap among species' resource requirements. In the absence of interspecific competition, intraspecific competition can determine the width of the habitat range of a species; optimal habitats may be exploited when populations are sparse but as population density increases, less favorable habitats also may be occupied, generally in their relative order of suitability (Kluyver and Tinbergen, 1953; Hilden, 1965).

Klopfer and Hailman (1965) hypothesized that the most important habitat variable orienting gulls to correct feeding, courting, and nesting habitat is the presence of other gulls, although other environmental cues are sampled as well. They maintained that the choice by early arrivals of one of the several possible sites determines the colony location for a particular year.

Studying nest site selection by Laughing Gulls, however, Borngiorno (1970) found that, if habitat were not changed, gulls nested within the same general breeding areas from year to year and in the same patterns in experimental quadrats. In contrast to Klopfer and Hailman's (1965) hypothesis, he concluded that Laughing Gulls first placed their nests in response to environmental features; further spacing depended on a bird's response to its neighbors.

Similarly, Burger (1974a) noted that Franklin's Gulls generally tended to return to display on colony sites of previous years. Such behavior has the selective advantage of reuniting members of a pair. Burger noted that cattail density and dispersion were environmental features most important for colony site selection. Nest sites were selected on the basis of minimal visibility to nearby nests. Similar results for nest-site orientation were later found for Black-headed Gulls (Burger, 1976). Of course, other variables are important as well; Burger and Shisler (1978) point out that nest-site selection is ultimately a compromise among various selection pressures of weather, cannibalism, predation, and other variables.

Prior breeding experience in an area may contribute significantly to the selection of one area over another for breeding (Klopfer and Hailman, 1965). Hilden (1965), reviewing the work of Austin (1940, 1945, 1949), stated that among Common Terns (*Sterna hirundo*) older birds returned faithfully to original nesting sites although vegetational changes over the years gradually rendered the substrate unsuitable for younger birds.

Borngiorno (1970) reviewed general tenacity in colony-site selection among gulls. Laughing Gulls may completely abandon former nesting sites, but many larids occupy the same general site over successive years, *e.g.*, Herring Gulls (Tinbergen 1952, 1961; Drost, Focke, and Freetag, 1961; Ludwig, 1963), Ring-billed Gulls (Southern 1967, 1977), Black-headed Gulls (Svardson, 1958; Beer, 1961), Glaucous-winged Gulls (Vermeer, 1963), Laughing Gulls (Stone, 1937; Noble and Lehrman, 1940; Noble and Wurm, 1943), Sooty Terns (Robertson, 1964), and Royal Terns (Kale, Sciple, and Tompkins, 1965). Brewer and Harrison (1975) also noted the same general phenomenon, citing the work of Nice (1937) and Haartman (1949). Occasional exceptions occur in species whose habitats are unstable, *e.g.* Black-billed Gulls (*L. bulleri*) (Soper, 1959; Beer, 1966), Franklin's Gulls (Burger, 1974a), Brown-hooded Gulls (*L. maculipennis*) (Burger, 1974b), and Ring-billed Gulls (Southern, 1977). Erwin (1977) has calculated an index to colony-site change rates for Herring Gulls as well as other species.

Brewer and Harrison (1975) suggested that for many species it seems likely that most individuals nest throughout their lives near the spot where they settled in their first year. McNicholl (1975) wrote that site tenacity generally has the selective advantage of reducing susceptibility to predation by familiarizing a bird with its surroundings as well as allowing it to return to sites where successful nesting previously took place. Of course, too strong a site tenacity could be disadvantageous if it promoted the continuous use of poor sites or those that have deteriorated (see the work of Austin, cited earlier). The degree of site tenacity within a population may reflect the stability of the habitat. McNicholl suggests that colony and nest-site tenacity is particularly well developed in highly stable habitats and reduced in unstable habitats. Group adherence—the association of several individuals from one year to the next—may be more important than site tenacity for species nesting in unstable habitats.

Variation of breeding success in relation to physical features of the environment is not well known (Birkhead, 1977). The factors determining the optimal breeding habitat of a species have been investigated for only a few species, *e.g.*, the Gray Partridge (*Perdix perdix*) (Southwood and Cross, 1969) and the Common Puffin (*Fratercula arctica*) (Nettleship, 1972). To adequately describe the relationship between the nesting success of a species and its habitat, information about environmental conditions throughout its total geographic range as well as its breeding success in representative areas should be known (Nettleship, 1972). In fact, there have been relatively few such systematic studies of the relationship between habitat and productivity. Most published accounts have been largely anecdotal or at least of limited scope, where habitat-productivity relationships were described as part of a larger study (*e.g.* Snow, 1960; Beer, 1966; Nelson, 1966; Brown, 1967; Coulson, 1971). Nettleship (1972) noted that colonial seabirds should make excellent study subjects for studies relating breeding success to habitat features; they tend to breed in high numbers at relatively traditional colonies where nests are abundant and where the number of environmental variables is small and relatively constant.

At Great Island, Newfoundland, Nettleship found Common Puffin density negatively correlated with distance from cliff edge and positively correlated with the degree of slope; close to the cliff edge where the angle of the slope was steep, the breeding success of puffins was significantly higher than on level habitat. Characteristics of the eggs in both habitats were approximately the same and egg-laying dates were similar, but the annual variation in egg characteristics was greater on the level than on the slope habitat. The frequency of infertile eggs was lower on the slope. Fledging success was higher on the slope. Frequency of chick deaths in the nest and disappearance before fledging was higher on level habitat in both years. Fledging success was higher for earlier-hatched chicks in both habitats, but the total breeding success was higher on the slope habitat.

Nettleship concluded that the difference in breeding success in the two habitats was due to higher exposure of chicks and eggs to gull predation on the level habitat. The primary cause of this differential exposure was that adults on slope habitats were less vulnerable to gull disturbance during incubation and gull robbery when feeding chicks. Breeding failures resulted from the interaction of food shortage and gull interference.

Burger (1977) recently investigated the comparative nesting success of Herring Gulls as they invaded previously unused *Spartina* salt marsh habitat in New Jersey. Gulls constructed larger and deeper nests in wetter as compared to drier areas. In wet areas, more complete repairs to damaged nests were effected. Hatching success was poorest in wet areas, much more successful in dry areas. Her results not only demonstrate a nice relationship between qualitative habitat differences and breeding success, but also indicate that the highly adaptable Herring Gull is making yet another successful shift into new areas because the species is able to give appropriate behavioral responses to previously unencountered habitat stimuli.

Summary and Conclusion

Various factors may account for observed declines in nesting success as the breeding season advances. For example, experienced birds can begin breeding earlier, can have larger clutches, and can be more successful in rearing young. Further, for some species food may be less abundant as time advances, resulting in less success among later-hatched young. Similarly, predation and intraspecific interference may increase nesting synchrony and nesting success, although not always at consistent periods within the season. Models have been proposed for the optimal timing of chick hatching by minimizing intraspecific and interspecific losses in gulls.

Breeding success often varies as a function of colony size. The increase in breeding success in larger colonies results from decreased predation per nest; there is a smaller proportion of vulnerable peripheral nests in larger colonies. Furthermore, fit and less fit individuals generally are not equally distributed within colonies. More experienced birds may acquire more desirable locations. Also, newer and often smaller colonies may be established by younger, less reproductively fit individuals.

The distinction between colony size and density within those colonies has not always been maintained. Nonetheless, the effect of density on reproductive synchrony and nesting success has been the relationship most often studied. There has been little unequivocal support for Darling's hypothesis of earlier breeding and intra-colony synchrony in large and dense colonies. Likewise, clear evidence for greater breeding success with increased density has not been found consistently. In fact, increased density and interspecific nesting associations may enhance opportunities for negative interactions through predation, cannibalism, or simple interference. Models have also recently been proposed relating optimal territory size to the amount of space necessary to prevent molesting of chicks by neighbors while at the same time allowing for sufficient clumping of nests for effective group defense against predators. These models attempt to resolve inconsistencies among reported results as well as predict simple relationships among spacing parameters and certain aspects of gull breeding success.

Colony and nest sites are selected on the basis of a variety of proximate and ultimate environmental characteristics. Numerous studies recently have described, in considerable detail, proximate features of breeding habitat of many colonial birds. Many studies have used sophisticated statistical techniques to enhance descriptions, *e.g.*, principal component analysis. Such descriptive studies have contributed to an evolving understanding among avian biologists of the relationship between habitat stability and nest- and colony-site tenacity.

Evaluation of differential reproductive success in relation to physical and other biological features of the environment has not kept pace with descriptive habitat studies. There is poor documentation of reproductive success in relation to the environmental factors which define the optimal breeding habitat of a species. Characterization of optimal or even sub-optimal habitat has suffered because of the lack of sufficient comparative data from the range of environments in which a species breeds. Seabirds have been proposed as a group whose study could elucidate such relationships between environmental factors and reproductive success.

For conceptual clarity and because of the way results have been reported in the literature, the effects of timing of breeding, spacing of nests, and habitat selection have been treated separately. Such simplification, of course, does not exist in the biological world. Interactions among variables occur, often in a nonadditive fashion. For example, dispersion of nests probably varies and influences reproductive success in quite a different fashion in sub-optimal habitats as compared to optimal habitats. Unfortunately, most published results do not permit assessment of such interactions. In the future, our planning and attention should be focused upon studies that will permit such evaluations.

It is encouraging that many of the results cited in this review generally fit relatively straightforward models, such as those proposed by Hunt and Hunt (1976). Most interesting, however, are those studies whose results do not fit the models. Many of those studies were conducted over short periods of time. Conclusions based on such limited samples of reproductive performance and the factors that influence it may be spurious. Moreover, such short-term studies may fail completely to allow for an opportunity to discriminate among the interactions of environmental variables. To better understand long-lived organisms, such as many colonially nesting birds, studies must be conducted over many years, using more systematic methods of data collection than have been attempted previously. It is through such investigations that we will eventually succeed in more completely determining the empirical relationships among timing of breeding, dispersion of nests, and habitat characteristics, and their effects on reproductive success in colonially nesting birds.

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COMMENTS

Burger: With respect to the cattails affecting the nesting behavior of Franklin's Gulls that you referred to, habitat variables were important and I was measuring them. The critical factor was that the social interactions were mediated by the vegetation. When you remove the cattails, there was an enormous increase in the amount of aggression. As cattails grew and reduced visibility, aggression decreased. Then removal of the cattails again resulted in increased aggression. Thus, it was the social factors, not the vegetation that were of primary importance.

McCrimmon: I am glad that you point out that multiple factors often interact.

Parkes: There has been an infinite number of studies of the effects on breeding success of seasonal food availability not only with respect to colonial birds, but everything from tropical fruit-eating passerines and hummingbirds to songbirds. There has been an infinite number of studies of effects of predation on breeding success. Do you know of any study that has tried to bring these two things together? Obviously, there will be a period in which the predator needs more food to feed its own young. Have there been any attempts to isolate the principal predator on a colonial seabird to see whether there is a correlation between the life cycle of the predator and the prey?

McCrimmon: No, not to my knowledge. That's an excellent idea.

Coulter: Tim Birkhead did look at the rooks and the guillemots on Skomer Island, Wales. Ray Pierotti is looking at the gulls in terms of Nettleship's puffin story from Newfoundland. Early work by M. P. Harris (*Ibis,* 1964) suggests a relationship between Great Black-backed Gulls and other breeding seabirds on Skokholm Island, Wales. Finally, Ian Spellerberg has been writing something on the skua–Adélie Penguin story, but I don't know whether it has come out yet; and Fritz Trillmich has an article on the skua-Adélie Penguin story in the 1978 *Auk.*

McCrimmon: Is the work by Birkhead in his dissertation in print?

Coulter: It came out in *Ornis Scand.:* Birdhead, T. R. 1974. (*Ornis Scand.* 5, 2: 71–81.)

McCrimmon: It is something I am not familiar with, and I couldn't get his dissertation in time to include in this review.

Gochfeld: I would like to emphasize one of the last points that Don was making. Most of us who have worked in the colonies year after year will find that there are a few years that fit the model perfectly and other years that show exactly the opposite. Inter-year variability in many of our breeding seabirds, as Don implied, is one of the most fascinating aspects of their biology.

McCrimmon: It is one of the most difficult to study and one that takes really long-term commitments.

Gochfeld: Evolution does look at these long-term changes. It's not particularly concerned with May of 1978.

Vuillemier: I was somewhat disturbed at your distinction between proximate and ultimate factors, and it seems to me that if we use the term in the sense that Lack originally used it, all or most of the factors that you've discussed today I would call proximate.

McCrimmon: Yes, that's true.

Vuillemier: Now, do you believe in ultimate factors in that sense, or do you use a different definition than Lack?

McCrimmon: I think the point is that some variables can occur in both a proximate and an ultimate fashion.

EFFECTS OF TOXIC POLLUTANTS ON PRODUCTIVITY IN COLONIAL WATERBIRDS

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This paper is a review of reported effects of toxic pollutants on productivity, or reproductive success, in colonial waterbirds. It is necessarily brief and somewhat speculative, because in fact we know very little about these effects. One problem is that it is very difficult to measure productivity in colonial waterbirds without reducing it by disturbance; there are surprisingly few precise and reliable measurements of reproductive success in the literature on colonial waterbirds or on other sensitive species. Most of the published reports of toxic effects either describe spectacular effects such as total reproductive failure and heavy chick mortality, or report measurements of something else, such as eggshell thinning, egg breakage, or embryonic mortality. Even if the scope of the review is broadened to include all effects on reproductive performance, we still know very little about the effects that may be taking place at the present time. Over much of North America and Western Europe, where most studies of these effects have been carried out, the levels of the two pollutants of greatest concern—DDE and dieldrin—have decreased markedly in the last five or 10 years. As a consequence, the reproductive performance of many affected species has returned almost to normal. One subject of this paper is the precise meaning of this phrase "almost to normal."

For the purposes of this review, I have divided the reported effects into four categories, listed in diminishing order of severity. I also include discussion of two more speculative categories of effects, which are the subject of recent and current research.

ACUTE POISONING OF BREEDING ADULTS OR OF NESTLINGS

There are remarkably few published reports that fall into this category. Most of them date from the 1960s and involve poisoning with cyclodiene insecticides.

1. The most spectacular incidents of this kind were reported in The Netherlands in the period 1962–1965 (Koeman, 1972). They were traced to residues of telodrin (and to a lesser extent, dieldrin) that were discharged in effluents from a manufacturing plant and accumulated in fish and shellfish. The species most severely affected was the Sandwich Tern (*Sterna sandvicensis*)—large numbers of adults and chicks were killed and the breeding population in The Netherlands was reduced by 97–98 percent (Koeman *et al.*, 1972; Rooth and Jonkers, 1972). Other species affected were the Common Eider (*Somateria mollissima*) (Swennen, 1972), and probably the Least Tern (*Sterna albifrons*), the Common Tern (*S. hirundo*), and the Spoonbill (*Platalea leucorodia*) (Rooth and Jonkers, 1972).

2. Severe mortality of waterbirds resulting from the use of aldrin-treated rice seed was observed in Texas and Missouri in the period 1967–74 (Flickinger and King, 1972; Flickinger and Meeker, 1972; Flickinger, 1979; Babcock and Flickinger, 1977). The species most severely affected were the White-faced Ibis (*Plegadis chihi*), in which large numbers of nestlings were poisoned by contaminated invertebrates fed to them by their parents, and the Fulvous Whistling-Duck (*Dendrocygna bicolor*)

and the Snow Goose (*Chen caerulescens*), in which large numbers of adults were killed.

3. Other reported effects on colonial waterbirds have been documented less conclusively. There is strong circumstantial evidence that the population crash and disappearance of Brown Pelicans (*Pelecanus occidentalis*) from the Louisiana coast in the early 1960s were related to the pollution of the Mississippi River with endrin (King *et al.*, 1977; Blus *et al.*, 1979a). Following the re-introduction of Brown Pelicans to Louisiana, a number were killed in 1975, apparently by poisoning with endrin and/or other cyclodienes (Blus *et al.*, 1979a). Poisonings and major population declines of the Bald Ibis (*Geronticus eremita*) in Turkey and of the Japanese Crested Ibis (*Nipponia nippon*) in Japan in the period 1956–1968 were also attributed to unspecified pesticides (Hirsch, 1977; Yamashima, 1977).

I have not found any documented accounts of mass poisonings of colonial waterbirds attributable to use of DDT (*cf.* Rudd and Genelly, 1956). Abrupt population declines have been reported mainly since 1956 and appear to be attributable primarily to cyclodiene insecticides.

DELAYED LETHAL EFFECTS

A number of incidents have been reported in which lethal poisoning of colonial waterbirds has been attributable to accumulation of persistent chemicals in the birds' tissues, followed by release of the chemicals into the bloodstream as a result of subsequent stress. There is some overlap between incidents in this category and the direct poisonings listed in the previous section.

1. One of the best documented cases is that of the Common Eider in The Netherlands, referred to above. Female Common Eiders accumulated telodrin and dieldrin in their tissues from feeding on contaminated shellfish, and were subsequently poisoned as they mobilized their fat reserves while fasting during incubation. In the period 1962–65 up to 60% of the breeding females died each year. After 1965 the mortality rate declined in parallel with the decline in cyclodiene residues; most deaths in the period 1966–68 were attributed to the combination of an otherwise nonlethal pollutant load with otherwise nonlethal infection with intestinal parasites (*Polymorphus botulus*) (Koeman, 1971; Swennen, 1972).

2. In the summers of 1969 and 1973, more than 100 Ring-billed Gulls (*Larus delawarensis*) were found dead in southern Ontario. On the basis of residue levels in the brain, their deaths were attributed to poisoning with PCBs, probably in combination with DDE and dieldrin (Sileo *et al.*, 1976).

3. The deaths of a number of Great Cormorants (*Phalacrocorax carbo*) in The Netherlands in the spring of 1970 were attributable to poisoning with PCBs, on the basis of residue levels in tissues (Koeman *et al.*, 1972, 1973).

4. In 1967, 1971, and 1972, unusual mortality of nesting female Snow Geese took place in a colony at McConnell River, Northwest Territories, Canada. The circumstances of the mortality were similar to those of the Common Eiders referred to above. The mortality followed poisonings of Snow Geese from the same population in Texas prior to spring migration, and dead birds had dieldrin residues in their brains (Flickinger, 1979).

5. Although the Bald Eagle (*Haliaeetus leucocephalus*) is not a colonial waterbird, it is pertinent that up to 15% of the eagles found dead in various parts of the United States since 1963 have had lethal residue levels of one or more chlorinated hydrocarbon pollutants in their tissues. Most of these deaths are attributable to poisoning with dieldrin, but a few birds have contained lethal or near-lethal residue concentrations of DDE, PCBs, and endrin; in some cases residue levels of heptachlor epoxide and oxychlordane were sufficiently high to have contributed to the lethal toxic effects (Reichel *et al.*, 1969; Mulhern *et al.*, 1970; Belisle *et al.*, 1972; Cromartie *et al.*, 1975; Prouty *et al.*, 1977; and unpublished data from the U.S. Department of the Interior).

6. Other miscellaneous reports in this category include deaths of Western Grebes (*Aechmophorus occidentalis*) in California attributable to poisoning with DDD (Hunt and

Bischoff, 1960), of Great Egrets (*Casmerodius albus*) in California attributable to poisoning with dieldrin (Faber *et al.*, 1972), of a Great Blue Heron (*Ardea herodias*) in South Dakota attributable to poisoning with DDE (Call *et al.*, 1976), and of a Glaucous Gull (*Larus hyperboreus*) at Bear Island attributable to poisoning with PCBs (Bourne and Bogan, 1972). The last report is especially noteworthy because it referred to a site remote from any likely point of discharge. Young *et al.* (1979) have recently shown that fish caught off southern California contain enough DDE to kill gulls and cormorants after prolonged feeding.

A noteworthy feature of the reports cited in this section is that they have involved a variety of different organochlorine compounds, including several of relatively low toxicity, such as DDD, DDE, and PCBs.

Effects on Reproductive Performance in the Absence of Overt Mortality

The principal reported effects that fall into this category are hatching failure and eggshell thinning. These two effects are closely related, although each can occur in the absence of the other (Ratcliffe, 1972; Blus *et al.*, 1974; Fox, 1976; Fyfe *et al.*, 1976). The examples listed below are the best documented cases in which reductions in productivity have been associated with residue levels of toxic pollutants.

1. *Brown Pelican.* Productivity in Brown Pelicans was severely reduced in both Atlantic and Pacific coast colonies during the 1960s, in association with high residue levels of organochlorine compounds (Anderson *et al.*, 1975; Blus *et al.*, 1972a, b, 1974, 1977, 1979b; Jehl, 1973; Keith *et al.*, 1970; Risebrough *et al.*, 1970). In California, almost complete hatching failure was associated with egg breakage and extreme eggshell thinning, which in turn were associated with residues of DDE (Risebrough *et al.*, 1970; Anderson *et al.*, 1975). In South Carolina, the degree of eggshell thinning was lower than in California and direct embryotoxic effects may have been more important. Nest failure was associated primarily with residues of DDE, although effects of dieldrin could not be excluded (Blus *et al.*, 1972a, b, 1974, 1977, 1979b). In both California and South Carolina, productivity increased rapidly as residues of DDE (and dieldrin) declined after 1972 (Anderson *et al.*, 1975; Blus *et al.*, 1979b).

2. *Common Tern.* Very low productivity in Common Terns nesting in Alberta in 1972 was attributed primarily to egg breakage and to embryonic mortality. The degree of eggshell thinning was comparatively minor in this population, and the effects were traced in part to disruption of eggshell structure, which reduced the oxygen supply to the embryo. Behavioral abnormalities were detected in chicks hatching from affected eggs. All these effects were statistically associated with DDE residues in the eggs (Fox, 1976). The circumstances are noteworthy because levels of DDE and other toxic pollutants were extemely low in the terns' local food supply: the residues responsible for the effects were probably acquired in Mexico during spring migration (Fox, 1976). Hatching success of Common Terns has also been unusually low at colonies in Lakes Erie and Ontario in the period 1972–77, in association with high residues of DDE, PCBs, and other toxic pollutants, but productivity has not been clearly affected since 1972 (Gilbertson, 1974b; Morris *et al.*, 1976; Courtney and Blokpoel, 1979). A small number of abnormal chicks was noted in 1971–73 (Gilbertson *et al.*, 1976). Low productivity of Common Terns was also reported at Clay Lake, in western Ontario, in 1971, and was attributed tentatively to severe local contamination with mercury (Vermeer *et al.*, 1973), but the evidence for this was only circumstantial.

3. *Herring Gull.* Reproductive failure of Herring Gulls (*Larus argentatus*) at a colony in Lake Michigan in 1964 was associated with flaking of eggshells, embryonic mortality, and high levels of DDE (Keith, 1966). Since 1971, productivity of Herring Gulls at colonies in Lake Ontario has been very low relative to that of other colonies on the Great Lakes (Gilman *et al.*, 1977). Reproductive failures are characterized by disappearance of eggs and nests, death of embryos during incubation, and death

of chicks around the time of hatching; parental behavior also appears to be abnormal (Gilbertson and Hale, 1974a, b; Gilbertson and Fox, 1977; Gilman *et al.*, 1977; Fox *et al.*, 1978). The effects are associated with elevated levels of DDE, PCBs, and Mirex, but a causal association has not been demonstrated (Gilbertson, 1974a; Gilbertson and Fox, 1977; Gilman *et al.*, 1977, 1978).

4. *Black-crowned Night Heron.* Productivity of Black-crowned Night Herons (*Nycticorax nycticorax*) on Pigeon Island, Lake Ontario, in the period 1972–76 was very low due to a combination of low hatchability of eggs and poor survival of young. The low hatching success was associated with egg breakage, eggshell thinning, and high residues of DDE, PCBs, and dieldrin (Price 1977). In an extensive study in the eastern United States and Canada, eggshell thinning in this species was more closely related to levels of DDE than to other pollutants, but evidence for effects on productivity was only circumstantial (Ohlendorf *et al.*, 1977).

5. *Great Blue Heron.* Reproductive failure of Great Blue Herons at Red Rock Reservoir, Iowa, in 1970–72 was associated with near-lethal levels of DDE and dieldrin in the tissues of newly hatched chicks (Konermann *et al.*, 1977). In other studies of Great Blue Herons, high levels of DDE and dieldrin have been associated with eggshell thinning and adult mortality, respectively, but not clearly with reduced productivity (Vermeer and Reynolds, 1970; Faber *et al.*, 1972).

6. *Great Egret.* Reduced reproductive success of Great Egrets as a colony in California in 1967–70 was associated with high levels of dieldrin in adults (Faber *et al.*, 1972).

7. *Gannet.* A decline in the breeding population of Gannets (*Morus bassanus*) at Bonaventure Island, Quebec, between 1969 and 1973 was associated with low hatching and fledging success during the 1960s, which in turn were associated with eggshell thinning and high levels of DDE (Pearce *et al.*, 1973; Nettleship, 1975). In Scotland, eggshell thinning in Gannets was statistically associated with residues of DDE, but a significant effect on productivity has not been shown (Parslow and Jefferies, 1977).

8. *Double-crested Cormorant.* Double-crested Cormorants (*Phalacrocorax auritus*) nesting off southern California and in the Great Lakes experienced almost total reproductive failure in the period 1969–71, associated with crushed eggs, thin and defective eggshells, and high levels of DDE, PCBs, and dieldrin (Gress *et al.*, 1973; Postupalsky, 1971). Eggshell thinning in this species is statistically associated with residues of DDE (Gress *et al.*, 1973; Anderson *et al.*, 1969). Reproductive success has increased in both areas since 1972 (R. W. Risebrough and S. Postupalsky, unpublished data). In a population of this species in coastal Maine, egg residues of DDE were only modest during the 1960s, but reproductive success was nevertheless unusually low (Kury, 1969).

9. *Cahow.* Reduced productivity in the Cahows (*Pterodroma cahow*) of Bermuda in the period 1966–70 was associated with high residues of DDT and its metabolites in eggs (Wurster and Wingate, 1968). Since 1972 residues of DDE have decreased in Cahow eggs, and eggshell thickness and productivity have increased (D. B. Wingate, personal communication).

EFFECTS ON REPRODUCTIVE PERFORMANCE WHICH DO NOT LEAD TO REDUCTION IN PRODUCTIVITY IN THE ABSENCE OF OTHER STRESS FACTORS

The outstanding effect in this category is eggshell thinning, which has been recorded in at least 30 species of colonial waterbirds in North America or Western Europe (Anderson and Hickey, 1972; Ratcliffe, 1970; Faber and Hickey, 1973; Koeman *et al.*, 1972; King *et al.*, 1978; Ohlendorf *et al.*, 1978; and other papers cited above). Indeed, it seems likely that most colonial waterbird species suffered from eggshell thinning in at least some areas in the 1950s and 1960s. In all cases where statistical analysis has been carried out, eggshell thinning is closely associated with residue levels of DDE, and there is no evidence that other pollutants make any contribution to eggshell thinning in wild birds (see references cited above, and Cooke, 1973; Peakall, 1975). According to a tabulation by Peakall (1975), Pelecaniformes and Ciconiiformes are highly sensitive to DDE-induced eggshell thinning, and Charadriiformes (Laridae) are moderately sensitive.

Although broken and cracked eggs have been noted in colonies of Common Terns and White-faced Ibises with only 3–4% eggshell thinning (Fox, 1976; King *et al.*, 1978), in most species egg breakage does not become significant until the degree of shell thinning exceeds 10%, and productivity is not usually reduced significantly until shell thinning exceeds 15–20% (Ratcliffe, 1970, 1972; Anderson and Hickey, 1972). Except for the nine species listed above, most of the reported instances of eggshell thinning in colonial waterbirds appear to have been below the threshold for significant adverse effects on productivity. However, it should be stressed that productivity is not often measured, and the few reported cases are not likely to represent the full range of populations affected.

In addition to eggshell thinning, a few other effects of toxic pollutants on reproduction have been reported, which were apparently insufficient to cause significant reductions in productivity.

1. In Grey Herons (*Ardea cinerea*) in Great Britain, the principal cause of egg loss was deliberate breaking and ejecting of eggs by the parents. Although more than half the pairs under study broke their eggs in some years, overall productivity of the colony was not markedly reduced, because most pairs repeatedly produced a new clutch (Milstein *et al.*, 1970). Egg breakage was associated with high levels of DDE and dieldrin in eggs (Cooke *et al.*, 1976), whereas eggshell thinning in this species is related primarily to DDE (Koeman *et al.*, 1972).

2. Deliberate egg breaking has also been reported in Great Blue Herons in Iowa, in association with high levels of dieldrin (Konermann *et al.*, 1977). In Alberta and California, productivity of Great Blue Herons was not clearly reduced in spite of eggshell thinning (Faber *et al.*, 1972; Vermeer and Reynolds, 1970).

3. Egg breakage in Shags (*Phalacrocorax aristotelis*) was apparently related both to social factors and to high levels of dieldrin, but only a few birds were affected (Potts, 1968).

4. In my studies of Common Terns in Massachusetts, I have found associations between failure of eggs to hatch, reduced porosity of eggshells, and residue levels of PCBs and/or DDE. However, hatching failures are rare (only 1–8% of eggs laid) and productivity is not measurably affected. I have also recorded behavioral abnormalities in chicks from the most contaminated colony, but preliminary data suggest that post-fledging survival is not affected. These effects are similar to those recorded by Fox (1976), but appear to represent only marginal effects on reproductive performance.

Although only a few effects of this kind have been described, they would be difficult to detect without detailed observation and measurement. The lack of baseline data on behavior, physiology, and breeding performance in colonial waterbirds in the pre-pesticide era makes it very difficult to establish the existence of subtle effects of this kind. Nevertheless, the pervasive occurrence of eggshell thinning (an effect for which it was possible to reconstruct baseline data from museum specimens) demonstrates that many colonial waterbird populations do show measurable sub-threshold effects of environmental pollutants. The occurrence of other physiological and behavioral effects is therefore likely. Even when such effects are below the threshold for causing significant reductions in productivity, they are potentially important because they may interact with other stress factors.

Effects in Search of a Cause

A number of other effects on reproductive performance in colonial waterbirds have been described. Although they have been reported primarily in highly contaminated populations, their relation to these contaminants is more speculative. In addition to the apparent behavioral anomalies in Herring Gulls, Common Terns, and Grey Herons referred to above, these effects include the following:

1. Abnormal feather loss and congenital anomalies in Common Terns and other species (Hays and Risebrough, 1972; Gilbertson *et al.*, 1976).

2. Reduced clutch size in Black-crowned Night Herons and Common Terns (Ohlendorf *et al.*, 1977; Fox, 1976).

3. Female-female pairing in Western Gulls (*Larus occidentalis*) (Hunt and Hunt, 1977) and Ring-billed Gulls (Ryder and Somppi, 1979).

The supposed relationships of these effects to toxic contaminants need further investigation.

CAUSES IN SEARCH OF AN EFFECT

In addition to the effects recorded in the field which can be associated more or less conclusively with residues of toxic pollutants, there are a number of other effects of toxic chemicals on reproduction in birds which have been detected in laboratory experiments, but which have not yet been matched by corresponding field observations. A short list of these effects includes the following:

1. Effects of petroleum hydrocarbons on egg hatchability (Albers, 1978; Coon *et al.*, 1979).
2. Effects of DDE and other toxic chemicals on behavior of chicks (Heinz, 1976).
3. Two-generation effects of dieldrin on reproductive performance and behavior (Baxter *et al.*, 1969).
4. Teratogenic and chromosomal effects of PCBs (Tumasonis *et al.*, 1973; Peakall *et al.*, 1972).
5. Effects of PCBs on incubation behavior (Peakall and Peakall, 1973).
6. Effects of methylmercury on reproductive success (Scott *et al.*, 1975).

Although all these effects have at least potential parallels in phenomena already observed in the field, much more detailed work is required to determine whether or not they are significant under field conditions.

SUMMARY AND CONCLUSIONS

Adverse effects of toxic pollutants on reproductive performance have been reported for at least 35 species of colonial waterbirds in North America or Western Europe. For about half the species, the reported effects included significant reductions in productivity; for the other half the principal effect reported was eggshell thinning, without measurable reduction in productivity.

Although eggshell thinning took place in some species before 1951, most of the more striking effects (mass mortality of adults or nestlings, or population crashes), did not occur until the period 1956–73. The latter effects are attributable primarily to dieldrin and/or other cyclodiene insecticides, whereas eggshell thinning and other effects on reproduction are attributable primarily to DDE. Combined effects of DDE and dieldrin may have been important in several cases.

There is little direct evidence that PCBs have had significant effects on reproductive performance in colonial waterbirds. Apart from one inconclusive case involving mercury, there are no reports implicating toxic pollutants other than chlorinated hydrocarbons as having significant effects on productivity.

With the general reduction in environmental levels of DDE and dieldrin in North America and Western Europe, the reproductive performance of several affected species has at least partially recovered. Most of the remaining effects of toxic pollutants are likely to be effects on eggshell thickness or structure, or on aspects of reproductive physiology or behavior that are difficult to measure without intensive study. However, such effects are important to study: (a) because they may affect productivity when acting in conjunction with other environmental stresses; (b) because they complicate interpretation of field data. *Without detailed study of potential sub-lethal toxic effects, no colonial waterbird species can be assumed to be normal in its reproductive performance, physiology, or behavior.*

Since DDT and dieldrin are still being used fairly widely in "Third World" countries, it is reasonable to assume that major effects on colonial waterbirds are still taking place there. However, almost no studies have been reported.

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COMMENTS

Schreiber: Ian, I would like to emphasize a point that you started out with: the effect of investigator bias on measuring reproductive success. I have been working with Brown Pelicans and Laughing Gulls and am finding it almost impossible to compare results between years, and certainly between investigators, because everyone is looking at the colony and checking nests on different cycles. The figures for productivity are not comparable between studies. It is something that behooves all of us, as students of colonial birds, to be very concerned about the "paper figure and population reality," as Joe Hickey called it in 1955. We need to look very carefully at the numbers we are publishing in our tables because other people use them without looking at our methodologies.

Nisbet: I didn't say so, but I agree with you very strongly. It is a major obstacle to measuring productivity and to comparing productivity. I believe we can do certain comparisons, however. There are certain species for which investigator bias doesn't affect clutch size very much, or doesn't affect hatching success very much even though it may affect chick survival.

Ohlendorf: Could you give PCB and DDE residue concentrations for the tern eggs that you mentioned?

Nisbet: The PCB concentrations which were associated with differences in eggshell structure and hatching success, and also chick behavior, were on the order of 20–30 parts per million in the whole egg. In the other colony the only significant difference I found was in DDE levels—a difference between 1.5 and 0.5 parts per million in the whole egg.

Ohlendorf: Those are wet weight?

Nisbet: Wet weight.

Gallegos: Do you have any knowledge at all of lead poisoning from environmental contaminants? I am asking this because in New Jersey we have a lead-shot ban during the waterfowl hunting season. It has been my belief that the lead-shot problem may not originate from just lead-shot deposition during the hunting season; it may also be from environmental contaminants.

Nisbet: In preparing for this talk I read a lot of papers on lead poisoning, and I did not find a single one on a colonial waterbird species. That is not to say it does not occur, but as far as I know it has not been documented.

Unidentified: Could you expand a little bit on your differences in your two tern colonies that were 50 km apart, which by our standards is very close, to show differences in residue levels? Can you explain the particular situation that allows the birds from the two different colonies to have different residue levels?

Nisbet: One is in Buzzards Bay, Mass., which is highly polluted with PCB's from a local point source. The other is on the outer part of Cape Cod, Mass., which is in the Labrador Current and has exceptionally clean water.

Bourne: I am rather worried about our situation at home with regard to the maintenance of routine monitoring. We had a good deal of trouble in the 60s and our Nature Conservancy, as it then was, was pretty militant in drawing attention to this; and steps were taken to deal with it. The people who are now doing the monitoring are at the Ministry of Agriculture. They are efficient and do apply pressure to the manufacturers, but they maintain a very low profile and don't make their results known on the same scale as previously. We no longer have the same level of public awareness and control. If this isn't happening in Western Europe, one very much wonders what level of monitoring is being maintained in the developing nations. While the effects of all these compounds are debatable, the information which is absolutely vital and which we need for the future is the way in which the levels are changing. We need fairly adequate samples so that if at some stage in the future we wish to look back and see what happened we do have a record. Personally, I am becoming increasingly worried about this and would hope that steps can be taken to maintain a better world record.

Nisbet: Monitoring is very important for a number of reasons. One global monitoring scheme which is being promoted by people in the United States is the Mussel Watch, which I think will have some value. But the theme of my paper was that the effect of toxic chemicals on reproduction in birds is primarily a research problem and is a good deal more difficult than it was 10 years ago when levels were higher and the effects were more overt. I don't think routine monitoring is going to help us very much with that research. To solve questions we will have to focus primarily on the individual bird, the individual colony, the individual egg, or the individual fish. If we are going to answer the difficult questions which I have raised here, we need a lot more precise measurement at that level.

THE INFLUENCE OF ANNUAL VARIATION IN RAINFALL AND WATER LEVELS ON NESTING BY FLORIDA POPULATIONS OF WADING BIRDS

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Introduction

Colonial wading birds are highly mobile species known to move throughout large geographical regions in response to environmental factors. Both the locations of nesting colonies and the number of birds in them are influenced by year-to-year changes in the locations of wader concentrations. Kushlan (1976) reported that White Ibis (*Eudocimus albus*) changed nesting sites in and adjacent to the Florida Everglades almost annually, and that the sequence in which colony sites were utilized corresponded with changes in feeding areas by the birds prior to each nesting season. In a later paper Kushlan (1977) also showed that the number of White Ibis that nested in southern Florida changed considerably from year to year. More birds nested during the two wet years, 1972 and 1973, than during the dry year 1971. Similar shifts in numbers of nesting birds and locations of colonies have been reported for the White-faced Ibis (*Plegadis chihi*) in Nevada and Utah (Ryder, 1967), for the Scarlet Ibis (*Eudocimus ruber*) in Trinidad and Surinam (ffrench and Haverschmidt, 1970), and for the Sacred Ibis (*Threskiornis aethiopicus*) in Ethiopia (Urban, 1974).

Although colonial species of ibis are frequent participants in colony relocations, other colonial waders apparently make similar movements. Byrd (1978) reported a tendency for wading birds banded as nestlings to return to colonies in the same geographical region in following years, although some banded birds returned in summer to colonies of regions that were great distances from where they had fledged. He listed Cattle Egrets (*Bubulcus ibis*) banded as nestlings in Alabama that appeared in Texas in a subsequent breeding season, a Black-crowned Night Heron (*Nycticorax nycticorax*) banded in a Saskatchewan colony and later recorded on the Atlantic coast, and a Glossy Ibis (*Plegadis falcinellus*) banded in a Virginia colony that was later found breeding in Maine. Circumstantial evidence of shifts from one area to another by herons and egrets has also been provided by repeated annual censuses of some colonies over a period of several years, where numbers of pairs may change considerably between consecutive years, while long-term trends by each species may be much more stable. The implication is that birds utilize a particular colony site only when local conditions are favorable. Such a pattern of use

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was shown, most strongly for Cattle Egrets and Louisiana Herons (*Hydranassa tricolor*) at Alligator Bay, North Carolina (Grant, 1971), and for Little Blue Herons (*Florida caerulea*) and Great Egrets (*Casmerodius albus*) at McKinney's Pond, Georgia (Shanholtzer *et al.*, 1970). Ogden (1978) provided additional examples of relocation of colonies by large numbers of waders, and pointed out the difficulty of determining population trends because of the high mobility of these species.

It appears that a major factor that influences waders to use different colonies in different years is food availability in wetland habitats. Kushlan (1978, 1979) reviewed wading bird feeding ecology and feeding behavior, and discussed the factors that determine colony and feeding locations. He suggested that, barring changes in colony site habitat, location of food resources is the major factor that determines colony sites. Urban (1974) speculated that there was a correlation between timing of nesting, food supply, rainfall, and the numbers of pairs of birds in Sacred Ibis colonies. Our observations in Florida suggest a strong correlation between the timing of nesting and the location of colonies and surface water levels. Although the extent and duration of surface flooding is an obvious factor that relates to colony locations, we assume that the influence of water on food resources is probably of ultimate importance.

As a basis for understanding regional population dynamics and long-term population trends by waders in the southeastern coastal plain, this study was designed to ascertain the frequency and magnitude of shifts in nesting sites by regional wading bird populations, the relationship between those shifts and climatological factors, and the effect of these relationships on nesting success. Specifically, we need to answer the following questions:

1. What are the number of birds and the location of nesting sites for each species of colonial wading bird?
2. Can we determine population trends, either on a regional or species basis, by comparing our census data with historical census data?
3. What are the characteristics of nesting sites presently being used by each species?
4. Are the annual variations in numbers and locations of nesting waders related to climatological factors?
5. Are the seasonal, annual, and regional variations in species productivity related to colony characteristics, colony locations, and climatological factors?

In this paper we report on our initial analysis of one phase of the project, the relationship between colony locations and size and annual climatological factors. These data were obtained during aerial surveys of all active nesting colonies in peninsular Florida, exclusive of the western Panhandle. We considered that a geographically large study area is essential in order to assess wading bird dynamics on a regional basis. For example, if the number of waders declines in one colony, or in one type of colony, does the number concurrently increase at other sites?

METHODS

We organized this study into two phases. The first consisted of a series of aerial surveys conducted by fixed-wing, single-engine aircraft during April–May, repeated in June–July, for three consecutive years, 1976 through 1978. Objectives of these surveys were to locate active nesting colonies, determine species composition and make gross estimates of numbers of each species, and determine various characteristics (vegetation substrate, presence or absence of standing water, proximity to human activities, etc.) of each site. North Florida surveys were flown by Nesbitt, east-central and southeastern Florida (south to Broward Co.) by Kale, and west-central and south Florida by Ogden. Colony data from Everglades National Park were provided by James Kushlan and Oron Bass.

The second phase of this study, to begin in 1979, will consist of ground studies to more accurately determine numbers of birds in selected representative colonies, and to correlate nesting success with colony type and annual climatological conditions. Limited aerial surveys will also be conducted during this second phase.

RESULTS AND DISCUSSION

For the following analyses we selected five *herodius*), Great Egret, Wood Stork (*Mycteria americana*), Cattle Egret, and White Ibis. The first three species listed were chosen because they nest conspicuously in the tops of woody vegetation, and the latter two species because they are white-plumaged and nest in easily recognizable dense aggregations. These characteristics of visibility are prerequisites for accurate aerial surveying of colonial birds.

Figure 1 shows the location of 295 wading bird nesting colonies that were active in at least one year in each region (southern, central, northern) of the peninsula. In some cases a symbol on the map represents more than one colony. The 295 colonies represent 211 inland and 84 coastal sites. We define coastal colonies as those in saltwater or brackish zones, including several colonies a few miles inland in the broad mangrove forest in extreme southwestern Florida. Data from a few south Florida colonies were not available in time for inclusion in these analyses.

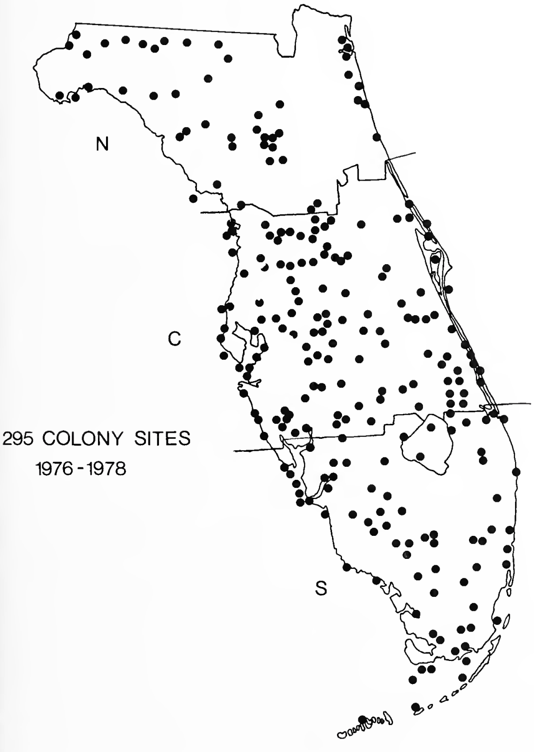

Figure 1. Location of 295 active nesting colonies of colonial wading birds, 1976–1978.

Rainfall data in each region are presented in Figure 2, which compares the historical mean rainfall with mean rainfall for each of the years, 1976 through 1978, as calculated from rainfall at eight scattered stations throughout Florida. These stations were Tallahassee, Jacksonville, Daytona Beach, Orlando, Tampa, Fort Myers, Belle Glade, and Homestead. Data are presented for the months January through July, the major wader nesting period, including the one or two months immediately preceeding actual nesting by most species. The combined means for each region were derived by adding the monthly mean rainfall from each station within that region.

In this preliminary analysis, we have not used surface water data because surface water conditions in most interior swamps and marshes in Florida are directly correlated with rainfall, and thus the extent and depth of water in fresh water wetland habitats increase proportionately with increasing rainfall. In coastal colonies surface water is related to sea level and varies imperceptibly between breeding seasons.

These data show that 1976 rainfall rates were slightly on the dry side of the historical means, that rainfall during 1977 was well below the means, and that 1978 was slightly wetter than the means. It is important to note the relative pattern of rainfall during the three years, as most changes in number and location of waders nesting each year appear to be related to this rainfall pattern.

Table 1 presents the combined total number of pairs of Great Egrets, Cattle Egrets, and White Ibis, and the mean number of pairs per colony for inland and coastal colonies in each year, 1976–78. Great Blue Herons and Wood Storks were omitted from this analysis because these two species, especially the latter, often nest separately in single-species colonies. These data were compiled from 82 colonies that were active all three years, and that contained one or more of these three conspicuous species. Colonies that were not detected until the second or third year of the survey were excluded from this comparison because in most cases we could not determine whether these colonies were inactive during the first survey year or were active and not detected.

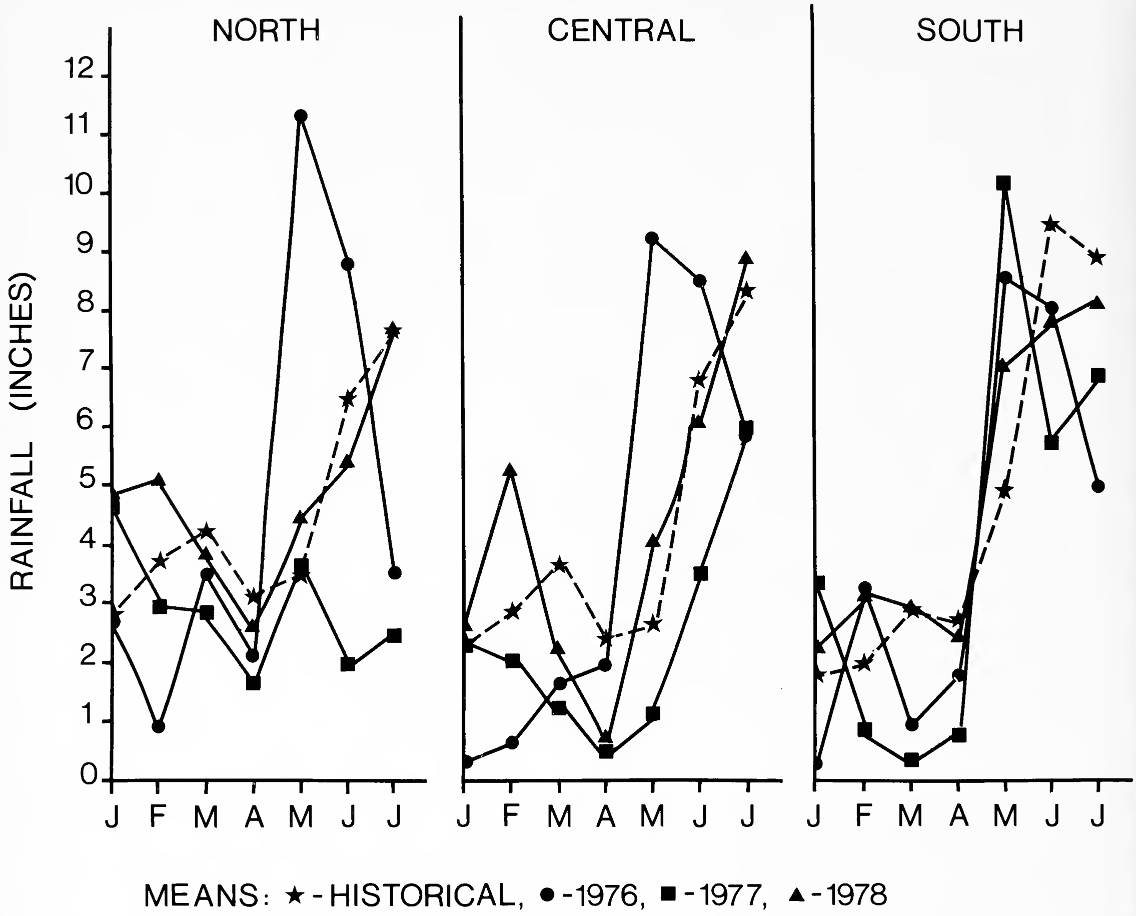

Figure 2. Comparison of historical mean rainfall in peninsular Florida with means from eight stations in 1976, 1977, and 1978.

TABLE 1
Nesting Pairs of Great Egrets, Cattle Egrets, and White Ibis
(in inland and coastal colonies which were active 1976 through 1978 in peninsular Florida.)

		Inland (n=42 colonies)	Coastal (n=40)	Combined (n=82)
1976	Mean No. of pairs	1922.1	787.5	1368.6
	Total No. of pairs	80,730	31,502	112,232
1977	Mean No. of pairs	1468.1	779.9	1132.4
	Total No. of pairs	61,663	31,196	92,859
1978	Mean No. of pairs	1634.4	1164.8	1405.3
	Total No. of pairs	68,646	46,595	115,241

Similar numbers of nesting pairs were present in the two near-average years, 1976 and 1978, with slightly more pairs present in the wetter year 1978. Approximately 20,000 fewer pairs nested during the dry year 1977, with the reduction occurring entirely in the inland colonies. The relative stability of coastal colonies when compared to that of the inland colonies is shown by the total number of colonies active in 1976 that remained active in 1978 (Table 2). Fewer than one-half (46%) of inland colonies were still active in the third year, while 78% of the coastal colonies remained active.

The relationship between rainfall and nesting for each species of wader is revealed by comparing the total number of inland and coastal colonies that contained these species, the mean number of pairs per colony, and the total numbers of pairs in all colonies in the dry and wet years, 1977 and 1978. These data are presented separately for each of the five species analyzed (Tables 3, 5–8).

For Great Blue Herons (Table 3), a total of 2328 pairs nested in 66 colonies in the dry year 1977, and 1397 pairs nested in 75 colonies in the wet year 1978. The reduction in number, 931 pairs, occurred in both coastal and inland colonies, but primarily in the former. We do not have a ready explanation for this dramatic decline between a dry and wet year, although temperature differences between the two years may have been a factor. Great Blue Herons are the earliest-nesting colonial wading bird in much of peninsular Florida, and lay as early as January (sometimes December) in some years (Howell, 1932). It is possible, therefore, that unusually low winter temperatures may affect either the timing of nesting or the number of pairs that attempt nesting. Table 4 shows deviations from historical mean temperatures at six Florida stations scattered throughout the peninsula for the main Great Blue Heron nesting months, January through April in each year 1976–78. Temperatures in 1976 were near normal, 1977 showed a cumulative 8.9 degrees below normal, and 1978 showed a cumulative deviation of 14.4 degrees below normal. Temperature and rainfall are compared with the pattern of Great Blue Heron nesting in Figure 3. Only colonies active in all three years are included in this comparison, so that the total number of pairs and colonies is less than that indicated in Table 3. Figure 3 shows a positive correlation between the number of pairs of Great Blues in inland colonies and cumulative temperature deviations from January through April, and a reverse correlation between numbers of pairs in coastal colonies and mean annual rainfall from January through July. More birds nested in inland colonies in the warmest spring of 1976, and fewer in the coldest spring of 1978, while more birds nested in coastal colonies in the dry year 1977, and fewer in the wet year 1978.

These relationships may not be fully understood until ground studies are concluded; how-

TABLE 2
Numbers of 1976 Colonies Still Active in 1978

	Inland	Coastal
1976	94	61
1978	44	48
Active in 1978	46%	78%

TABLE 3
Comparison of 1977 and 1978 Great Blue Heron Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Total	Inland	Coastal	Total
No. colonies	33	33	66	34	41	75
Mean no. pairs per colony	29.79	40.76		20.59	17.00	
Total no. pairs all colonies	983	1345	2328	700	697	1397
% total	42%	58%		50%	50%	

TABLE 4
Deviations from Historical Mean Temperatures for January through April at Six Florida Stations

	1976					1977					1978				
					Cum.					Cum.					Cum.
					Sta.[a]					Sta.[a]				Sta.[a]	
	J	F	M	A	Deviation	J	F	M	A	Deviation	J	F	M	A	Deviation
Tallahassee	−5.2	2.0	2.6	−1.1	−1.7	−8.7	−5.6	3.6	−0.5	−11.2	−7.8	−9.6	−4.0	−1.6	−23.0
Gainesville	−3.4	2.3	4.5	−1.2	2.2	−8.7	−4.1	5.2	−0.5	−8.1	−5.2	−7.7	−1.7	−0.1	−14.7
Orlando	−3.8	2.2	4.5	0	2.9	−9.7	−4.1	3.8	−0.7	−10.7	−3.5	−5.7	0.4	2.1	−7.5
Tampa	−3.8	1.3	4.5	−1.4	0.6	−9.2	−4.3	4.9	−0.5	−9.1	−5.4	−8.6	−1.8	0.3	−15.5
Ft. Myers	−2.6	0.3	3.0	−2.1	−1.4	−7.6	−3.7	2.4	−1.9	−10.8	−4.3	−7.5	−2.8	−0.5	−15.1
Belle Glade	−1.9	0.5	3.9	−0.2	2.3	−5.7	−1.6	4.5	0.7	−3.5	−3.6	−6.0	−0.8	−0.2	−10.6
Monthly Mean Deviation [b]	−3.4	1.4	3.8	−1	0.7[c]	−8.2	−3.9	4.0	−0.5	−8.9[c]	−4.9	−7.5	−1.7	0.0	−14.4[c]

[a] Cumulative station deviation derived by totaling January-April deviations for each station.

[b] Monthly mean deviation derived by averaging station deviations for each month.

[c] Four-month total of monthly mean deviations.

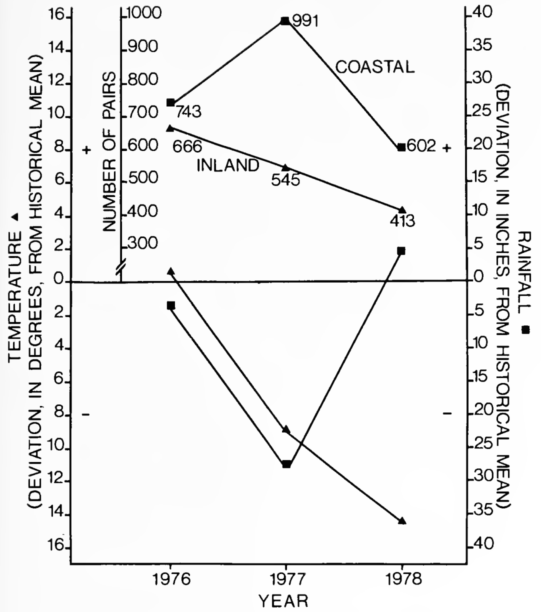

Figure 3. Correlations between rainfall, temperature, and number of nesting pairs of Great Blue Herons in peninsular Florida, 1976 through 1978.

ever, it appears that Great Blue Herons in peninsular Florida are a relatively mobile population that shifts nesting locations in response to several complex environmental factors. Two patterns appear to be evident from these three years of observations. First, the increase in numbers in coastal colonies in 1977 may be a result of birds forced to move from inland sites where many swamps were dry. Secondly, extremely cold temperatures late in winter, such as occurred in 1978, may have depressed the total number of Great Blues in both coastal and inland colonies. We do not know if fewer pairs initially attempted to nest in 1978, or if greater nesting failures resulted from the cold weather early in the nesting season before our surveys were conducted. The fact that the decline in numbers in 1978 was less in inland colonies than it was in coastal colonies may have been a result of better nesting conditions inland due to higher water levels.

With the four remaining species—Great Egret, Cattle Egret, Wood Stork, and White Ibis—patterns of nesting were compared only with rainfall, because these species initiate nesting in most of peninsular Florida later than Great Blue Herons, generally between late February and April when temperature is usually not a limiting factor. Thus far in our analyses, we have detected no relationships between low winter temperature and numbers or location of nesting sites by these four species, as seemed to occur with the Great Blue Heron.

The dry year-wet year nesting pattern of Great Egrets is shown in Table 5. Total numbers of nesting pairs in the two years were similar, 11,546 *vs.* 10,755. The greater rainfall of 1978, however, created numerous inland nesting sites that were not available to, or at least not used by, Great Egrets in 1977. Seasonal marshes and swamps, ponds, and low ground in pastures, all dry in 1977, were flooded in 1978. The result was a shift from coastal to inland sites by approximately 1500 or more pairs, and a 30% increase in inland colonies. The widely scattered nature and small size of many of the new inland colonies in 1978 suggests that it is very unlikely that all colonies were located during our surveys.

TABLE 5
Comparison of 1977 and 1978 Great Egret Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Total
No. colonies	53	47	101	76	50	126
Mean no. pairs per colony	110.7	120.7		93.6	72.7	
Total no. pairs all colonies	5869	5677	11,546	7119	3636	10,755
% total	51%	49%		66%	34%	

The distribution of Great Egret colonies in 1977 and 1978 is presented in Figure 4, which shows that most new colonies formed in central and south Florida, mainly located in a region of prairie, pasture, and phosphate-mining country and extending south into the Big Cypress Swamp. Colonies that contained Great Egrets both years were primarily those at the relatively stable coastal sites. As with most other wading birds in Florida, Great Egrets nest in woody vegetation over dry ground only when they nest on islands. We do not know if the shift to inland sites in 1978 was because the higher surface water levels created more nesting sites over water or because feeding conditions in the area were improved, but we suspect a combination of both factors. Cypert (1958) reported that the number of Great Egrets in the Okefenokee Swamp region is primarily regulated by local surface water conditions, with more birds scattered throughout the marshes when they are well flooded. A comparison of 1978 nesting success by Great Egrets at two inland colonies during spring nesting (relatively low water) and at one inland colony during summer (higher water) revealed that 50% of 76 nests in the spring colonies produced full-sized, feathered nestlings, while only two of 16 (13%) nests in the summer colony produced large young (B. Warren, unpub. data). If this pattern is representative, which we doubt, it would suggest that high water years may provide good nesting habitat, but not necessarily provide good feeding conditions. In the case of the summer colony, water was generally 8 to 15 inches or more in depth over most of the country within several miles of the colony.

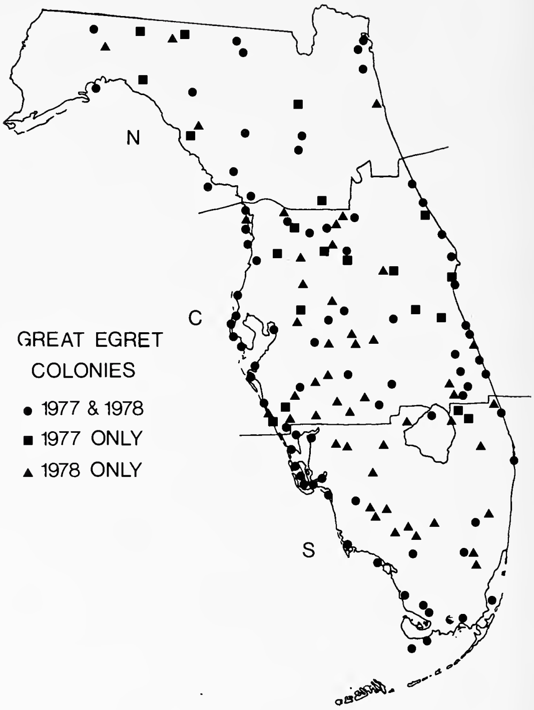

Figure 4. Distribution of Great Egret nesting colonies in peninsular Florida in 1977 and 1978.

The number of pairs and number of colonies of Cattle Egrets in both inland and coastal sites showed considerable increase, 38% and 35%, respectively, in the wetter year 1978 (Table 6). The higher inland numbers resulted primarily from establishment of new colonies, while the increase in the coastal zone was caused by greater numbers of pairs in the existing colonies. The mean colony size in inland colonies did not increase, suggesting that Cattle Egrets

TABLE 6
Comparison of 1977 and 1978 Cattle Egret Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	67	17	84	108	28	136
Mean no. pairs per colony	1353.1	700.0		1227.8	1138.3	
Total no. pairs all colonies	90,658	11,900	102,558	132,608	31,875	164,483
% total	88%	12%		81%	19%	

more often formed new colonies rather than enlarging existing colonies. This phenomenon may provide evidence for the existence of some factor(s) regulating maximum (= optimum?) colony size of Cattle Egrets in Florida, which may involve more than simply the effects of limited nesting substrate at each site. Numerous colonies that we examined from the air in 1978 appeared to be surrounded by broad belts of identical but unused habitat.

Studies of Cattle Egrets in South America and Africa (Lowe-McConnell, 1967; Siegfried, 1971) have shown that Cattle Egrets were stimulated to nest by the initiation of the rainy season. Our survey appears to be the first to show a positive correlation between numbers of nesting pairs and magnitude of rainfall. It is not clear why Cattle Egret nesting is correlated with rains in Florida, because this species generally does not feed on aquatic organisms (Fogarty and Hetrick, 1973). As in the case of Great Egret nesting, higher rainfall results in a greater number of potential nesting sites, and numerous 1978 colonies were located in sites that were dry in 1977. The correlation between rainfall and initiation of nesting in Cattle Egrets may be related to their origin in the dry regions of Africa (Siegfried, 1978), although wading birds (especially Cattle Egrets?) appear to be sufficiently flexible in many other respects to suggest that this consideration is probably unimportant.

The numbers of nesting pairs and active colonies of Wood Storks were both higher in the dry year 1977 (Table 7). This species has been intensively studied in Florida (Kahl, 1964; Ogden *et al.*, 1976; Browder, 1978). The stork's grope feeding technique for obtaining food requires the presence of relatively high concentrations of small fish, especially when food requirements are greatest during the nesting season. Favorable feeding conditions occur when fish are concentrated by dropping water levels, such as happens during annual dry seasons and in dry years. Studies in the Florida Everglades show good correlation between drying rates and timing of colony formation by storks (Kushlan *et al.*, 1975). Colony formation is delayed, or storks are most likely to desert established colonies, when water levels are high or are rising. Thus, a pattern of increased nesting in the drier year 1977 was not surprising. The change in percentage of storks nesting in inland versus coastal colonies between the two years, as shown in Table 7, is primarily a result of the failure of three major coastal colonies in the Everglades region to form in 1978. Our aerial surveys covered essentially the entire breeding range of the Wood Stork in the United States (excluding 1–3 very small intermittent colonies in southeastern Georgia). Hence our counts confirm that in years when habitat conditions are poor for stork feeding, not all adult storks attempt to nest.

Both the total number of pairs of White Ibis and the number of colonies that contained ibis were similar during 1977 and 1978 (Table 8). Between the two years, mean colony size declined in inland sites and increased in coastal sites, and the percentage of ibis in coastal colonies increased during the second year.

Although our figures do not indicate a great amount of shifting of nesting sites by White Ibis, it does appear that they may have re-

TABLE 7
Comparison of 1977 and 1978 Wood Stork Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	15	5	20	13	2	15
Mean no. pairs per colony	194.3	281.6		145.2	200.0	
Total no. pairs all colonies	2915	1408	4323	1888	400	2288
% total	67%	33%		82%	18%	

sponded to the heavier rainfall in 1978 by either forming smaller inland colonies or moving to the coastal colonies. Just why this may have occurred is uncertain, although ibis, like storks, are more efficient feeders when water levels are low or dropping. Kushlan (1976, 1978, 1979) reported that peak nesting by White Ibis in subtropical zones occurs during dry seasons when food is concentrated, and that heavy rains during dry seasons can cause colony abandonment. Ibis colonies in Florida typically form during March, late in the annual dry season. The spring of 1978 in peninsular Florida was characterized by above normal rainfall during February, which presumably either dispersed ibis food or increased the depths of water over nearby feeding grounds to the point where ibis could not feed immediately prior to the normal time of colony formation. Although heavy rainfall affects all wetlands, coastal estuaries subject to tidal influence are less affected than inland basins and may provide better feeding habitats when water is high inland. An indication that this is so is seen annually in the Everglades region, where feeding flocks of ibis move to the coast during the summer rainy season. Thus in 1978 some ibis may have shifted to coastal colonies in response to the heavy February rains. Further indication that inland marshes in 1978 did not provide adequate food for ibis, at least locally, was the absence of ibis at the Andytown East colony in the interior Everglades, where they nested in large numbers in prior years. In addition, they also abandoned another inland site in the Okaloacoochee Slough when many of their nests already contained eggs.

Conclusion and Summary

The three years of aerial surveys over peninsular Florida demonstrated that both total numbers of nesting pairs and the location of nest colonies varied between years in response to rainfall, and for at least one species, in response to low temperature as well. Although it appears that wading birds may move over large geographical regions when selecting nesting sites, precise information about the distance that individual birds move will require marking large numbers of birds in such a way as to recognize colony of origin.

Each of five species of wading birds analyzed here showed different responses to the 1977–78 rainfall pattern. Total numbers of Great Egrets and White Ibis remained approximately the same between dry and wet years, with the majority of egrets in inland colonies and an increase in numbers of ibis in coastal colonies in the wetter year. Great Blue Herons showed a shift to coastal colonies in the dry year, while the number of nesting pairs was reduced during the breeding season of 1978 following the coldest winter on record. Higher rainfall in 1978 was correlated with a sharp increase in the number of nesting pairs of Cattle Egrets, and a reduction in the number of nesting Wood Storks.

Acknowledgments

We thank Larry Riopelle for his superb piloting and sharp eye for colonies during the aerial surveys. Colony data from Everglades National Park were provided by James Kushlan and Oron Bass, of the National Park Service.

TABLE 8
Comparison of 1977 and 1978 White Ibis Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	12	15	27	15	14	29
Mean no. pairs per colony	1048.7	1301.2		689.2	1680.9	
Total no. pairs all colonies	12,585	19,518	32,103	10,339	23,533	33,872
% totals	39%	61%		31%	69%	

Barbara Warren assisted in several of the surveys, provided preliminary data for her field studies, and prepared the figures for this paper, and both she and Lorraine Waddell, of the National Audubon Research Department, assisted in the preparation of the manuscript. Alexander Sprunt, IV, and Barbara Warren commented on the several versions of the manuscript.

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COMMENTS:

Unidentified: There are several parameters interacting with several species. You probably have considered this; but in the case of Cattle Egrets, they apparently like to nest in associations over water. On the one hand, water may stimulate large numbers to breed; on the other hand, it will also either directly or indirectly produce more prey items for Cattle Egrets. If you take this strategy and apply it to Great Egrets, it doesn't necessarily work.

Ogden: I am not sure that I understand yet why a lot more water will produce more food for Cattle Egrets. At least in these subtropical areas both Cattle Egrets and Great Egrets are capable of breeding for a good part of the year, and what actually triggers nesting may be the creation of nesting sites, the summer rains for instance. Of these 280 sites, except for colonies that were on islands, I think 57% of them were in vegetation over standing water. So, at least in Florida, it looks like they require either isolation by being on an island, or they require vegetation over standing water. Both Cattle Egrets and Great Egrets might have been stimulated to breed by the creation of nesting sites. I agree that once they start nesting the rising water might have different effects on food for the two species of egrets.

Blacklock: Colonial waterbirds have been counted in Texas since 1967. One observation of particular interest is that during dry periods many colonial waterbirds apparently do not attempt to breed. Breeding populations during wet periods are almost double that for populations during dry periods.

Thompson: In 1957, R. P. Allen wrote a paper on populations of wading birds entitled, "An Urgent Appeal for Information on the Wading Birds," *Audubon Field Notes,* 11: 458–460. He documented population declines in numerous species nesting in Florida up to that time. He also described a sudden influx of Great Egrets into the upper Midwest in 1947 and 1948. Apparently egrets were displaced from Florida and established new colonies far to the north. This is another example of the need for a large study area when monitoring population trends.

Ogden: Yes, it may turn out that the peninsular of Florida is not a big enough study area for us to see the full extent of seasonal or year-to-year shifts in wader populations.

CENSUS METHODS FOR GULF COAST WATERBIRDS

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Abstract

Various census and sampling methods were used to enumerate the abundant colonially breeding waterbirds of coastal Louisiana, Mississippi, and Alabama in 1976 and 1978. Nesting habitats and substrates of the more common nesters are described, and criteria for selecting specific inventory techniques are explained.

In the past several years, the censusing of colonial waterbirds has been facilitated by a considerable federal commitment, both in the United States and Canada, to locate, measure, and monitor concentrations of coastal birds that could be adversely affected by petrochemical expansion within the estuarine and marine environment. Recent research efforts have been directed toward obtaining much more precise and comprehensive census data than were previously required and obtained by local resource managers. The goal has been accurate and repeatable regional censuses that allow detection of significant annual changes in breeding populations.

Federally backed increases in personnel and research funds have allowed more careful consideration of factors affecting apparent breeding abundance, such as habitat type, reproductive stage, and breeding bird conspicuousness. These complicating factors, which often act to confound accurate inventories, also control the development of inventory methodology and the final selection of census methods. It has become evident that most accurate censuses result from individually applying specific methods (and precise timing) to each colony during each season.

During the entire 1976 nesting season, and again for two short periods in April and June 1978, I had the opportunity to work on the census of colonial waterbirds of the northern Gulf of Mexico. Much of this region remains undeveloped, except for oil and gas operations, and contains very large and practically unstudied populations of colonial seabirds and waders (Ogden, 1978), nesting in a variety of habitats. I first arrived on the north Gulf coast in August 1975 with very little practical experience in the censusing of colonial birds, and with very little knowledge of their specific breeding habits in this region. Thus unencumbered by methodological prejudices, I reviewed the available literature, spoke with experienced field workers, and spent considerable time over, under, and among colonial birds to develop a set of census methods that seemed to apply to the specific nesting situations encountered on the north Gulf coast.

My purpose here is to describe these associated methods and nesting situations, discuss the reliability of census results, and present a classification system of census methods, ordered by species, habitat, and degree of expected reliability.

Study Area and Nesting Situations

In a previous paper (Portnoy, 1977), I described and quantified habitat types of the 2.4 million ha study area, and discussed the relative use of these types by 26 species of nesting waterbirds. Specific nest sites of the most common species are briefly reviewed here.

On the unvegetated barrier beaches, Black Skimmers (*Rynchops niger*), Sandwich Terns (*Sterna sandvicensis*), Royal Terns (*S. maxima*), and Least Terns (*S. albifrons*) nest in large colonies or closely adjacent subcolonies. Immediately behind the beaches, Laughing Gulls (*Larus atricilla*) commonly nested concealed in *Spartina patens* or exposed on saltmarsh islands. Forster's Terns (*Sterna forsteri*) also nest on marsh islands at the seaward edge of the Louisiana salt marsh.

Within saline coastal bays, on either side of the Mississippi Delta, are occasional Black-Mangrove (*Avicenna germinans*) islands popul-

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ated with nesting herons, egrets, and ibises. In the brackish water of the Delta itself, emergent "islands" of *Phragmites communis* serve as the predominant heron nesting sites. Louisiana Herons (*Hydranassa tricolor*), Snowy Egrets (*Egretta thula*), Great Egrets (*Casmerodius albus*), Black-crowned Night Herons (*Nycticorax nycticorax*), White-faced Ibis (*Plegadis chihi*), and White Ibis (*Eudocimus albus*) are the most abundant species in both saline and brackish areas.

Farther north in freshwater marshes, large wader colonies occur on emergent woody vegetation, usually Buttonbush (*Cephalanthus occidentalis*) in floating marshes. Where oil-drilling activities have created islands of dredged material, the invasion of Black Willow (*Salix nigra*) onto these spoil islands has often been followed with the colonization by ciconiiform birds. Common species in both floating marsh and in spoil island colonies are Snowy Egret, Little Blue Heron (*Florida caerulea*), Great Egret, Louisiana Heron, White-faced Ibis, Cattle Egret (*Bubulcus ibis*), and Black-crowned Night Heron. In the freshwater marshes of southwestern Louisiana, colonies often include Roseate Spoonbills (*Ajaia ajaja*) and Olivaceous Cormorants (*Phalacrocorax olivaceus*), in addition to the waders mentioned above.

Still farther north in the Baldcypress (*Taxodium distichum*)-Water Tupelo (*Nyssa aquatica*) swamps, Great Egrets and Great Blue Herons (*Ardea herodius*) usually nest atop tall trees in distinct groups separate from the smaller ardeids. The smaller wading birds—Snowy and Cattle Egrets, Louisiana and Little Blue Herons, and White Ibises—generally nest on shrubs (*Cephalanthus, Salix,* and small *Taxodium*) that emerge from ponds in the swamp forest.

Except for small colonies of Forster's Terns and Least Terns, nesting aggregations in all the above-mentioned habitats normally contain thousands of nesting pairs.

Finding Colonies

A small fixed-wing aircraft (*e.g.*, Cessna 172) operated at about 200 m altitude and 160 km/hr speed is completely satisfactory and the best choice for finding colonies of conspicuous species in extensive habitat. Helicopters are much more expensive to charter and their slower speed capability is not enough of an advantage to justify their use when simply searching for colonies of all species except highly cryptic and diffusely nesting Least Terns on barrier beaches.

Census Methods

Selection of an ideal environmental barometer. Much of the federal push for colonial waterbird inventories was directed toward monitoring coastal bird populations as indicators of environmental contamination or habitat destruction. Although no provision was included in recent inventories to concurrently monitor estuarine pollution flux or habitat loss along with coastal bird populations, the principal idea was to closely follow an easily censused (thus colonial), discrete population (thus comprehensive, coastwide inventories) as an indicator of ecosystem stability. Ideal "indicators" would be: 1) conspicuous and thus easy to find; 2) predictable in nesting location and timing, and thus easy to find; 3) reproductively synchronous within and among colonies; 4) quickly and inexpensively censused; 5) censused with minimal disturbance to breeding birds. (A sixth requirement, not addressed in the present study, would of course be that these indicator species truly reflect habitat degradation important to the whole system.) In many habitats, field workers would find it difficult to select a "best" species, whose nesting characteristics would at least approximate what is required to employ methods that produce comparable annual counts.

The following methods are rated according to ease of application in obtaining reliable breeding-pair counts on the northern Gulf of Mexico coast. Ease of application is based upon my subjective judgment from having employed all these methods in the field; reliability is based upon an objective appraisal from comparisons of various census results. Note that the reliability and applicability of each method is intimately associated with characteristics of specific species at specific nest sites.

Aerial photography. Prints from 35 mm or 6 × 7 cm black and white aerial photographs of Great Egret, Royal Tern, and Sandwich Tern colonies clearly show each nesting attempt (*i.e.* incubating bird or attendant pair) currently active on colonies. Aerial photo counts and the visual estimates of two observers were generally comparable during an April 1978 Great Egret survey (Table 1). Tern colonies were ground-checked during the 1976 census to verify that individuals recorded on aerial photographs were in fact incubating eggs or brooding young.

Aerial photography is also useful for censusing Black Skimmer colonies, even though the relationship of birds (or pairs) to active nests within a given nesting area is not one to one. A total count from aerial photographs taken at midday (1000 to 1400 h) of skimmers present within the nesting area during late incubation will yield a reliable active nest estimate when divided by a correction factor generated for this specific time of day and reproductive stage (Portnoy, 1978). This technique should be appropriate for other conspicuous species nesting in exposed areas where total counts of adults present within the nesting area are obtainable from aerial photographs.

TABLE 1
Comparison of Aerial Photographic Counts and Visual Estimates of Great Egret Breeding Pairs at Louisiana Colonies in April 1978

Colony	Visual Estimate[a]	Count from Photographs
Atchafalaya 1	300	432
Atchafalaya 7	75	84
Atchafalaya 8	1500	1015
N of I-10	500	598
NW of Maurepas	135	122
SE of Ponchatoula	400	360
S of Maurepas	300	359
S of I-10	130	136
S of I-10	700	799
Creole	60	66
Sidney I.	1300	2434
Grand Chenier	400	448
Lake Misere	160	161
Deadman I.	250	380
Avery I. tupelo	225	241
Lake Fausse Pointe	120	123
Amelia	1400	2163
E of Lake Verret	1200	1176
Queen Bess I.	800	1035

[a] The estimates of two observers were averaged.

Aerial estimation of breeding birds or "pairs." Visual estimates of abundance are quickly made by observers in aircraft, but are of limited reliability with very large colonies, cryptic species, or birds that nest under vegetation, unless related to contemporary ground counts (Kadlec and Drury, 1968). Table 2 indicates that the percentage error of visual estimates, compared with concurrent "ground counts" (either photographic counts or the results of transect sampling), is correlated with nesting bird conspicuousness. Nesting Louisiana Herons and Black-crowned Night Herons were grossly underestimated or often completely missed. In 1976, in mangrove colonies where I had estimated from the air a few hundred Louisiana Heron pairs, I counted about that number in only a *10% sample* of the nesting area.

Wide variation in percent error of visual estimates (Table 2) appears to preclude generation of correction factors, at least for these large colonies surveyed by fixed-wing aircraft. The use of helicopters would probably increase the accuracy of visual estimation, assuming that successive bird counts could be accurately tallied while hovering over a typical 30-ha and 15,000-pair heronry.

Aerial estimation is unfortunately the only method currently available for censusing most wading birds (except for Great Egrets) in large swamp and floating marsh colonies, where ground counts or samples are impossible because of the lack of a solid substrate to walk upon, and where aerial photographs do not completely record cryptic and/or concealed species.

Transect sampling of active nests. In large colonies with species that cannot be totally seen or photographed from aircraft, and with a substrate firm enough to support the observer's weight, the preferred method is some sort of random sample collected across the entire nesting area. The belt transect scheme used during the 1976 Gulf coast survey has been described

TABLE 2
Visual Estimates of Adult Birds *vs.* Contemporary Nest Counts at Gulf Coast Heronries During Incubation

(Estimates of adult birds were made by two observers in a fixed-wing aircraft; nest "counts" were from aerial photographs [for the Great Egret] or from transect sampling [smaller ardeids].)

Species	Colonies	Mean Colony Size (nests)	Average Error of Visual Estimate (%)[a]	SD
Great Egret	33	511	−4.2	12.2
Snowy Egret	6	1992	−8.7	92.0
Louisiana Heron	8	3192	−79.1	25.1
Black-crowned Night Heron	7	573	−84.4	14.7

[a] I assumed that each bird observed from the aircraft represented an active nest. Thus bird estimates and nest counts have the same units.

TABLE 3
Typial Results of 10% Belt Transect Sampling on Gulf Coast Heronries (1976) with 95% Confidence Limits Calculated from Nest Densities Per Transect

Nesting Substrate	Transects Required	Nest Estimate	Confidence Limits (nests)
Willow shrubs	12	3,240	810
Willow shrubs	35	5,012	1498
Spartina patens	91	7,775	2752
Mangrove shrubs	33	12,666	1337
Mangrove shrubs	8	2,522	560
Mangrove shrubs	14	9,683	2738
Mangrove shrubs	54	14,279	1809
Mangrove shrubs	31	14,938	3090
Mangrove shrubs	19	4,502	1422
Mangrove shrubs	136	16,880	2672

(Portnoy 1977; also see Eberhardt 1978 for theoretical considerations). Total nest estimates from belt transect sampling and confidence limits generated from nest densities per transect are presented for typical heronries (Table 3). An expected maximum error of 3000 nests may seem unacceptable in a 14,000-nest heronry, but when compared with other methods, transect sampling appears the only way to at least measure order of magnitude in such large colonies—and for all nesting species regardless of conspicuousness (as long as nests can be separated by species).

In addition to mangrove and spoil island heronries, randomly spaced belt transects were applied to Laughing Gull colonies in *Spartina patens* and Forster's Tern colonies on *Spartina alterniflora*. The 95% confidence limits of a 10-percent-sampled Laughing Gull colony was ±2326 nests with a total nest estimate of 17,326; total nest estimates from sampling on a few large Forster's Tern colonies were within 25% of concurrent total nest counts. Belt transects also produced estimates that closely approximated total nest counts on some Herring Gull (*Larus argentatus*) colonies and heronries on Massachusetts coastal islands in 1977 (Erwin, pers. comm.).

Total ground nest counts. Because of time limitations, this is practical only in small colonies, and even here the disturbance to nesting birds appears considerable (Ellison and Cleary, 1978). Although total active nest counts are desirable, if not requisite, for evaluating other census methods, field workers involved in extensive regional surveys rarely have the time to totally count nests in very large shrub or treetop heronries by carefully demarcating counted versus uncounted sections. In 1976, I found this method appropriate and quick for censusing barrier beach skimmer colonies and salt-marsh Forster's Tern colonies.

Ground estimation of adult birds. This too applies only to small colonies. To visually estimate the total adult population of a colony without duplication or omission, an observer must be able to see the whole nesting group at once. At large colonies in vegetation this is generally impossible.

I used this method in 1976 to census beach-nesting Least Terns, by counting and/or estimating the number of adults flushed from colonies as I walked along the beach berm. It was assumed that each singly flushed adult represented a nesting attempt, but this was never tested by concurrently counting nests.

Classification of Census Methods

I find it useful to summarize the above methods and their applications on the northern Gulf of Mexico coast in a simple diagram (Figs. 1 and 2). For each species and nesting situation there follows a list of census methods, in decreasing order of reliability, that could be physically applied. Similar priority listings of appropriate census methods might be useful to field workers in other habitats. Although observers in each region and habitat type must individually choose, adapt, and implement the most appropriate census methods for their area, it might facilitate information exchange, in addition to clarifying coastwide inventories and regional comparisons, if researchers agreed on a universal procedure for census method selection. A universal classification of colonial waterbird inventory methods, similar in organization to Figs. 1 and 2, would at least outline the state of the art of waterbird inventory, put each specific method in perspective of overall applicability, and encourage careful consideration of the range of utility of each method.

Acknowledgments

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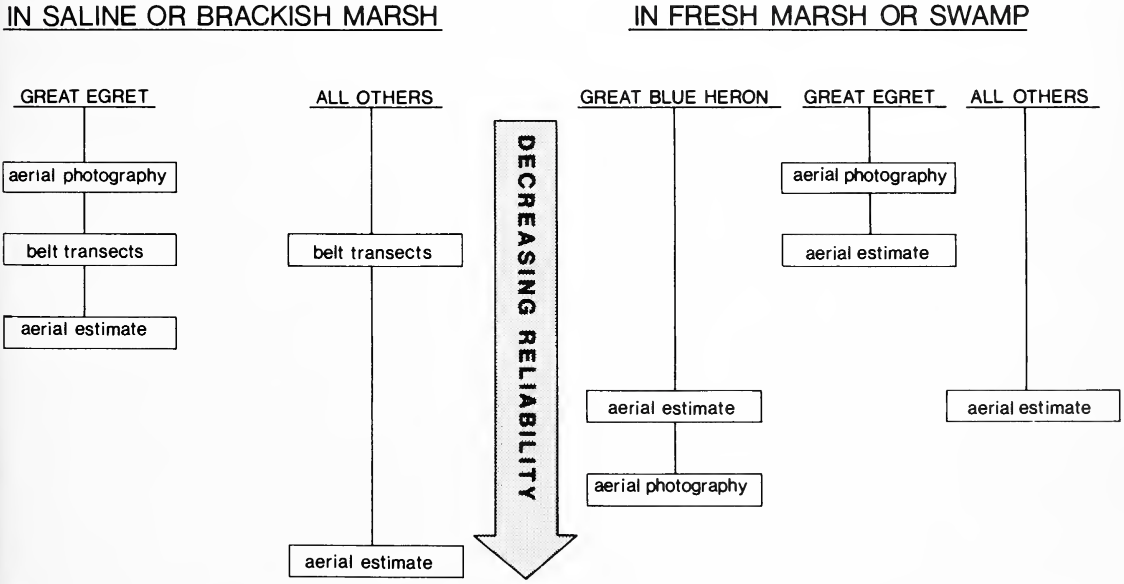

Figure 1. Relative reliability of inventory techniques for wading bird colonies in coastal Louisiana-Mississippi-Alabama.

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COMMENTS

Gochfeld: I appreciated your emphasis on the fact that any census technique is a trade-off between how much you are willing to disturb the birds in question and how accurate an estimate you think you need for a particular problem. We in the Northeast rarely see colonies of such magnitude as you describe for the Gulf coast, and therefore our whole approach toward estimating tends to be quite different. I noticed when you showed the belt transect that the confidence limits around the mean estimates didn't seem to be correlated with the actual mean value. In other words, it didn't seem that the confidence limits varied directly. Is there any consistency to that?

Portnoy: If I could fit all the data on this slide, I think you would see that in larger colonies there is a greater variation in nest density.

Gochfeld: The second comment I have pertains to skimmers. I have done a lot of aerial estimating of skimmer numbers in the Northeast, and I wonder if you have had the opportunity to compare your 2.2 ratio, which is higher than we usually have, both diurnally and across seasons?

Portnoy: The seasonal change in the bird to nest ratio?

Gochfeld: Yes.

Portnoy: Yes, in 1976 the counts were made at the end of June, the peak of incubation, and the ratio was 2.2 at midday. I flew again at the end of July, and the ratio was much reduced in all the colonies I checked. I have forgotten what the ratio was. Also, the bird to nest ratio was higher at midday than during early morning or late afternoon.

Blokpoel: I noted that for the Great Blue Heron you consider aerial estimates to be more reliable than aerial photography. Is that correct?

Portnoy: Right.

Blokpoel: Is that because when you get close with the aircraft the birds flush?

Portnoy: No, you probably could census Great Blue Herons using aerial photographs. I

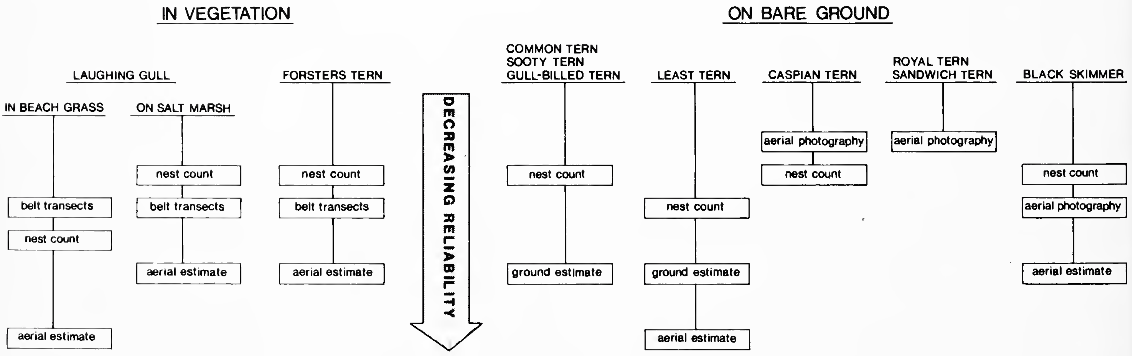

Figure 2. Relative reliability of inventory techniques for seabird colonies in coastal Louisiana-Mississippi-Alabama.

know Mike Erwin has. In small colonies you could get the whole colony on the relatively small negative size that I was using. With the large colonies that I had, I didn't have the time to stay up high and get all the colony in the frame for censusing Great Egrets, and then later go down low and take overlapping close-ups that would show Great Blue Herons. I was aiming mainly at Great Egrets, and they will show up on high-altitude photography. The photo census of Great Blue Herons on these large colonies would require very many overlapping photographs that would be difficult to juxtapose in such uniform habitats.

F. G. Buckley: Are you aware of any studies on human perceptual difficulties in estimating large numbers? I am very impressed by the large-sized colonies you have, and we don't really have that problem here in the Northeast.

Portnoy: I should think that the psychologists would have done something with this. There are really a lot of psychological factors involved in the estimation.

F. G. Buckley: If anyone in the audience is aware of such studies, I would like to learn of them.

WHY ARE THERE DIFFERENT KINDS OF HERONS?

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ABSTRACT

The number of diurnal fish-eating herons increases from north to south along the eastern coast of North America. Species differ in the size and kinds of prey taken, foraging behavior, degree of foraging sociality, and use of habitat. All seem equally good at capturing prey. The increase in diversity as latitude decreases is best explained by the greater year-round productivity of southern habitats. This argument is supported by the low heron diversity on the Great Barrier Reef (Australia), where foraging conditions limit prey availability to only half that of marine habitats in eastern North America. As habitats become more productive of food for herons, species are initially "packed in" along a resource-size spectrum. The first heron is the largest, the second the smallest, and so on. The largest heron is able to breed successfully in northern latitudes because it is able to take all sizes of prey encountered and hence hunts with optimal efficiency. As productivity increases, additional species are packed in as foraging or habitat specialists. Particularly rich environments support a "giant" heron (*e.g., Ardea goliath* in Africa and *A. herodias occidentalis* in Florida), which specializes in very large prey. The pattern by which herons are added with increasing productivity along the eastern coast of North America is duplicated on other continents. It can be concluded that there are different sizes of herons because there are different sizes of prey, and that there are different kinds of herons because there are different kinds of prey. By itself competition is not a satisfactory explanation of differences between heron species. Selection for foraging efficiency during periods of reduced prey availability resulting from weather or seasonal changes or fluctuations in prey numbers should be considered of equal or greater importance.

INTRODUCTION

Twelve species of herons (Ardeidae) occur along the eastern coast of North America. Seven of these are predominantly fish eaters that forage during the day and frequent open-water habitats. The others, including bitterns, night herons, and the Cattle Egret (*Egretta ibis*), either avoid open waters, hunt mostly at night, or forage on invertebrates. Although they differ in size, the guild of diurnal fish-eating herons ("day herons") are basically similar in their morphology (long legs, long necks, long bills) and use many of the same hunting behaviors (Palmer, 1962; Kushlan, 1976, 1978; Parkes, 1978). The habitats frequented by these birds are effectively two-dimensional, and where they occur together spatial segregation is possible only in a horizontal plane. Because of this, herons hunting in the same habitats are potentially exposed to the same prey resources and apart from segregation by water depth, resource partitioning should be by selection of different kinds or sizes of prey and by different foraging strategies. Studies by Meyerriecks (1962), Jenni (1969), and Willard (1977) have shown that resource partitioning among herons foraging in the same habitats does occur in the ways suggested.

The observation that herons use different resources when foraging in the same habitats is not surprising. Studies of coexisting species have invariably demonstrated resource partitioning (Schoener, 1974; Cody, 1974), a result that conforms to current theory (*e.g.* MacArthur and Levins, 1967; Levins 1968). What is not clear are the reasons why coexisting species use different resources. There has been a tendency on the part of many ecologists to explain resource partitioning primarily as a means of avoiding or minimizing interspecific competition, but alternative explanations may be equally reasonable (see Kikkawa, 1977, for an interesting discussion on this). Species may differ in size, foraging behavior, or prey selection because specialization may promote foraging efficiency and could thus evolve even in the absence of competitors; that is, there may be large and small herons because there are large and small fish, and not because there are different herons.

The group of diurnal fish-eating herons is particularly suited to tackling these kinds of problems. The large size of herons and the ease with which their prey can be identified as it is captured mean that data are relatively easy to obtain on the use of resources by predators exposed to the same prey populations.

During 1965 and 1966, we studied the foraging ecology of herons on the eastern coast of the United States, and between 1967 and 1972, we investigated the foraging ecology of the Reef Heron (*Egretta sacra*) on the Great Barrier Reef in Australia (Recher, 1972; Recher and Recher, 1972). We were interested primarily in the way different species used resources (resource partitioning), in foraging behavior, and in foraging efficiency. Two main questions were asked—"Why are there different kinds of herons?" and "Does the use of resources change with the number of coexisting species?." Related to these questions were the obvious ones of species diversity—"What determines the number of coexisting herons?" or "Why are there more species of herons in Florida than (say) New York?" Our hypothesis was that if resource partitioning were the result of competition, then as species number increased niche breadth should decrease. If, however, competition were unimportant, then niche breadth would remain unchanged for species with a wide distribution; species with a restricted distribution would be specialists. We also hypothesized that the number of coexisting species should increase as new resources were added to the resource spectrum or as increased productivity and resource stability allowed specialization.

To test these hypotheses we needed the following kinds of information: 1) censuses of foraging herons demonstrating a range of species diversity from simple communities to highly diverse ones; 2) an estimate of productivity, including food availability and diversity; 3) a measure of niche breadth (in this instance we measured foraging distribution and the kinds and sizes of prey taken by herons); and 4) a comparison of foraging efficiency. In this way niche breadth could be compared at different species densities and in areas of greater or lesser productivity. Observations were restricted to birds foraging together, and the measure of foraging efficiency provided an estimate of the ability of each species to survive and reproduce in that habitat.

In this paper we present the results of our observations in eastern North America and on the Great Barrier Reef and consider the question—"Why are there different kinds of herons?"

STUDY SITES AND METHODS

In the United States, observations were made in Florida, New Jersey, and New York. The Florida data were obtained mainly in the Everglades National Park at Flamingo, but we also looked at herons in the Florida Keys. The New Jersey observations were made in the Tuckerton Meadows and at Brigantine National Wildlife Refuge. The New York work was carried out at Montezuma National Wildlife Refuge. With the exception of those in New York, all observations were in marine environments. The work on the Great Barrier Reef was done on Heron and One Tree Reefs in the Capricorn Group. Table 1 summarizes the time of observations at each study site, the number of birds from which data were recorded, and the number of prey taken.

In Florida we obtained data on the Great White Heron (*Ardea herodias occidentalis*), Great Blue Heron (*A. herodias*), Great Egret (*E. alba*), Reddish Egret (*Egretta rufescens*), Little Blue Heron (*E. caerulea*), Snowy Egret (*E. thula*), Louisiana Heron (*E. tricolor*), and Green Heron (*Ardeola striata*). Nomenclature follows Payne and Risley's revision of the Ardeidae (1976); as ecologists we find their classification of the subfamily Ardeinae ("day herons") much more pleasing than previous classifications that scattered these birds among a plethora of monotypic genera. Payne and Risley (1976) consider the Great White Heron (*A. h. occidentalis*) a subspecies of the Great

Blue Heron (*A. herodias*). We treat these two herons separately in this account wherever we have sufficient data, and for ease of discussion consider the Great White as a separate species.

With the exception of the Great White Heron and the Reddish Egret, the same species were studied in New Jersey. In New York we obtained data for only the Great Blue Heron and the Green Heron.

At all localities the herons studied were breeding species, but we could not be certain that the individuals were breeding birds. In Florida some may have been wintering individuals, and in New Jersey some immature Little Blue Herons may have been birds dispersing north from southern breeding colonies. The Reef Herons nests on the islands of the Great Barrier Reef, and all individuals studied were breeding.

In Florida the observations were made during late winter and early spring (March–May); in New Jersey, during summer and autumn (June–October); and in New York, in summer (August). The Reef observations were made in spring and summer (October–January). All the data for each area have been combined. Observations were made with a telescope (25× and 40×) and required two persons. One person kept the heron under observation while the second recorded all data. Generally observations were confined to birds within 50 m and individuals selected as they were encountered. Where we had a choice of two or more individuals or species, we chose the nearest bird and the species on which we had the fewest data. Observations continued until the heron moved out of the range of the scope for easy identification of prey.

Prey were identified and their length estimated as they were held by the heron. Prey length was gauged against the bird's bill: we assumed that all individuals of a species had the same bill length. Morphological measurements of North American herons were compiled from the literature and from museum specimens and are available from the authors on request. Measurements of Reef Herons were taken from live birds captured for banding on

TABLE 1
Summary of Observations

A. Minutes of observation of foraging birds (numbers of individuals)

Heron	Florida	New Jersey	New York	Great Barrier Reef
Great White Heron	3605 (64)	—	—	—
Great Blue Heron	740 (15)	2157 (53)	644 (41)	
Great Egret	234 (14)	682 (29)	—	—
Reddish Egret	166 (9)	—	—	—
Little Blue Heron	854 (39)	603 (51)	—	—
Snowy Egret	139 (6)	391 (33)	—	—
Louisiana Heron	528 (32)	71 (5)	—	—
Green Heron	324 (7)	51 (2)	452 (10)	—
Reef Heron	—	—	—	1509 (?)

B. Number of items of prey

Heron	Florida	New Jersey	New York	Great Barrier Reef
Great White Heron	137	—	—	—
Great Blue Heron	55	122	264	—
Great Egret	219	256	—	—
Reddish Egret	132	—	—	—
Little Blue Heron	511	634	—	—
Snowy Egret	85	501	—	—
Louisiana Heron	297	148	—	—
Green Heron	87	16	64	—
Reef Heron	—	—	—	1083

One Tree Island. Prey length was converted to prey weight with species length/weight curves that were obtained from fish and invertebrates seined at our study sites (unpub. data). Regular seining of prey in the places where herons were feeding kept us familiar with the kinds of prey available to herons and made the identification of prey held by the bird fairly simple. Prey that could not be identified as to genus or species was treated as "fish" and weight determined from a generalized length/weight curve. The greatest difficulties in the identification of prey and the estimation of size were with the smallest prey (<2.5 cm in length), but there is relatively little difference in weight for prey this small and use of a generalized length/weight curve is appropriate.

Stopwatches were used to record the intervals between attempts at prey capture, successful captures, and the length of interruptions to hunting (*e.g.* aggression, preening, defecation). With large prey, the time required for swallowing was measured; but for the smallest prey, swallowing was almost immediate (Recher and Recher, 1968; Kushlan, 1978). These data provide the basis for estimating foraging success and foraging efficiency.

In addition to details of prey, the depth of water in which a bird was feeding was measured by recording its position on the heron's leg. All individuals of a species were assumed to have the same leg measurements. The time spent at any depth was recorded with a stopwatch as part of the foraging observations. Foraging behavior itself was described and recorded, but the duration of a particular behavior was not measured.

Regular counts of the herons foraging on our study sites were made, and these were used to calculate species diversity of herons foraging in the same habitats. As an index of diversity, we used the Shannon-Weaver function [$H = \Sigma_i(p_i \log_e p_i)$ where P_i is the proportion of the i^{th} species], and use it here as the number of equally common species (e^H). Additional information on diversity was obtained from the distribution maps in Palmer (1962).

Species Density

Including the Great White Heron, all North American herons (Ardeidae) with the exception of the American Bittern (*Botaurus lentiginosus*) occur as breeding birds in southern Florida (Palmer, 1962; Robertson and Kushlan, 1974; Custer and Osborn, 1977, Ogden, 1978). Meyerriecks (1962) has recorded as many as nine species feeding on the same shoal in Florida Bay, and we commonly observed eight species foraging on our study areas near Flamingo. The number of species decreases south along the Florida Keys and north along the Atlantic coast (Fig. 1), but nine species extend to New Jersey and eight of these forage in the marine habitats of Brigantine refuge. In their survey of wading-bird breeding colonies, Custer and Osborn (1977) also found that the number of species declined from south to north. However, if they discounted colonies with only one or two nesting species, the median species richness of

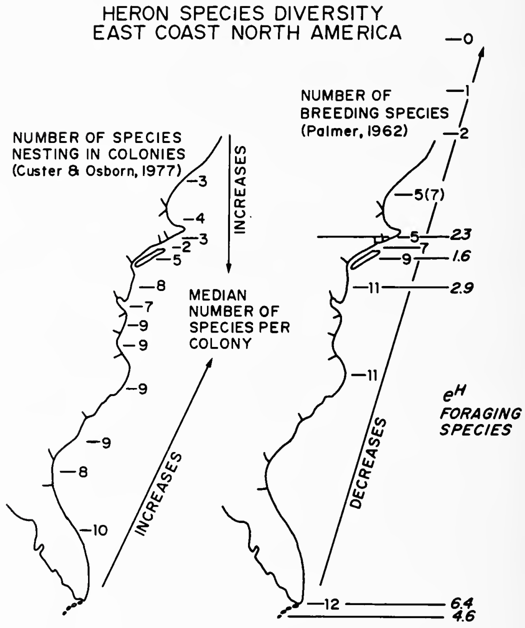

Figure 1: The number of heron species decreases from south to north along the eastern coast of North America. However, Custer and Osborn (1978) reported that nesting colonies were most diverse in the mid-Atlantic states. Censuses of foraging herons are shown here as the number of equally common species (e^H). This shows the latitudinal trend in species diversity to be more precipitous than indicated by the number of breeding species and illustrates the rarity of some herons in the northern part of their breeding range.

colonies was greatest in the mid-Atlantic states (Virginia-New Jersey). Of the diurnal fish-eating guild, the Reddish Egret and Great White Heron are confined to Florida (30° N) and the Louisiana Heron and the Little Blue Heron were uncommon in our New Jersey foraging bird censuses (40° N). As a result of these changes in species abundance, we found that heron species diversity decreases precipitously from south to north (Fig. 1). Kushlan (1978) has also shown the foraging aggregations of wading birds are richer in species in Florida than in New Jersey. Five ardeids, including the Great Blue Heron and Green Heron, nested in New York at the Montezuma refuge. The Great Blue Heron nests north to the Gaspé Peninsula (49° N), where it is the sole member of the diurnal fish-eating guild (Palmer, 1962).

In late summer and autumn, many herons disperse northward (Townsend, 1931; Palmer, 1962; Byrd, 1978). This movement is primarily of young birds and is most conspicuous among Great Egrets and Little Blue Herons (Byrd, 1978; Odgen, 1978). Young birds may also be sedentary or move in directions other than north, but it is the northward dispersal that is of greatest interest as it takes birds beyond their breeding range. As illustrated by Willard's (1977) data this can result in substantial increases in the number of herons and of heron species in northern latitudes. With colder weather herons migrate south, and at Brigantine only the Great Blue Heron overwinters in any numbers (Willard, 1977; pers. obs.). Robertson and Kushlan (1974) also point out that the numbers of herons in southern Florida show a marked seasonality. Numbers are greatest during winter, when resident birds are augmented by wintering individuals.

The number of coexisting ardeids (12) in southern Florida is probably as great as anywhere else. For example, there are 10 or 11 potentially coexisting species in northern Australia (Reader's Digest, 1976), 13 to 15 in Guatemala (Land, 1970), and 13 to 15 in India and Ceylon (Ripley, 1961). On all continents the maximum number of resident heron species found foraging together is about eight or nine. The group of herons on Florida Bay thus represents the maximum number of heron species that occur together in an aquatic environment. In contrast, the Reef Heron is the only heron that nests abundantly on the Great Barrier Reef, although the Mangrove Heron (*Ardeola striata*) occurs in small numbers (pers. obs.) and the White-faced Heron (*Egretta novaehollandiae*) is common during the winter (Domm and Recher, 1973). Our observations of foraging herons therefore extend from the most diverse heron communities to the least and include two sites of intermediate diversity.

At the beginning of our studies we considered it likely that by virtue of its warmer climate and longer growing season Florida Bay would be more productive of food for herons than New Jersey, and that New Jersey would be more productive than central New York. The kinds of prey (*e.g.* species of fish) would also be greater in Florida than New Jersey and greater in New Jersey than New York. As shown in Table 2, herons do take more kinds of fish species in Florida than in New Jersey and more in New Jersey than in New York. Similarly, we viewed the Great Barrier Reef as a rich environment for herons with an abundance of fish and a high diversity of fish species (Table 2). The presence of only one species of heron on the Reef, therefore, seemed anomalous and contradictory to the latitudinal trend in species number seen in eastern North America.

Species Diversity and Productivity

On a year-round basis, New York, New Jersey, and Florida differ significantly in productivity. As an indication of the greater productivity of Florida, the "growing season" in southern Florida is 300 days, in New Jersey 120 days and in New York (Montezuma) 100 days. Florida also has a more diverse fish fauna than New Jersey or New York and therefore offers greater foraging opportunities for fish-eating birds. Coral reefs are among the world's most productive and diverse communities. The reefs at One Tree Island and Heron Island where we studied the Reef Heron are not exceptions and should be considered as productive as Florida Bay. However, if we let the herons measure "productivity" in terms of food actually available (grams of prey captured per minute of hunting), there are no sharp differences between Florida, New Jersey, and New

York. The Great Barrier Reef is less productive of food for herons than any of the North American sites (Table 5). The Reef and Florida do have a more diverse fish fauna, and this is reflected in the greater diversity of fish species taken by herons in these places (Table 2).

The similar amounts of food taken by herons in Florida, New Jersey, and New York are an artifact of our observations; New Jersey and New York were studied in late summer and early autumn, when food is probably maximally abundant. Times of peak food abundance probably have less effect on heron survival and by extension on heron species diversity than times when it is limited. The decrease in the number of breeding species between Florida, New Jersey, and New York is probably related to the prey available during the spring when nesting by herons commences.

Heron species diversity in New Jersey and New York increases during late summer (Willard, 1977; pers. obs.) with the northward movement of young birds and is probably explained by the greater availability of food at this time of year. Given the lower efficiency of young herons at prey capture, their northward dispersal is an important survival strategy. By moving north young herons are able to exploit a rich food source and do not have to contend with adult herons, many of which defend foraging territories.

Food and Foraging Behavior

Herons are opportunists. Given the chance, they will feed on any animal they are able to catch and swallow. Insects, spiders, crustaceans, birds, mammals, reptiles, fish, and amphibians are all part of their diet (Bent, 1926; Palmer, 1962; Kushlan, 1978). As a result, the diets of individual species differ from place to place according to the habitat in which the bird is feeding and to the kinds and sizes of prey that are available. In our marine study areas, herons fed principally on fish and crustaceans, but in New Jersey Snowy Egrets also took numbers of annelids. Frogs were a major food item for Green Herons in New York. Because of the herons' catholic feeding habits, the kinds and sizes of prey taken by herons should be compared only between birds feeding in the same places. In theory, birds foraging in the same places are exposed to the same prey. Any difference in diet will therefore reflect differences in hunting strategies and not differences in the time or place of foraging.

Despite the scope of their diets, it is unikely that herons take all items of prey as they are encountered. Except during periods of scarcity, predators do not choose prey in proportion to their abundance but are selective (Schoener, 1971; Stein, 1977). Large prey may be hunted in preference to small prey, or an abundant

TABLE 2
Number of Fish Species Taken by Herons

Heron	Florida	New Jersey	New York	Great Barrier Reef
Great White Heron	14	—	—	—
Great Blue Heron	10	5	3	—
Great Egret	12	6	—	—
Reddish Egret	7	—	—	—
Little Blue Heron	13	4	—	—
Snowy Egret	5	6	—	—
Louisiana Heron	12	2	—	—
Green Heron	7	2	2	—
Reef Heron	—	—	—	29
Total for all herons	22	9	3	29
Total fish species in area	?	?	?	700+
Fish species taken by seining	19	12	n.d.	100+

food item may be selected over those that are scarce. No doubt there are many reasons why predators are selective, including "individual choice" (see Kushlan, 1978), but prey should be chosen to maximize the intake of energy and minimize its expenditure (MacArthur, 1972; Pulliam, 1974). For example, Recher and Recher (1968) showed that herons differed in their ability to handle some kinds of fish and suggested that herons avoided species where the time expended in handling the prey after capture was excessive. Also, herons hunt in different ways, and this exposes them to different kinds of prey.

The effect of foraging behavior on diet is best illustrated by a comparison of the prey taken by the similar-sized Little Blue Heron, Louisiana Heron, and Snowy Egret (Table 3). We found that the Little Blue Heron hunted in a slow and methodical fashion, often peering intently under floating matter or carefully searching aquatic growth. The others hunted more actively and are aptly described as pursuers; the Little Blue is a searcher. As a result of these differences, in Florida, where a great diversity of prey was available (Table 2), Little Blues captured a much greater proportion of crustaceans and took more bottom-dwelling or

TABLE 3
The Percent of Prey Types Taken by Herons

Prey Species	Heron Species (Number of prey items)							
FLORIDA	Great White Heron (137)	Great Blue Heron (55)	Great Egret (219)	Reddish Egret (132)	Little Blue Heron (511)	Snowy Heron (85)	Louisiana Heron (297)	Green Heron (87)
Fish:	84.0	95.8	91.4	97.7	78.3	82.5	83.8	74.7
Free-swimming	42.9	52.2	65.2	96.8	51.9	93.9	91.2	72.3
Sedentary	57.1	47.8	34.8	3.2	58.1	6.1	8.8	27.7
Crustacea:	16.0	4.2	8.6	2.3	21.4	16.3	16.2	25.3
Prawn	10.0	?	100.0	?	80.7	92.3	97.7	72.7
Crab	90.0	?	0	?	19.3	7.7	2.3	27.3
Other	0	0	0	0	+	0	0	0
NEW JERSEY	—	(122)	(256)	—	(634)	(502)	(148)	(16)
Fish:	—	91.9	96.7	—	88.8	65.9	98.6	53.3
Free-swimming	—	98.0	98.0	—	99.6	98.7	100.0	?
Sedentary	—	7.8	2.0	—	0.4	1.3	0	?
Crustacea:	—	6.3	0	—	17.5	16.3	0.7	46.7
Prawn	—	?	—	—	92.3	90.4	?	?
Crab	—	?	—	—	7.7	9.6	?	?
Other	—	1.8	3.3	—	0	17.8	0.7	0
NEW YORK		(264)						(64)
Fish:	—	98.9	—	—	—	—	—	45.2
Free-swimming	-	100.0	—	—	—	—	—	100.0
Sedentary	—	0	—	—	—	—	—	0
Crustacea:	—	—	—	—	—	—	—	—
Prawn	—	—	—	—	—	—	—	—
Crab	—	—	—	—	—	—	—	—
Insect	—	—	—	—	—	—	—	22.6
Frog	—	1.2	—	—	—	—	—	32.2

slow-swimming fish than either the Snowy Egret or the Louisiana Heron (Table 3). In New Jersey, where prey diversity was less, the three took similar prey when feeding together. However, Willard's (1977) observations of these birds at Brigantine are different and resemble our data from Florida. He suggested that the Snowy Egret and Louisiana Heron exploited open-water prey (free-swimming), which the Little Blue rarely used. In another study that compared the diets of these three herons, Jenni (1969) also showed that Little Blues take a greater proportion of slow-moving prey than the other two species. Sixty-six % of the diet of Little Blues was amphibians and insects, and only 33% fish. In contrast, 96% of the diet of Louisiana Herons and 88% of the diet of Snowy Egrets were fish. Each of the herons took many of the same species of fish, but in different proportions. Jenni (1969) attributed the different diets of these three similar-sized herons to their different feeding behaviors and to the fact that they tended to hunt in different places.

Meyerriecks (1962); Kushlan (1976, 1978) and Willard (1977) have described and compared the foraging behavior of North American herons. Recher and Recher (1968, 1972) have described the foraging behavior of the Reef Heron. Kushlan (1976) identified 28 feeding behaviors used by North American herons, but noted that no one species used the full range.

Each species of herons has a distinct repertoire of foraging behaviors that is used and that in the absence of any other clues permits an experienced observer to identify the species with relative ease. Of the herons considered here, the Great White Heron, Great Blue Heron, Great Egret, and Green Heron have the most limited range of feeding behaviors (pers. obs.). They forage principally by the "stand and wait" or "walk slowly" methods. The Little Blue Heron is somewhat more active and has a more diverse foraging repertoire, but also relies mostly on "stand and wait" and "walk slowly" methods. The Snowy Egret, Louisiana Heron, and Reddish Egret have the most diverse behavior patterns and are much more active foragers than any of the others. The foraging behavior of the Reef Heron is most like that of the Little Blue.

Herons also differ in the extent to which they form foraging flocks or defend foraging territories. Although all herons will aggregate where prey is concentrated (*e.g.* a drying pond), only three of the species we studied regularly hunted in flocks—Great Egret, Snowy Egret, and juvenal Little Blue Heron. All three have white plumage, which Kushlan (1978) has shown facilitates flocking. The foraging flocks formed by these herons appeared to range widely from day to day and were seemingly an adaptation to exploit transient patches of prey. Other species, including the dark-plumaged adult Little Blue Heron, were most often solitary and territorial when foraging (*e.g.* Recher, 1972). The difference in foraging socially between adult and juvenal Little Blue Heron is striking and is probably related to the dispersal of young birds and their exploitation of seasonally abundant prey in northern latitudes.

Because of the diverse array of behavior that a foraging heron may use, it is useful to compare foraging strategies. Herons use two basic strategies—they can either be described as searchers or as pursuers. A searcher hunts methodically, spending most of its time looking (or in the case of many herons, "waiting") for prey and little or no time chasing or pursuing prey. In contrast, a pursuer is an active hunter that expends a relatively large amount of time and energy chasing prey after it has been located.

We considered the Great White Heron, Great Blue Heron, Great Egret, Little Blue Heron, Reef Heron, and Green Heron to be searchers. The Louisiana Heron, Snowy Egret, and Reddish Egret are pursuers. Given the extensive foraging repertoires of these birds, the distinction is of course not absolute. The Snowy Egret in particular has a wide range of hunting behaviors and at times is a searcher and at others a pursuer. Although simplistic, the distinction between searchers and pursuers allows some predictions about diets of herons.

Large herons and searchers should have more diverse diets than small herons and pursuers. By virtue of its size, a large heron should take a greater size range of prey than a small heron and be able to handle prey that easily escapes from smaller birds. Searchers should encounter more kinds of prey than pursuers; pursuers tend to locate prey at a distance, spend relatively long periods chasing sighted prey, and stay with schools of fish once located. By hunting schooling prey, pursuers will tend to restrict their diet to the kinds and sizes of prey found in schools, and this will necessarily be less diverse than the total available array of prey.

Restricting comparisons to the broad categories of prey in Table 3, large herons and searchers had more diverse diets than small herons or pursuers. Among the similar-sized species, the Little Blue Heron (a searcher) also took a greater diversity of prey sizes than the Snowy Egret or Louisiana Heron (pursuers) (Table 4). Jenni's (1969) data also show that the Little Blue Heron had a more diverse diet than either the Snowy Egret or the Louisiana Heron.

PREY SIZE

Herons are of different sizes, and one might expect a sharp partitioning of resources on the basis of prey size. However, this does not appear to be the situation, and the sizes of prey taken by different species of heron broadly overlap (Table 4; Fig. 2a, b). Willard (1977, unpub. data) has also found a broad overlap in prey size among herons of different sizes in New Jersey and Venezuela. Although large prey items provide a large amount of a heron's diet by weight, most of the prey items that we recorded taken by herons were less than 10 cm in length. The preponderance of small prey probably reflects its abundance in the environments where herons were foraging. However, in terms of the maximum size of prey that a heron can capture and swallow, large herons (*e.g.* Great Blue Heron) do take larger prey than small herons (Fig. 3), and for these birds large prey items are the most important part of their diet by weight.

All herons are able to swallow prey larger than the largest fish they can capture. Thus Green Herons in New York fed on frogs (*Rana* spp.) weighing up to 125 g, but were not seen to take fish larger than 10 g (Fig. 3). As discussed by Recher and Recher (1968), body shape and manner of struggling after capture also affect the ability of herons to handle certain kinds or sizes of prey.

TABLE 4
Size of Prey Taken by Herons

A. Mean Weight of Prey and Variance (grams)							
Heron	Florida		New Jersey		New York		Great Barrier Reef
Great White Heron	73.5	(190.8)	—		—		—
Great Blue Heron	48.8	(139.4)	15.8	(35.1)	13.3	(63.0)	—
Great Egret	1.3	(2.2)	2.3	(6.0)	—		—
Reddish Egret	1.5	(1.8)	—		—		—
Little Blue Heron	1.2	(2.1)	0.7	(0.7)	—		—
Snowy Egret	1.1	(2.1)	0.6	(1.6)	—		—
Louisiana Heron	1.0	(1.5)	0.5	(0.2)	—		—
Green Heron	0.7	(1.1)	0.9	—	6.9	(16.8)	—
Reef Heron	—		—		—		0.5
B. Prey Length Diversity $\bar{H} = -\Sigma_i(p_i \log_e p_i)$							
Great White Heron	2.374		—		—		—
Great Blue Heron	2.067		1.846		1.062		—
Great Egret	1.269		1.291		—		—
Reddish Egret	1.160		—		—		—
Little Blue Heron	1.420		0.760		—		—
Snowy Egret	1.110		0.600		—		—
Louisiana Heron	1.170		0.340		—		—
Green Heron	0.909		0.563		1.079		—
Reef Heron	—		—		—		0.660

Most fish taken by herons are grabbed, but large fish may be speared (Recher and Recher, 1968; Kushlan, 1978). Either way the prey struggle vigorously, and the size of fish that a heron can handle is related to both the size of the heron and the shape of its bill. The stouter bills of the Little Blue Heron and Reef Heron should enable them to handle larger and therefore stronger prey than the relatively slender bills of the similar-sized Snowy Egret and Louisiana Heron. The Little Blue Heron does take larger prey than either Snowy Egrets or Louisiana Herons feeding in the same habitat (pers. obs.). Jenni (1969) found that the prey taken by Little Blues averaged larger than that taken by the Snowy Egret or Louisiana Heron and that even the average size of the same fish species differed. The Reef Heron takes fish as large as those taken by the Little Blue and larger than those taken by the similar-sized White-faced Heron feeding in the same places (pers. obs.).

The overlap in the sizes of prey taken can be deceptive. Schlorff (1978) has shown that more than 84% of the prey of the Great Egret at Humboldt Bay, California, is less than five cm in length, but these contribute less then 36% of the bird's energy intake. Only 2% of the prey was in excess of 10 cm in length, but these provided 43% of an egret's energy intake. If prey length is converted to weight and plotted by size class, there is an increased separa-

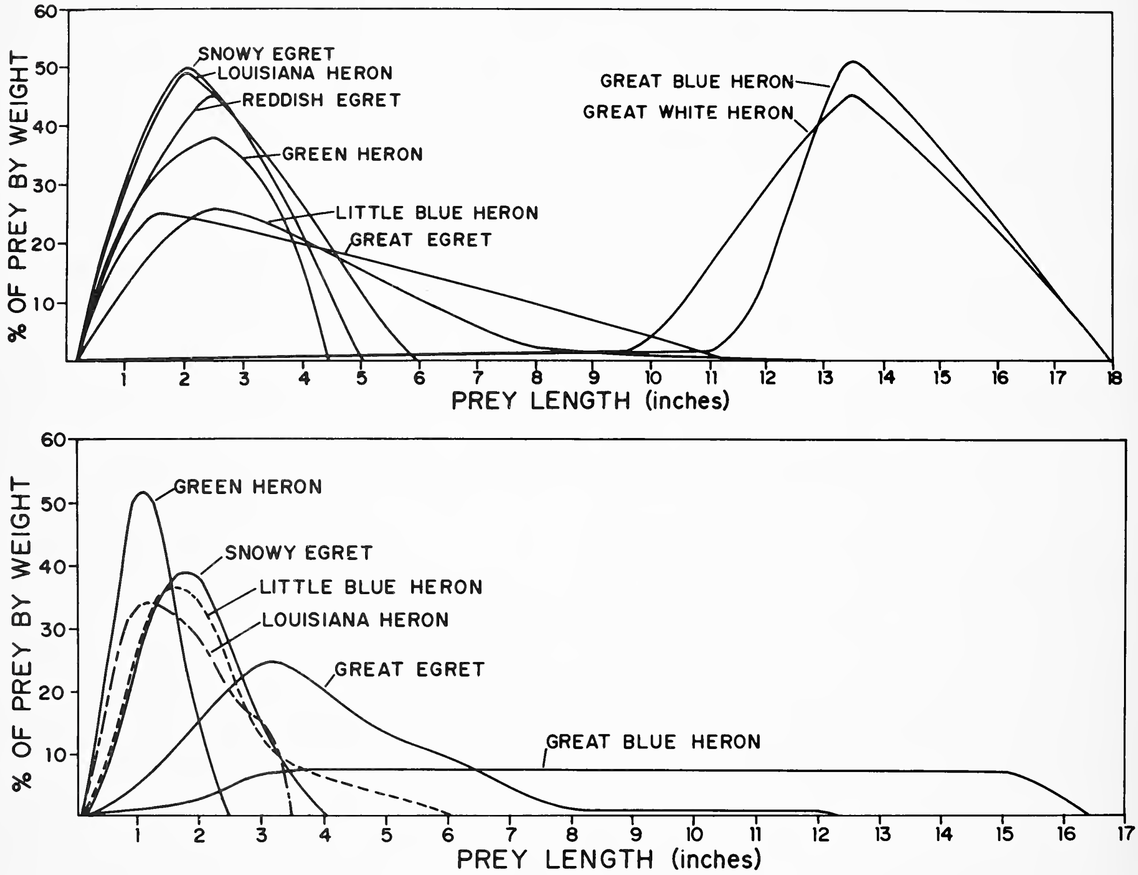

Figure 2, a and b: The percent of prey weight is plotted for prey length categories for Florida (2a) and New Jersey (2b). Two species that were uncommon in our New Jersey censuses of foraging birds are shown as dashed curves. The remaining species are well separated along the resource size spectrum. Species were more equally abundant in Florida, and their utilization curves broadly overlap along the size spectrum.

tion in the diets of the different-sized herons. The separation is most pronounced for the Great White and Great Blue Herons; although few large fish are taken, they contributed the greatest weight to the diet of these birds in Florida, New Jersey, and New York. Although large herons take many small prey items, large prey—even the occasional large item of food—contribute most of the weight of prey taken. This is illustrated in Fig. 2a and 2b, where food size is expressed as the percentage of weight of prey in each length category. In New Jersey, the Great Blue Heron and the Great Egret take substantially larger prey than the smaller herons. The size range of prey, the average size of prey, and prey-size diversity are all greater for these two birds (Table 4; Fig. 2a & b) than for any of the smaller herons. The Little Blue Heron, Louisiana Heron, and Snowy Egret took similar-sized prey, but as discussed above there was a tendency for the Little Blue to take larger fish and to have a more diverse diet. The Green Heron does not take fish as large as the other herons, but the average size of the organisms it does take is similar to that taken by the Little Blue (Table 4). Considering that the Little Blue Heron and Louisiana Heron were uncommon in our New Jersey study areas, the four most common day-feeding herons are well separated by the size of prey that contributes the greatest weight to their diets (Fig. 2b). Willard (1977) did not identify prey as to species, and it is not possible to convert his data on prey length to prey weight. However, his results appear quite similar to ours. In New York, the Green and Great Blue Herons took very different kinds and sizes of prey (Tables 3 and 4).

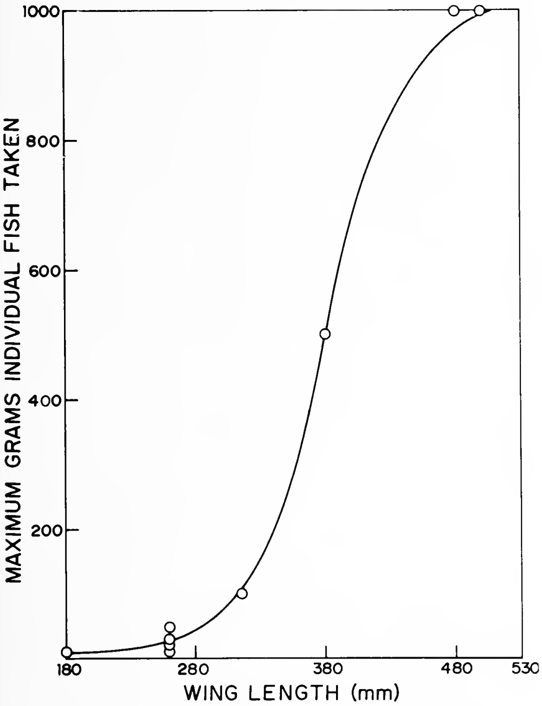

Figure 3: Regardless of the size of the bird, most fish taken by herons are small. A comparison of the largest fish that each species has been seen to take is therefore useful in illustrating the extent to which species differ in their ability to use different-sized fish. Fish were the most important prey taken by herons on our study area. The herons shown in order of increasing size (wing length is used as a measure of body weight) are: Green Heron; Little Blue Heron, Snowy Egret, Louisiana Heron, and Reef Heron (all of equal size); Reddish Egret; Great Egret; Great Blue Heron; Great White Heron. The data for Reddish Egret and Great Egret are from Willard (in press) and are for birds in Venezuela and New Jersey respectively.

The separation of species by prey size is least clear among the herons foraging on Florida Bay (Fig. 2a). The Great White and Great Blue Herons took very large prey, and it was our impression that small fish were taken incidentally to the hunting of large fish (*e.g.* mullet). The other six species for which we have data tended to take prey of the same size when foraging together. The Great Egret did take fish twice as large as any taken by the other smaller species and the Little Blue Heron did take larger fish than the Louisiana Heron and Snowy Egret, but the differences are not great enough to separate these herons along a resource size spectrum (Fig. 2a). Willard (*in litt.*) has data from Venezuela that differ from our Florida Bay observations only to the extent that Little Blue Herons and Great Egrets took fewer large prey. The length of fish taken by Snowy Egrets, Little Blue Herons, Great Egrets, Louisiana Herons, and Reddish Egrets broadly overlap; Willard has no data on Green Herons or the larger species from Venezuela.

Foraging Depth

The foraging depth distribution of herons is shown in Fig. 4. As anticipated, the larger birds tended to feed in deeper water than the smaller herons, but there is considerable overlap between species. Willard (1977) also found that the Great Blue Heron and Great Egret foraged in deeper water than the smaller Little Blue Heron, Snowy Egret, and Louisiana Heron. He found that the three smaller species foraged in similar depths and overlapped greatly. Our own data from New Jersey show that these herons overlap in their foraging depths, but that the Little Blue hunted in slightly deeper water than the Snowy Egret and that the Louisiana Heron fed in the shallows. All three fed in the same depth of water on Florida Bay. Custer and Osborn (1977b) also found that Snowy Egrets and Louisiana Herons foraged in the same depth of water, but that the larger Great Egret fed in deeper water. Although water depth was the most important variable separating these species, productivity, vegetation, and water clarity also helped explain their foraging distribution. The difference in foraging depth distribution that we recorded between New Jersey and Florida (and the difference between our data and Willard's) reflects differences in the availability and distribution of food resources with depth from place to place (and between seasons and years). Thus Green Herons in New York hunted in deeper water than Green Herons in New Jersey and Florida, which mostly hunted along the edge of marsh or mangrove vegetation in the shallowest water. In New York the Green Heron hunted frogs at the edge of submerged weed beds, but in New Jersey it hunted small fish and invertebrates in tide pools at the upper edge of the intertidal zone.

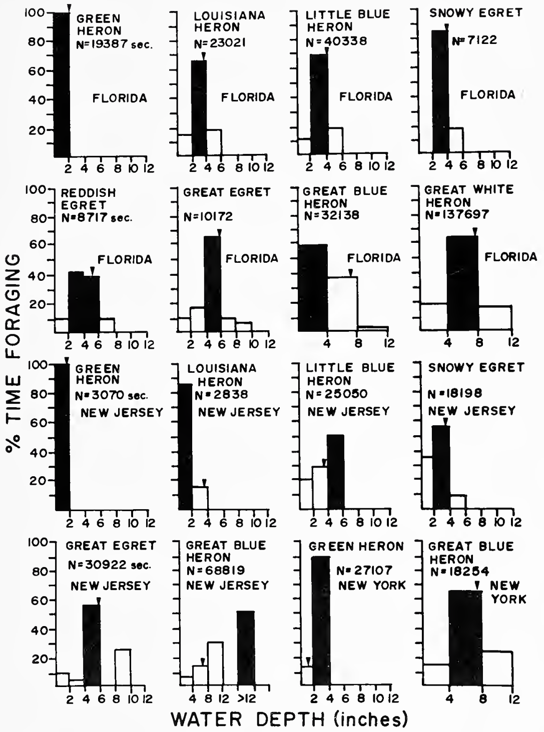

Figure 4: The foraging depth distributions of herons feeding in the same habitats are shown here for Florida (Everglades National Park, Florida Bay), New Jersey (Brigantine National Wildlife Refuge and the Tuckerton Meadows), and New York (Montezuma National Wildlife Refuge). In New Jersey, many Great Blue Herons hunted fish from the edge of channels in water deeper than wading depth, which is shown here as greater than 12 inches. The depth(s) in which the birds spent 50 percent or more of their foraging time is shown in black. Most birds feed in water that is about "ankle" deep; ankle deep is indicated by the small triangles in each plot. (In deference to our original measurements, depth is expressed in inches.)

Variations in the foraging depth distributions between localities of the Little Blue, Snowy Egret, and Louisiana Heron have similar explanations. Jenni (1969), for example, reported that Little Blue Herons fed in deeper water than the Snowy Egret and tended to frequent heavily vegetated areas. Snowy Egrets fed in open areas and along the edges of openings. Louisiana Herons fed still deeper than Little Blues and often foraged in water up to their bellies, but also actively pursued fish in the shallows. In the freshwater habitats near Lake Alice, Florida, where Jenni conducted his studies, each of these species took different prey, which reflects their different foraging depth distributions and foraging behaviors.

Foraging Success and Foraging Efficiency

The foraging efficiency of herons was measured by recording the proportion of times that attempts at prey capture were successful and the weight of prey obtained per minute of hunting effort. These data are also useful as an index of the amount of food available to herons. If one assumes that herons feed at a constant rate so that foraging ceases when satiated, the amount of food captured is a measure of the availability of prey. In the absence of data on prey biomass or production, we made this assumption, used the grams of prey captured by herons per minute of hunting as an index of prey availability, and set this equal to prey production (environmental productivity). The data are summarized in Table 5.

Are herons equally good in exploiting the food resources of the habitats they share? Or are there differences in foraging efficiency that might result in competitive exclusion? If herons differ in their use of resources because of past competitive interactions where a more efficient species has excluded a less efficient species from some part of the resources spectrum, then where herons forage together we should expect measurable differences in their abilities to use common resources. Previously we demonstrated that adult and immature Little Blue Herons differ significantly in their abilities to capture prey and in the amount of prey obtained per minute of hunting (Recher and Recher 1969). We were unable to find such differences between species. Instead, we found that large herons obtain a greater quantity of food per minute of hunting than the smaller species. Similar-sized herons, such as the Little Blue Heron, Snowy Egret, and Louisiana Heron, catch equal amounts of food even though their foraging methods differ, and the more active foragers, such as the Snowy Egret, Reddish Egret, and Louisiana Heron, missed on a greater proportion their attempts at prey capture than did searchers, such as the Little Blue and Green Herons (Table 5). However, this did not reduce the amount of food taken; the lower capture rate was compensated for by more frequent attempts at (or opportunities for) prey capture. Although additional data are required—especially on the actual expenditure of energy during foraging and on foraging abilities when prey is scarce—

TABLE 5
Foraging Efficiency of Herons

A. Grams of prey obtained per minute hunting

Heron	Florida	New Jersey	New York	Great Barrier Reef
Great White Heron	2.8	—	—	—
Great Blue Heron	3.6	0.9	5.5	—
Great Egret	1.2	0.9	—	—
Reddish Egret	1.2	—	—	—
Little Blue Heron	0.7	0.7	—	—
Snowy Egret	0.7	0.8	—	—
Louisiana Heron	0.6	1.1	—	—
Green Heron	0.2	0.3	1.0	—
Reef Heron	—	—	—	0.3-0.4

B. Number of food items per unsuccessful attempt

Heron	Florida	New Jersey	New York	Great Barrier Reef
Great White Heron	1.3	—	—	—
Great Blue Heron	1.6	1.0	2.8	—
Great Egret	1.9	1.0	—	—
Reddish Egret	0.6	—	—	—
Little Blue Heron	1.8	2.0	—	—
Snowy Egret	0.5	1.2	—	—
Louisiana Heron	0.7	0.8	—	—
Green Heron	3.9	2.0	3.9	—
Reef Heron	—	—	—	2.1

our observations indicate that all of the species studied were capable of capturing in excess of their requirements for survival and reproduction in relatively few hours of hunting.

Junor (1972) estimated that herons (and other fish-eating birds) required approximately 16% of their body weight in fish each day. His estimates were based on hand-rearing birds from Lake Kyle in Rhodesia and are similar to Siegfried's (1973) estimate for the weight of insects required by Cattle Egrets in South Africa. The relationship between body weight and daily food requirements holds for other wading birds and over a wide range of body sizes (30 to 5000 g) (Kushlan, 1978). In most circumstances the herons we studied were able to obtain this quantity of food in 2 to 3 hours of foraging. Reef Herons (Recher and Recher, 1972), juvenal Little Blue Herons (Recher and Recher, 1969), and Great Blue Herons in New Jersey required longer and took up to six hours to catch 16% of their body weight in fish. There was considerable variation in foraging success between individuals and from day to day. Wind, rain, and turbid water were seen to interfere with the ability of herons to forage efficiently. Owen (1960) attributed poor foraging success by Gray Herons (*Ardea cinerea*) during rain to increased turbidity. Krebs (1974) also found a negative relationship between foraging rate and turbidity for the Great Blue Heron. Schlorff (1978), however, found that in most instances environmental variables such as tide, cloud cover, wind speed, and air temperature had little effect on prey capture rate for Great Egrets.

Variation in individual foraging success of the herons we studied appeared to be related to the patchy distribution of prey, and birds that failed to catch prey generally moved. Betts and Betts (1977) found that the movements of Green Herons were related to foraging success, and both Krebs (1974) and Kushlan (1977) found that herons remained at a site only if feeding success were high. Our own work supports these conclusions, but the "optimal foraging strategy" of herons will be considered in another paper. Here we are concerned only with comparing the relative foraging efficiency of herons.

Although our impression is that all herons are equally good at prey capture, it does not mean that they would be equally good across a variable environment. Our collection of data was restricted to fine weather and to seasons when food was abundant. The test of a heron's efficiency as a hunter would come during periods of inclement weather and seasons when food is scarce. Kahl (1963) has shown that the time of greatest heron mortality in North America is during the winter and that young birds are the most affected. Our data on Little Blues showed that young birds were only half as good as adults at hunting. During the times of maximal food abundance in late summer and autumn, the lesser efficiency of the young means only that they need to hunt longer to obtain their needs. As food becomes less abundant and the time available for foraging decreases with shortening days, young birds can be expected to starve and mortality to increase. At these times, aggressive interactions with adult birds may further stress the ability of young herons to feed themselves and may deny them access to the best foraging sites (Bayer, 1978; Woolfenden *et al.*, 1976). Bayer (1978) found that territorial adult Great Blue Herons had nearly twice the survival rate (70 to 80%) of either nonterritorial or territorial juvenals (less than 50%) during the winter.

Adults as well as juvenals will be affected by a shortage of prey or poor foraging conditions. Owen (1960) has shown that the reproductive success of Gray Herons can vary substantially between years. Reduced nesting success and increased mortality are correlated with a shortage of food during periods of wet weather. Siegfried (1973) found that Cattle Egrets in the "man-modified" habitats of the southwestern Cape (South Africa) seldom succeeded in raising more than two chicks out of broods of three or four. He concluded that the larger clutch size was adapted to undisturbed habitats where larger prey is available. However, most studies of nestling survival among herons have shown that starvation is the principal cause of pre-fledging mortality (*e.g.* Teal, 1965; Tenni, 1969; Owen, 1960). Mortality among nestlings is greatest during the first two weeks, when growth is rapid and parents forage only one at a time (Kushlan, 1978).

Our data on foraging efficiency suggest that under ideal conditions all herons should be able to raise full clutches. In the real world, conditions are not always ideal or easily predicted. This is reflected in the relatively large clutches that herons lay and in the asynchronous hatching of young. We agree with Owen (1960), who concluded that " . . . the adaptive value of asynchronous hatching is that when food is short the smallest young in the nest die, but when food is more plentiful all the young are raised." Owen also pointed out that the nesting of herons is timed to coincide with the maximum availability of food. Shortages of food or the absence of suitable prey prevent successful reproduction (Milstein *et al.*, 1970; Owen, 1960). Thus when considering the distribution of herons, their movements, and the limits to heron species diversity, it is necessary to emphasize times of least food abundance and not times of peak productivity.

RESOURCE SEPARATION AND SPECIES DIVERSITY—AN OVERVIEW

As demonstrated by previous workers (Meyerriecks, 1962; Jenni, 1969; Willard, 1977; Kushlan, 1978), the day herons differ in their use of common resources. One way of illustrating the separation of the day herons through their use of resources is shown in Fig. 5. From our own observations we have tended to emphasize size and kind of prey, foraging behavior, and use of habitat as the most important ways in which the foraging ecology of these herons differ. However, foraging sociality and specialization as marine species may be equally important if we are to understand why there are different kinds of herons and the environmental factors that limit the number of coexisting species.

There is one feature of Fig. 5 that requires some explanation. We have indicated that the Great Egret takes small and large prey, but that the Great Blue Heron takes large and small prey. This is not intended as a play on words. We suggest that the Great Blue heron be viewed principally as a hunter of large prey and that its ability to survive and reproduce depends on the availability of large prey organisms. Smaller prey merely permit the Great Blue to hunt more efficiently and use habitats that are otherwise marginal. In contrast, the Great Egret is a medium-sized heron masquerading as a large bird. It forages principally for smaller prey, but its size allows it to take the occasional large prey (Fig. 3). We again suggest that this enables the Great Egret to forage with maximum efficiency. These are different strategies, different ways of exploiting the available array of prey, and they should not necessarily be viewed as the result of competition between the two species. If we are correct, the Great Egret in Australia, which is the largest heron over most of the continent, should take different sizes of prey in much the same proportion as the Great Egret in North America. It is a prediction we intend to pursue.

It is useful to note that the Green Heron as the smallest species has a particularly heavy bill (Fig. 6). This permits it to take fairly large prey such as frogs, but not large fish or other animals that struggle when caught (Fig. 3). The medium-sized herons—Little Blue Heron, Louisiana Heron, and Snowy Egret—fit between the Green Heron and the Great Egret in the size of prey taken (Fig. 2) but appear to us to be narrower in their use of different sizes of prey. Thus the prey-size spectrum is broken into four major classes, which are defined by exploitation strategies rather than by a mean or median prey size. In particularly productive marine habitats, the Great White Heron is a "big bang" species specializing in very large prey. The Reddish Egret is also restricted to productive marine habitats where it exploits small schooling prey in shallow water, but has the option seen in the Great Egret of taking large prey animals when these are easily caught.

The pattern of resource separation is also illustrated by the way herons are added as species richness increases from north to south (Fig. 6). The most northerly-breeding day heron is the largest, while the smallest is the second most northerly. The next two added are the Great Egret and the Snowy Egret, which fit between the Great Blue Heron and Green Heron in size. Thus the first four species are neatly spaced along a size spectrum (see also Fig. 2b) and represent the four size classes referred to above. As additional species are added, they are "superimposed" on the first four along the prey-size spectrum (see Fig. 2a)

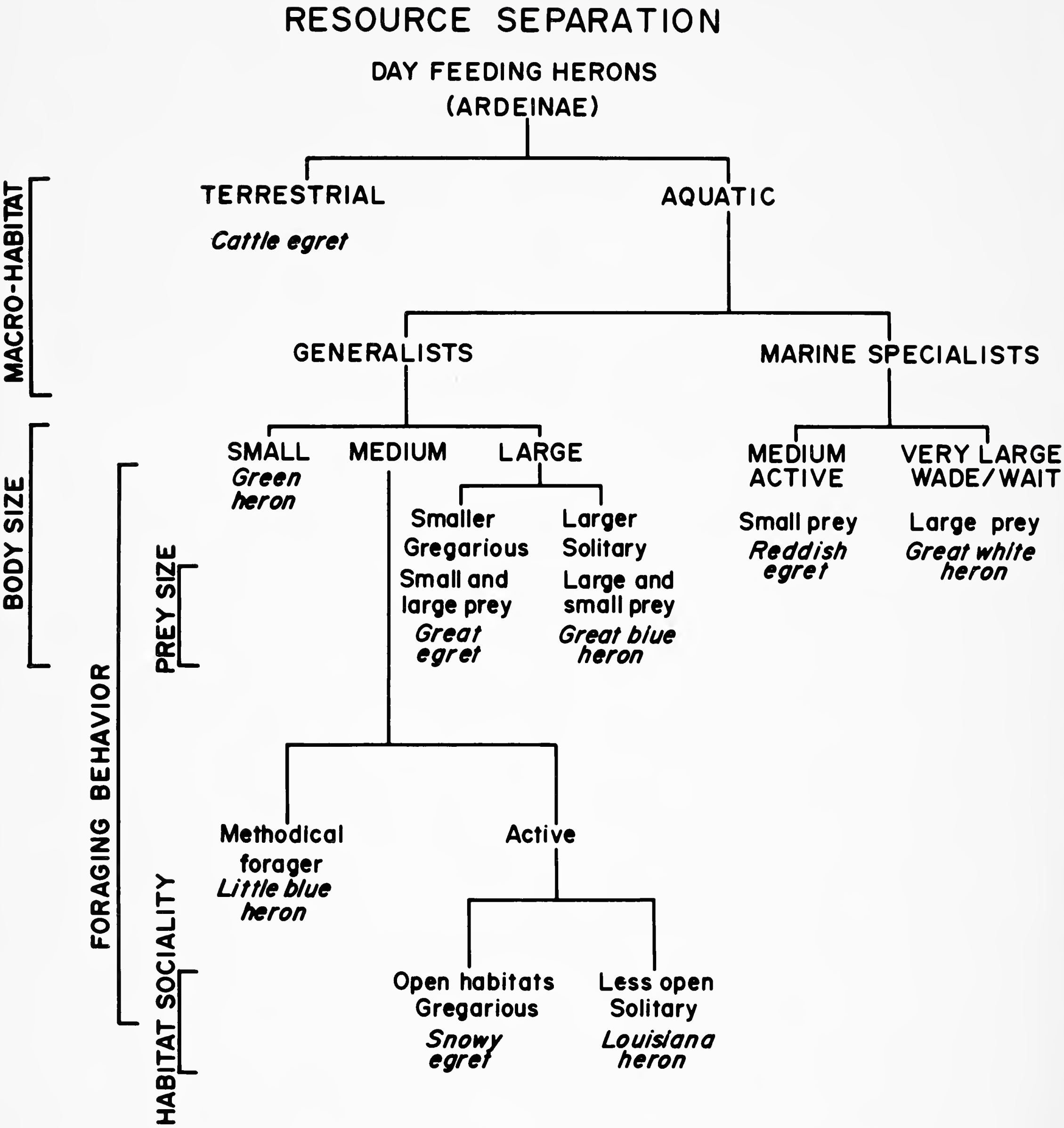

Figure 5. The "day herons" (Ardeinae) are separated by habitat, body size, and foraging behavior. In addition, the more social foraging behavior of the Snowy Egret and the Great Egret may be an important difference in the way they use resources, distinguishing them from other species that take some of the same-sized prey.

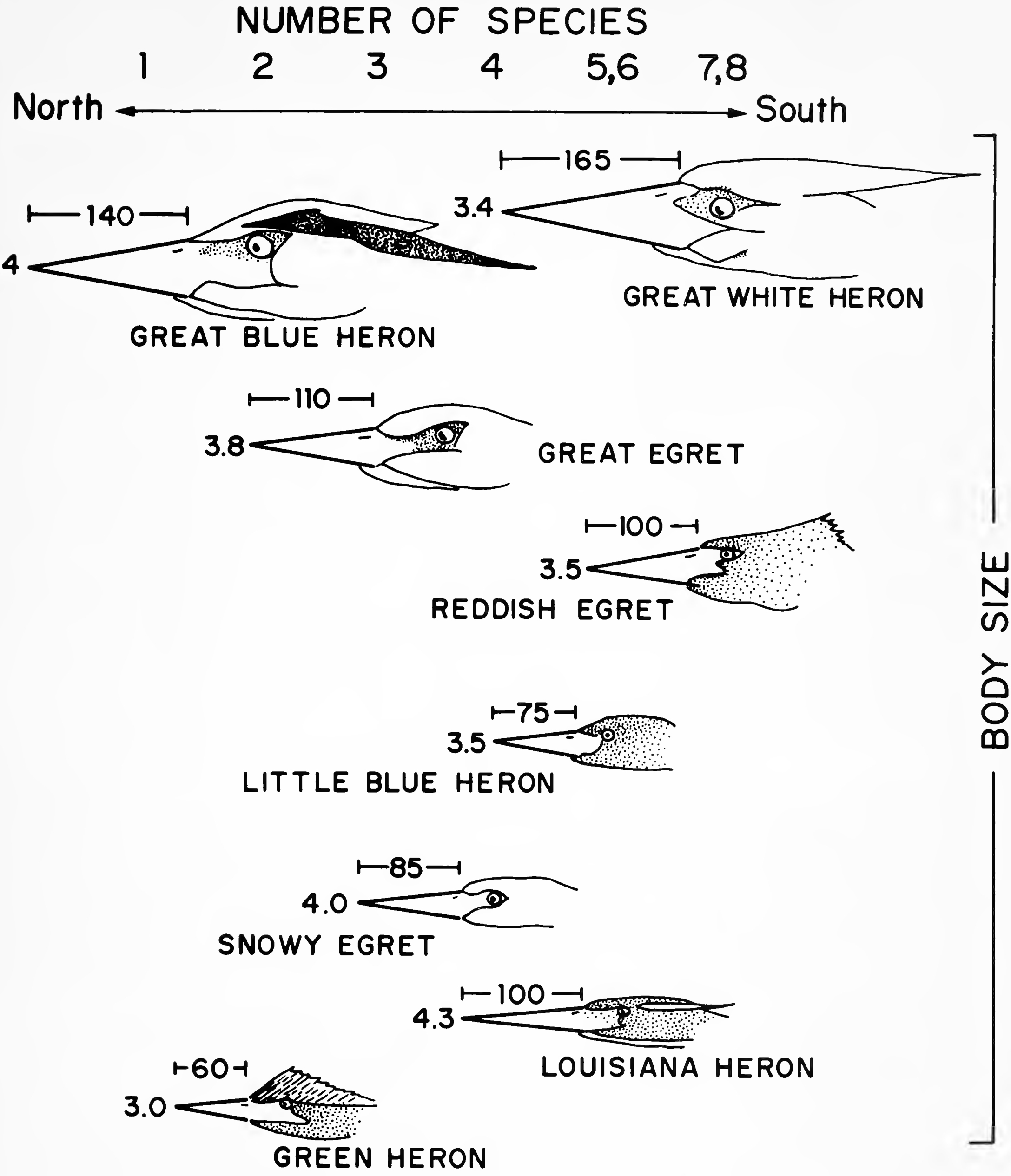

Figure 6: The most northerly breeding of the day herons is the Great Blue Heron. The Green Heron is the second most northerly, with the Great Egret and the Snowy Egret the third and fourth most northerly breeding species. Thus, with increasing diversity species are first added along a resource-size spectrum. As environmental productivity increases, additional species are "packed in" as habitat or foraging behavior specialists. The Great White Heron is a "big bang" species specializing in very large prey; not surprisingly, it is confined to the most productive habitats. [The measurements given are culmen length (mm) and the ratio of culmen length to bill depth at the nares (the number at the tip of the bill)].

but differ in foraging behavior or habitat (Fig. 5). The Great White Heron and the Reddish Egret are marine specialists, while the Little Blue Heron differs in its foraging behavior from the similar-sized Snowy Egret. Because our observations were restricted to birds foraging together in a limited array of habitats, we found only minor differences between the Snowy Egret and Louisiana Heron (*e.g.* Fig. 4). However, observations of the bird in other places and Jenni's (1969) results suggest that the Louisiana Heron may be a habitat specialist frequenting areas with more emergent vegetation than those used by the Snowy Egret.

The Great Blue Heron is the most northerly breeding (and wintering) heron because it is the largest and therefore able to use all sizes of prey as they are encountered. We suggest that the smallest heron is the next to be added along the species richness gradient because it is the most different from the Great Blue in size and because we would expect the smaller sizes of prey to be abundant than larger prey classes. Foraging efficiency relative to the abundance of available prey sizes is, in our view, the major factor determining the sequence in which species are packed into a community. In a single-species community, as on the Great Barrier Reef, the heron present will always be the largest species possible given the size distribution of prey.

The Great Blue Heron and the Green Heron can be considered prey-size generalists. Note that the Green Heron has the relatively stoutest bill of the species considered (Fig. 6) and is able to take very large prey for its size (Table 4). The ability of these two herons to take a wide range of prey and prey sizes enables them to exploit less productive environments than more specialized species. With increasing productivity, additional herons are added (Fig. 6). The last species to be added, the Great White Heron and the Reddish Egret, are highly specialized and restricted to the most productive environments. Productivity as measured through the year appears to be the major variable determining heron species diversity.

Continental Comparisons

Although data are lacking on which species actually forage in the same habitats, a comparison of the heron species density on different continents (Fig. 7) further illustrates the ways in which resources are apportioned and the limits to heron species diversity. The initial separation of species is again made most easily by size. Each continent has at least one heron in the large, medium, small, and very small size categories. In the most productive tropical environments, a very large heron is added. The extreme example of this is the Goliath Heron (*Ardea goliath*) of Africa, which is nearly twice the size of the next-largest heron. There is never more than one giant species of heron, and these birds tend to be uncommon and solitary. Additional species diversity is reached by adding species to the other size categories.

As species are added to any of the smaller sizes, they are either habitat specialists (generally using more densely vegetated areas) or have different foraging behaviors, as discussed previously for the similar-sized Little Blue Heron, Louisiana Heron, and Snowy Egret, which occur together in eastern North America. The addition of species in one size category may exclude additions to another. If corrections are made for this factor, three is the maximum number of heron species packed into any size group, and these are separated by habitat preferences, foraging behavior, and degree of sociality when foraging.

Africa and southern Florida appear to be the only places where two large herons commonly occur together. The Gray Heron and the Black-headed heron (*Ardea melanocephala*) coexist in both East and West Africa, but the Gray Heron is considered uncommon or local and is more restricted to aquatic habitats than the Black-headed. The Great Blue and Great White Herons are considered conspecific, but we have some data that suggests that they are separated to some extent by habitat and food size preferences. The Great White is typically a bird of open tide flats and shallow marine waters, but in the same region the Great Blue tends to feed in shallower water, hunts nearer to mangroves, and also frequents fresh and brackish waters avoided by the Great White.

The Great Egret occupies an intermediate position in terms of size and is a foraging generalist. It must fit in between larger and smaller herons, which may be more efficient at exploiting particular kinds or sizes of prey and

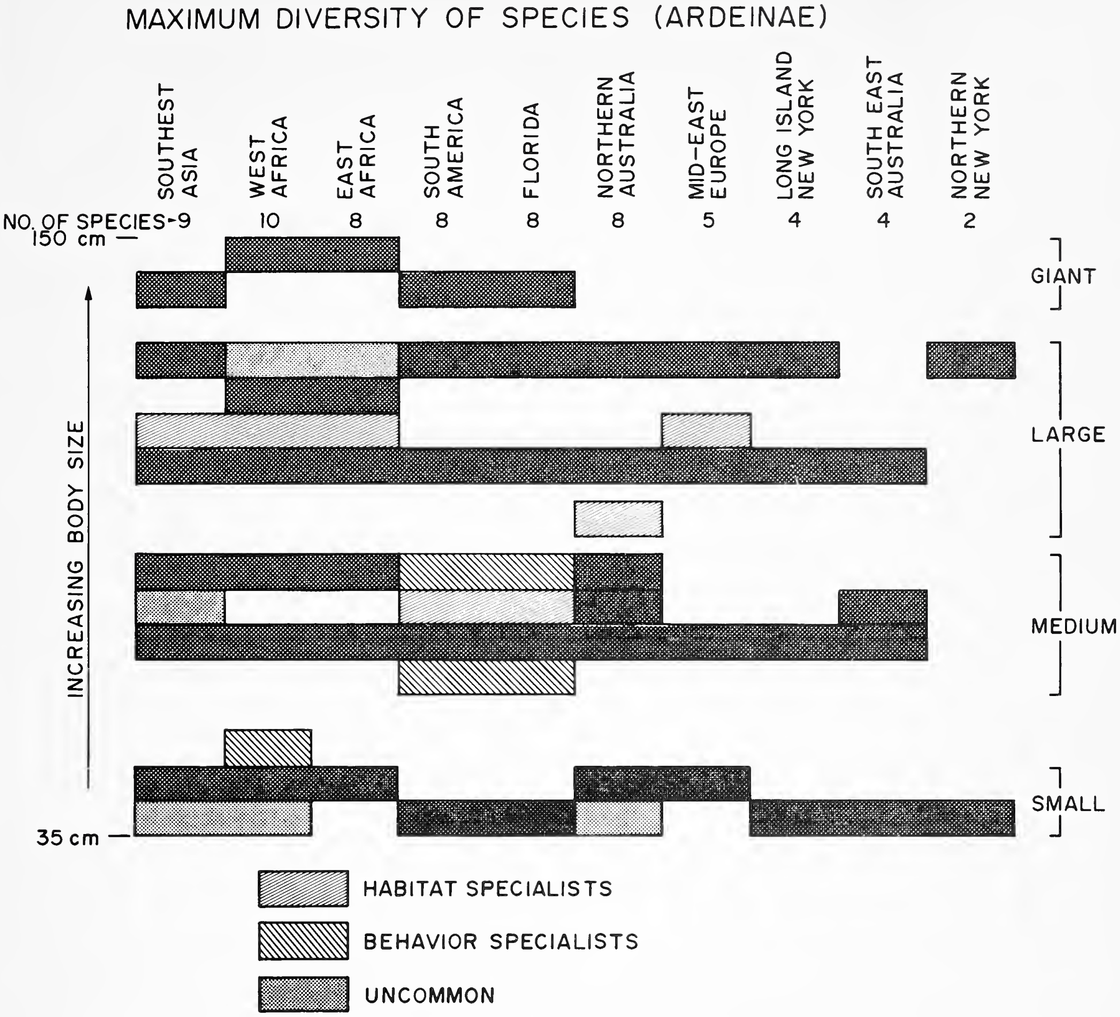

Figure 7: The same patterns of resource allocation can be found among heron communities on different continents as is seen along the eastern coast of North America. With increasing diversity, new species are first "packed in" along a prey size spectrum and are then added as habitat or feeding behavior specialists. It appears that the greatest number of species can be packed into the medium and large body-size classes and rarely or not at all as small or giant birds. It also appears that the addition of species into one size class may reduce the opportunities for new species in the adjoining size category.

The data for this figure are drawn from regional lists with references given in Literature Cited, and refer only to breeding species of the diurnal fish-eating guild. In order of increasing size, the species for each locality are: central New York (*Ardeola striata, Ardea herodias*), Southeastern Australia (*Ardeola striata, Egretta garzetta, E. novaehollandiae, Ardea alba*), Long Island, New York (*Ardeola striata, E. thula, Ardea alba, A. herodias*), Middle East and Europe (*Ardeola ralloides, E. garzetta, Ardea alba, A. purpurea, A. cinerea*), northern Australia (*Ardeola striata, E. picata, E. garzetta, E. novaehollandiae, E. intermedia, Ardea pacifica, A. alba, A. sumatrana*), Florida (*Ardeola striata, E. caerulea, E. thula, E. tricolor, E. rufescens, Ardea alba, A. herodias, A. herodias occidentalis*), South America (*Ardeola striata, E. caerulea, E. thula, E. tricolor, E. rufescens, Ardea alba, A. herodias, A. cocoi*), East Africa (*Ardeola* sp., *E. garzetta, E. intermedia, Ardea alba, A. purpurea, A. melanocephala, A. cinerea, A. goliath*), West Africa (*Ardeola striata, Ardeola* sp., *E. ardesiaca, E. garzetta, E. intermedia, Ardea alba, A. purpurea, A. melanocephala, A. cinerea, A. goliath*), Southeast Asia (*Ardeola striata, A. ralloides, E. garzetta, E. eulophotes, E. intermedia, Ardea alba, A. purpurea, A. sumatrana, A. imperialis*).

habitats. Murton (1972) described the Great Egret's cosmopolitan but patchy distribution as "relict," but both its cosmopolitan distribution and patchy abundance are more likely to be the result of its generalist position among herons in terms of size and feeding habits. It occurs with the similar-sized Purple Heron (*Ardea purpurea*) in Europe, Africa, and Asia and with the White-necked Heron (*A. pacifica*) in Australia. The Purple Heron is described as "skulking" and frequents densely vegetated aquatic habitats. The White-necked Heron also frequents densely vegetated places though it is not a skulker. Both species are separated by habitat and feeding habits from the Great Egret, which generally hunts by wading and walking and uses areas of shallow, open water.

The greatest number of herons on all continents are medium-sized or small. The Little Egret (*Egretta garzetta*) and the Plumed Egret (*E. intermedia*) are widely distributed in Africa, Asia, and Australia and differ primarily in foraging habits and sociality while foraging. The Little Egret is similar to the Snowy Egret of North and South America. It has a wide foraging repertoire and tends to be an active hunter (pursuer) and is social (pers. obs). The Plumed Egret tends to be less social while foraging and hunts more in the fashion of the Great Egret (searcher). In Asia both egrets occur with Swinhoe's Egret (*E. eulophotes*), which seems to have broadly overlapping habits but is uncommon. Murton (1972) attributes its rarity in part to competition with other egrets, but not enough is known of its habits or the effects of humans to readily accept Murton's ideas. Swinhoe's Egret was hunted for its plumes and, like the Reddish Egret of North America, may not have recovered from excessive hunting. The Reddish Egret and the Black Heron (*E. ardesiaca*) of Africa are separated from other herons by their active foraging behavior and habitat preferences. The differences between the North American Snowy Egret, Little Blue Heron, and Louisiana Heron have already been discussed. In Australia the White-faced Heron fills a unique position. Intermediate in size between the Little and Plumed Egrets, the White-faced is a habitat generalist (pers. obs.). It occurs in all aquatic habitats across the continent and is often found on pastures and rough grazing land. Except for its tendency to hunt very small prey, in aquatic habitats it is perhaps most comparable to the Little Blue Heron as a slow and methodical hunter and is thus separated from the Little Egret.

Australia is a dry continent with a highly variable rainfall. In the southern and central parts of the continent, aquatic habitats are limited and may vary in extent significantly from year to year. It is probably for these reasons that Australia lacks a large heron south of the tropics; the Great Egret is the largest heron over most of the continent. The variability of rainfall probably also explains the ecology of the White-faced Heron as a bird able to exploit a wide range of habitats and foods and not be confined to aquatic environments.

The smallest herons are the Green or Mangrove Heron (*Ardeola striata*) and the paddy or pond and squacco herons (*Ardeola* spp). One or the other of these species occurs on all continents. *A. striata* is absent from East Africa and Europe, while other *Ardeola* species are absent from Australia and North and South America. The pond herons and the Green Heron seem complementary, and where they occur together they are separated by habitat. Generally, pond herons frequent more open areas and are more social than *striata*. Where a pond heron is abundant, Green Herons may be scarce, as in Southeast Asia. In Australia, the Pied Heron (*E. picata*) may be a replacement for the pond herons.

Conclusion

There are different kinds of herons because there are different kinds of resources. Herons differ in size because there are both large prey and small prey. They differ in foraging behavior, use of habitats, and formation of foraging flocks because prey species themselves differ in their behavior and the ways in which they are distributed through time and space. The efficient exploitation of prey therefore requires some degree of specialization on the part of the heron; a large heron can not forage efficiently on very small prey, nor can a small heron take big fish. We should therefore expect differences to evolve between herons in response to the different kinds of prey available and the need to forage with maximum efficiency during periods of reduced prey availability or when nestlings are being fed. Selection for foraging efficiency may be especially intense on young birds regardless of any interaction that may or may not occur with other individuals.

It would be easiest to accept a competition argument for the differences in resource use between heron species. Such an argument would contend that past competition between species for common resources has selected for differences that minimize competitive interactions. It would not be necessary to demonstrate that competition existed in the present (although herons probably do interfere with each other when foraging and may do so aggressively), but it would be necessary to accept an argument that foraging herons significantly reduce prey availability and thereby depress the reproductive success of birds using the same habitats and feeding on the same prey. We find this a difficult argument to accept in its entirety. Without rejecting competition as a factor in the ecology of herons and their evolution, it is necessary to put its role in perspective. Changes in the availability and abundance of prey are most often the result of weather and climate and not of predation by herons. This is particularly true of seasonal patterns or variations in prey availability from year to year, which are the events most closely linked to increased mortality or lowered productivity of herons (*e.g.* Kahl, 1963; Owen, 1960). At these times, the capture of prey by other herons (exploitation competition) or the interference with foraging (interference competition) may well occur and would serve to intensity the impact of effects by climate on availability of prey. Despite this, we consider it more productive to view competition between species of herons as a "honing device" sharpening differences in behavior and morphology, differences that have evolved principally to optimize foraging efficiences during periods of reduced prey availability resulting from weather and climatic variations or other factors influencing prey numbers.

If we turn over our original question and ask "Why are there so few kinds of herons?" then we might give more weight to competitive interactions between species. It seems reasonable that once a set of resources is fully exploited by a species, a second species cannot use those resources or the two species coexist. There is a limit to the similarity of coexisting species. Nonetheless we did find broad overlaps between herons in their use of resources; coexisting species took many of the same kinds of prey, foraged in the same depths of water, and generally hunted in the same places. Without question this reflects the very favorable foraging conditions during which we made our observations and the abundance of food at these times. It may also indicate that there is a high level of variability in the environments used by herons, with the advantage shifting first to one species and then to another. In such circumstances, with chance events exerting a greater effect on the evolution of species and the structuring of communities, competitive exclusion is unlikely.

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COMMENTS

Lester Short: I wonder to what extent you really can talk of a heron community in terms of interference factors from other organisms, especially at the higher and lower ends of the spectrum. One can visualize, for instance, Green Herons competing as much with kingfishers as they would with other herons. The Great Blue, of course, reaches the point of competition with other large fish-eating birds. Also, what interference would there be from the nocturnally feeding herons entering into the picture, and from ibises and other kinds of birds feeding in similar ways?

H. Recher: I really can't answer that question. We deliberately restricted our observations to a very cohesive group of organisms. I've listened to David Willard and others who have worked in South America, where they have attempted to look at the entire galaxy of fish-eating organisms—fish, mammals, reptiles, and birds of all sorts. I don't think one can come up with simple answers to that kind of complexity. What we were trying to generate is a simple model for a small part of the fish-eating community, in the hope that it stimulates additional questions. Moreover, I don't think we could have, in a physical sense, coped with the full range of organisms.

Gochfeld: I am personally very gratified that the theoretical model relating heron size to foraging depth and prey size has been borne out in these studies. Having fiddled with heron observations, I have found it very difficult along Long Island to actually see what they are getting, and I am particularly interested in how you were able to discern, for each of these species, the kinds of fish they were taking, whether they were bottom or surface species. It has been my understanding—I am not much of a fish person—that there is both diurnal variation and also age variation in the heights at which certain fish are found in any given estuarine area.

Recher: Bear in mind that our observations were of birds in water of less than one foot in depth, which doesn't allow much scope for movement up and down of fish species. We restricted our observations to birds which were quite close to us. In Florida we dealt with about 15 or 16 species of major prey items above one inch in size, with which we became familiar through catching the prey and handling it. We didn't find it difficult to identify prey. Below one inch in size, yes, it gets hard to identify fish as to species. If you plot weight/length curves for all the species of fish available to the herons, they converge so closely that we were able to use a generalized prey weight/length curve for that small prey which was identified only as fish. On the Great Barrier Reef, where herons took over 100 species of fish and where they had 700 species potentially available to them, we simply categorized fish by shape; length/weight curves were on that basis.

Drent: I was tantalized by your statement that the Reef Heron had a food requirement of 16% of its body weight per day and my question is—Is this a measured value for that species, or are you deriving this from some theoretical equation?

Recher: I'm taking it from the empirical studies of people like Junor in Africa where they have done it for a range of fish-eating birds. That has been summarized, at least up until 1976, by Kushlan in his paper in the wading bird proceedings. It has not been measured for the Reef Heron.

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