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Technical Report 197

A report on the guano-producing birds of Peru [“Informe sobre Aves Guaneras”]

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William Vogt[1] with translation and notes by David Cameron Duffy[2]

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This technical report series began in 1973 with the formation of the Cooperative National Park Resources Studies Unit at the University of Hawai'i at Mānoa. In 2000, it continued under the Pacific Cooperative Studies Unit (PCSU). The series currently is supported by the PCSU.

The Pacific Cooperative Studies Unit at the University of Hawai'i at Mānoa works to protect cultural and natural biodiversity in the Pacific while encouraging a sustainable economy. PCSU works cooperatively with private, state and federal land management organizations, allowing them to pool and coordinate their efforts to address problems across the landscape.

CONTENTS

Abstract.-- (Modified from the original) Vogt studied the Guanay Cormorant (*Phalacrocorax bougainvillii*), Peruvian Booby (*Sula variegata*), and Peruvian Pelican (*Pelecanus thagus*) for almost three years (1938 - 1940). The nesting range of these species extends from $04^0$35'S to 38^0S, covering an area of considerable geographical diversity. The climate is briefly described. The report contains details of the oceanography and marine biology of a part of the nesting range of the birds, and a rejection of the theory that a warm southward-flowing surface current causes major changes on climate and breeding season for guano birds. The histories of past abnormal years and their effects on the birds are reported.

The average density of Guanay Cormorant nests is 313.9 ± 3.76 per 100 m^2. The ecological efficiency of the islands and their microclimates are linked. The Guanay Cormorant is limited to nesting on the windy parts of the island, which are the coolest, as there is an inverse relation between wind and temperature.

A detailed description of the social behavior of the Guanay Cormorant, including its feeding and nesting, is given. Nesting is concentrated in spring and summer. The breeding season keeps the adults on the island for four months every year. The average Guanay Cormorant clutch size is 3.13 ± 0.101 eggs and incubation lasts 27 days. Nesting in large colonies protects nests because fewer birds are at the edges in larger colonies. Various causes of mortality are described. The only significant predator of the Guanay Cormorant may be the Andean Condor (*Vultur gryphus*).

Food is probably the most important limiting factor for the birds. There is a correlation between the abundance of food for birds and the abundance of diatoms. Each Guanay Cormorant eats approximately 215 g/day of food and no more than 316 g/day.

Annually, each Guanay Cormorant eats 78.4 to 115.4 kg/year of the Peruvian Anchoveta (*Engraulis ringens*) and produces approximately 15.8 kg of guano per year. The quantity of fish consumed by birds in the year prior to the guano harvest of 1940 was between 711,903 and 917,150 metric tons.

Based on extensive data, this is much lower than previous estimates. Each ton of guano is the result of 4.95 - 7.3 tons of fish consumed, but the guano that the company removes from the islands is only a small proportion of the guano that the birds deposit at sea, where it may act as an important fertilizer for plankton.

Preliminary studies suggest that anchoveta are migratory. I have rejected, because of a lack of supporting data, the theory that anchoveta are still present during food shortages, but at depths too great for them to be taken by birds. A preliminary study of 1,427 anchoveta indicated a marked reduction in the year-classes hatched in the spring and summer of 1939 and 1940, when the birds died of hunger. Anchoveta spawned in 1938 were the most abundant. The Peruvian Anchoveta appears similar in biology to the California Sardine (*Sardinops sagax caerulea*). The commercial anchoveta fishery should be carefully monitored as it represents one of the most serious potential threats to the guano industry.

Various interactions of the birds and humans are discussed. I review the history of the guano birds, based on available data, from the pre-Columbian period to the present. The ecologies of the Peruvian Booby and Peruvian Pelican are discussed. Each species seems to occupy a distinct niche so that, within broad limits, the three do not compete with one another. Interactions or the synecology of plants and animals connected with the guano birds appear to be so complex that they require more thorough study. Various

management methods are suggested that might allow an increase in the numbers of birds and the proportion of guano harvested.

Key words: E1 Niño, Peruvian Anchoveta *Engraulis ringens*, Guanay Cormorant *Phalacrocorax bougainvillii*, Peruvian Booby *Sula variegata*, Peruvian Pelican *Pelecanus thagus*, upwelling.

A NOTE CONCERNING THE TRANSLATION

After I finished my own work in Peru on guano birds and had learned enough Spanish to begin to understand the importance of this paper, I spent more than a decade periodically trying to recover Vogt's original English-language manuscript, tracking down leads from four continents. Being unsuccessful, I decided instead to translate the surviving Spanish into English.

A translator usually tries to achieve two things: accuracy and preservation of the author's style. The latter is, in this case, almost impossible since I have had to translate back into English a document originally written in English but surviving only in Spanish. Enrique Avila, the Peruvian who originally translated the document into Spanish, apparently tried to keep the translation more or less literal, but as Spanish is a more loquacious language than English, there is the customary proliferation of introductory and parenthetical phrases which Vogt is unlikely to have used in the original. Avila at times had to invent Spanish equivalents for English scientific words and jargon.

In some cases, the English originals followed in the Spanish text, but in others, recovery of the original sense was difficult. Additionally, some of the words and expressions are idiomatic, being peculiar to the Peruvian Spanish of the period. Finally, the typesetters and copyeditors have not been kind. Many of the numbered references were omitted and several phrases altered through omissions or "typos." Two photographs, of an unidentified plankton and of Peruvian Boobies nesting on artificial ledges, have been included but at limited quality because of difficulties of reproduction.

I have tried to make my translation as concise as possible without sacrificing the sense of the "original" Spanish. I have cut redundant sentences wherever possible and reformed others, often pruning supplementary or reinforcing phrases. The translation is thus rather more “free” than literal. Emphasis has been on “readability” and context while respecting the fact that this report to the Peruvian guano company was meant to be both practical and informative.

William Vogt was a remarkable man and this is a remarkable piece of work, done in isolation more than six decades ago, but still as current as much of the work being done today. It would be preferable to read the English original, but I hope my translation has done justice to both the man and his work. Superscripts in the text refer to footnotes that I have added, to update or expand on Vogt's work. These updates extend to 1985. A review of the subsequent literature would be a paper in itself.

This translation and the notes benefited from the help of a great number of people. Manuel Plenge introduced me to William Vogt's work and was a constant source of friendship and advice in Peru. My wife, Maria Jose Campos de Duffy, and her father, Luis Campos Martinez, helped me with difficult passages in the text. Wendy Liell-Cock and Ione Davies transformed my nearly unintelligible script into a readable manuscript. Pat Lauber proofread the text and Marie-Pierre Touchard and my wife redrew the figures. Georgia Fredeluces Hart rescued the manuscript when I thought we had lost it to an archaic electronic storage system and she also coordinated the final copy editing, figure reproduction and publication process. Helen Chesbrough carefully copy edited the final English manuscript. Joanna Griffith, AIA, artfully re-produced the figures from scanned hardcopies.

Finally, I thank Professor W. Roy Siegfried for allowing me to use the facilities of the Percy FitzPatrick Institute of African Ornithology. The Alaskan Natural Heritage

Program of the University of Alaska and the Pacific Cooperative Studies Unit of the University of Hawaii Manoa provided the resources to see the manuscript into its final shape. The Frank M. Chapman Memorial Fund provided much-needed support.

A number of people helped in my efforts to learn more of William Vogt: Mr. Stephen Catlett (American Philosophical Society), Mr. Huntington Eldridge, Jr. (Ducks Unlimited), Ms. Myriam Figueras (Columbus Memorial Library, Organization of American States), Dr. Quentin M. Geiman (Professor Emeritus, School of Medicine, Stanford University), Mr. Lindsey Hayes (National Biological Service), Dr. Helen Hays (Chair, Committee on Bibliography, American Ornithologist's Union), Professor Joseph J. Hickey (University of Wisconsin), Professor G. E. Hutchinson (Yale University), Ms. Mary Le Croy (American Museum of Natural History), Professor Ernst Mayr (Museum of Comparative Zoology), Mr. Ray Norman (University of Alaska Anchorage), Ms. Barbara K. Rodes (The Conservation Foundation), Dr. Mary Sears (Woods Hole Oceanographic Institute), and Mr. Richard J. Wolfe (Countway Library of Medicine).

David Cameron Duffy

INTRODUCTION

Three species of birds are so important in the production of guano in Peru that they merit the name "guano birds." They are, in order of importance, the Guanay Cormorant (*Phalacrocorax bougainvillii*), hereafter also guanay, the Peruvian Booby or Piquero (*Sula variegata*), hereafter also booby, and the Peruvian Brown Pelican (*Pelecanus thagus*), hereafter also pelican. Earlier writers mentioned other species as major guano producers, but these are not presently of importance, whatever the historical situation.

My field studies of the guano birds began a short time after my arrival in Callao, Peru, on 25 January 1939 and continue as of this writing. My first objective has been to determine the factors that limit the numbers of birds so that, if some of these could be altered, bird populations would increase. The second objective of the study has been to suggest improvements in the management of the birds, to allow recovery of a greater proportion of all the guano produced.

In considering the results of these studies, two aspects should be kept in mind. First, the birds do not merely exist in their environment, but are an integral and essential part of it. They have to be constantly considered in relation to the places where they nest, rest, feed, or migrate; to wind, temperature, rainfall; and to all the other organisms, plants or animals with which they associate. All of these, owing to their abundance or scarcity, cooperation, competition, or predation, affect the guano birds.

Second, the birds evolve over time. The life histories of the birds are the result of selection over thousands of years. Each species has responded differently to the environment and each has its own niche. The guanay exists because of certain conditions of food and climate, but these same conditions place limits on its activities. The booby is unaffected by certain conditions that govern the guanay so that the former can exist where the cormorant cannot. The pelican occupies yet another niche, feeding and breeding under conditions which would be impossible for the guanay.

All three species have been profoundly influenced by man, apparently in different ways. To understand the current situation, we must study not only the pre-Columbian period, but also conditions during the Spanish colonial and Republican periods in Peru.

To be complete, such a study would require much more than these three years (1939 - 1941) of work by a biologist. Coverage of only the most important aspects would require a team of experts for many years. However, I have been able to study various aspects, some in considerable detail, thanks to the cooperation of specialists in various disciplines, especially pathology and marine biology. The reports of these experts will be published later because of the need for additional study (cf. Sears 1954).

I wish to express my gratitude to various persons and institutions. Above all, I wish to thank Sr. Francisco Ballen and the Directorate of the Compañia Administradora de Guano for the type of support often desired but rarely encountered by a scientist. This support was essential to the success of this project. My assistant, Enrique Avila L., has, during the last year and a half of these studies, accumulated many meteorological and oceanographic data on which I have based my conclusions. His careful work allowed me to investigate aspects that would otherwise have been inadequately examined. He is also the translator of this report. Dr. Robert Cushman Murphy of the American Museum of Natural History assisted with his advice, especially in the initiation of this study. Dr. G. Kingsley Noble of the same institution offered valuable suggestions related to the study of lizards. Dr. Quentin M. Gelman of the National Institute of Hygiene and Public Health and of Harvard Medical School is studying the pathological material. His contribution has been invaluable.

Dr. Mary Sears of Wellesley College and Woods Hole Oceanographic Institution not only examined plankton samples that I sent to the United States, but also came to Peru to study the biology of the Humboldt Current in cooperation with me. Her investigations contributed greatly to the understanding of very important aspects of marine biology related to the food of the birds. She has also given valuable advice concerning numerous other matters.

The Woods Hole Oceanographic Institution provided planktometers, devices for the quantitative collection of plankton. The Bureau of Plant Industry, U.S. Department of Agriculture, identified the ticks and gave advice on their control. The Fish and Wildlife Service of the U.S. Department of the Interior studied the stomach contents of the lizards and, through its banding office, helped to gather the dispersed data on banding recoveries from most of the west coast of South America, from Buenaventura, Colombia, to Ancud, Chile. The Servicio Nacional de Meteorología and the Escuela Naval of Peru kindly provided data on the climate of the Peruvian coast. Dr. Daniel Lehrman of New York made useful suggestions concerning the study of the birds' behavior. From the employees of the Compañia Administradora del Guano, I received constant and generous aid. I especially wish to thank Victor Miranda who graciously endured my interruptions of his work.

Unfortunately, this report was written without access to a good library. The bibliography is incomplete. Many topics could only be touched upon since they require reference to technical publications. In some cases I have been obliged to cite authors from memory. The most important investigations of the seabirds of the area have been made by Murphy (1925, 1936), Coker (1918, 1919, 1920, 1921, 1935), Forbes (1914 and an unpublished report), LaValle (1914, 1917, 1920, 1925), and Vogt (1939; 1940a, b; 1941). Reports on geography and oceanography have been produced by Gunther (1936), Schott (1933), Schweigger (1931, 1940), Sverdrup (1930), Romero (1939), Bowman (1916), and Vogt (1940a,b; 1941). Unfortunately, most of these are based on field work of only a few months' duration. None of the reports covered a long enough period to be considered definitive. Because of the marked climatic cycles discussed below, a study of at least eight years is necessary, while fifteen years would be preferable. Even longer periods might be necessary.

GEOGRAPHY

General Description of the Area

The study area extended from the Isla Lobos de Tierra (6° S) to the Bahia de la Independencia (14°16'S). However, Guanay Cormorants nest as far south as Isla Mocha (38°20'S) (Murphy 1936: 900). The Peruvian Booby also nests that far south, and the Peruvian Pelican has done so in the past (A. W. Johnson, pers. comm.). The nesting range of the guanay extends north to Lobos de Tierra, that of the booby to the area of Punta Parinas ($4^0$35'S) (Murphy 1936: 839), while the pelican nests on Lobos de Tierra.

The northern part of the range of the guano birds is rather uniform. It is located in a zone of southeast winds, but is protected by the Andes from the winds' intense humidity. It includes a narrow desert band where life finds refuge in valleys or wherever engineering skill has irrigated fields with water from Andean rivers or from wells. The islands themselves, with the exception of the islands Lobos de Tierra and Lobos de Afuera, are typically desert with no sign of plant life, apart from algae that flourish because of the humid winds. The island Lobos de Tierra has two locust trees, indicative of its position at the edge of the desert zone. On this island in late August 1939, rain rattled on the roof. This was the only time it rained during my entire stay on the Peruvian coast. Several islands with higher elevations support vegetation during the winter. The only one of the higher islands that holds an appreciable number of guano birds is San Lorenzo, off Callao (12°02'S), but the area occupied by the cormorants is well separated from the humid summit.

It is interesting to compare the conditions encountered by the birds nesting in Peru with those found along the Chilean coast in the most southerly part of the breeding ranges. Almost half the island of Mocha "is mountainous and covered with virgin forest." The ranches, pastures, and marshy areas are cut by numerous gullies, none of which is permanent. Their mouths present nesting places for the birds. The sides of the island, with their woods and thickets, present a totally different habitat, primarily occupied by a restricted fauna (Murphy 1936: 251). Few data are available at present, but it seems that the extreme south of the nesting range of the guano birds is again at the edge of two climatic zones. The first of these receives an austral-summer precipitation of 250 - 500 mm and 500 - 1000 mm in winter, while in the second zone the summer precipitation is 500 - 1000 mm and in winter, 1000 - 1500 mm (Anon. 1937).

The uniformity of the Peruvian landscape suggests little variation in meteorological conditions from north to south, but the guano birds appear so susceptible to even slight differences that these require further study, as will be discussed below. In addition, conditions on the islands are different from those of the coast itself, but we have few reliable data from the islands. Nevertheless, coastal weather data give an indication of the climatic variation of the area.

Figure 1 gives climatic diagrams for three meteorological stations: El Alto (4°16'S; 295 m elevation), Lima ($12^{0}5'$S; 25 m elevation), and Cañete ($13^{0}7'$S; 36 m elevation). The mean and maximum temperatures as well as means of humidity have been extracted from the archives of the National Weather Service of Peru. These data leave much to be desired for purposes of comparison and they can be considered only a first approximation to conditions encountered by the birds.

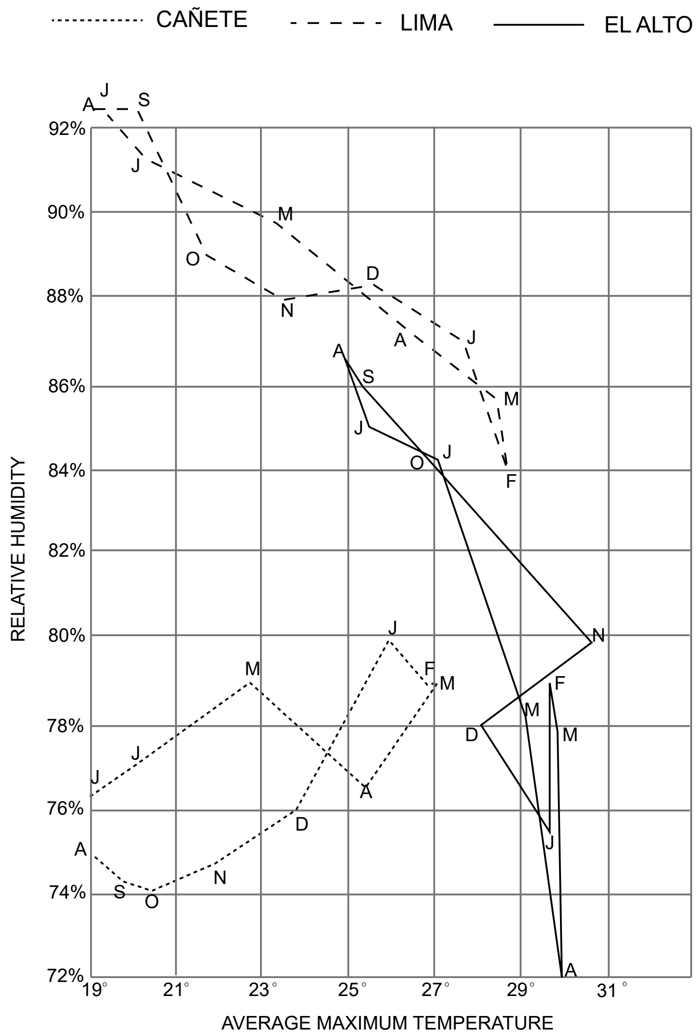


Figure 1. Maximum temperatures recorded at three sites along the Peruvian coast: El Alto (04⁰16'S, 295 m); Lima (12⁰05'S, 25 m); and Cañete (13⁰7'S, 36 m).

The stations selected are located at different elevations and distances from the coast and cover only slightly more than half the coast of Peru used by the birds. However, the three stations provide the best available data and thus a key to avian distributions.

The high temperatures of El Alto indicate conditions that would be intolerable to the guanay, which reaches its northern limit 240 km to the south of the station. The pelican has the same nesting limit, but its non-breeding range extends many miles to the north, as will be shown below. Conditions vary so much from place to place and the birds are so strongly affected by microclimates that more meteorological data are essential for reliable conclusions.

The same can be said of wind conditions. Since each island inhabited by guanays presents a different aerodynamic situation, as we shall see below, detailed and continuous studies are needed if we wish to understand the effect of wind. However, observations made during the last three years offer some indication of the causes of climatic cycles and periodic great mortalities of the birds.

The literature concerning the coast is full of references to southeast winds (Bowman 1916, Gunther 1936). Bowman noted southwest winds, but these occurred, at least partially, during 1911, a year in which there were heavy rains. During 1940 and part of 1941, observations of winds were made three times daily on Isla Chincha Norte. There was a large proportion of south and west winds, differing from what was expected on the basis of previous publications (Fig. 2). The extent of the deviation from normal cannot be determined because of various interruptions in the observations. However, Figures 3 - 6 show that 1938 and 1940 were years with a high proportion of southwest winds while 1939 had a low proportion. Unfortunately, there are no comparable observations for other islands.

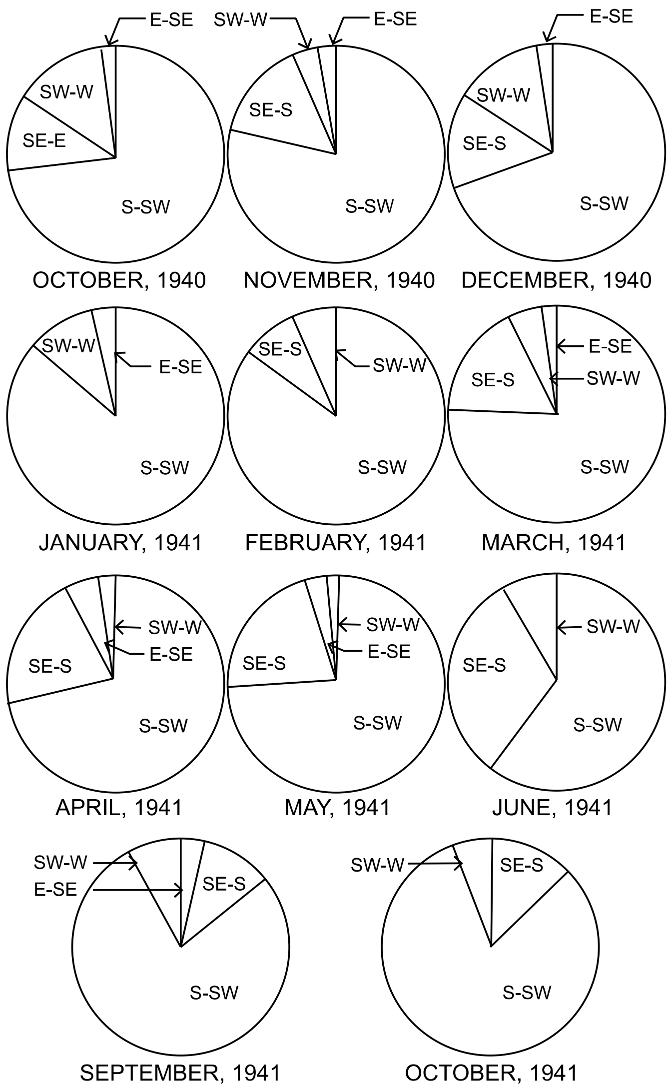


Figure 2. Relative frequencies of southerly winds on Isla Chincha Norte: October 1940 - October 1941.

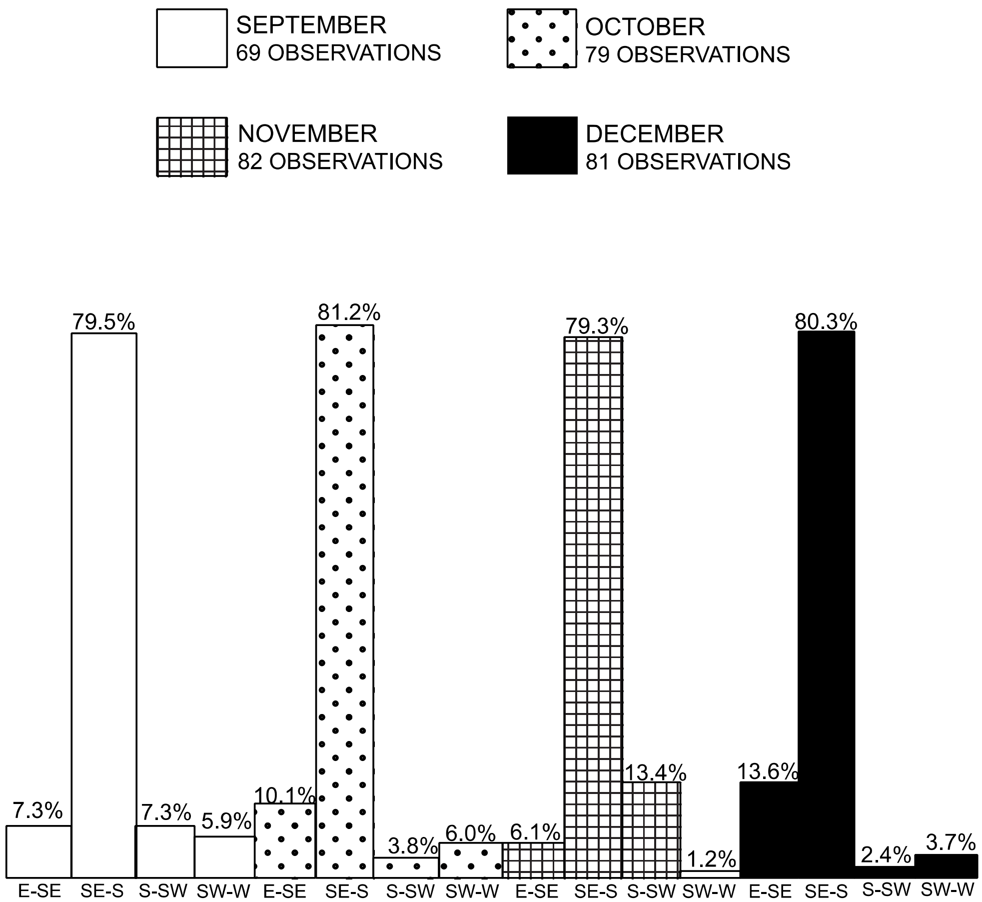


Figure 3. Distribution of southerly winds at the Naval Academy, Callao: September - December 1937.

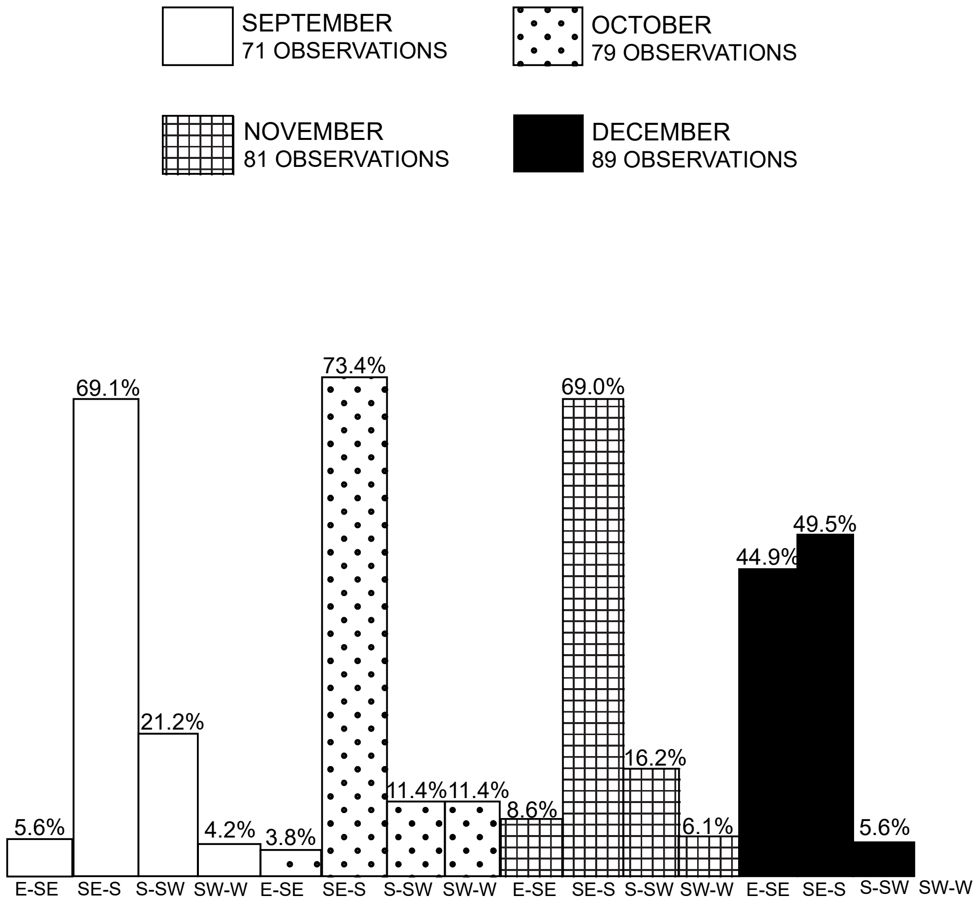


Figure 4. Distribution of southerly winds at the Peruvian Naval Academy, Callao: September - December 1938.

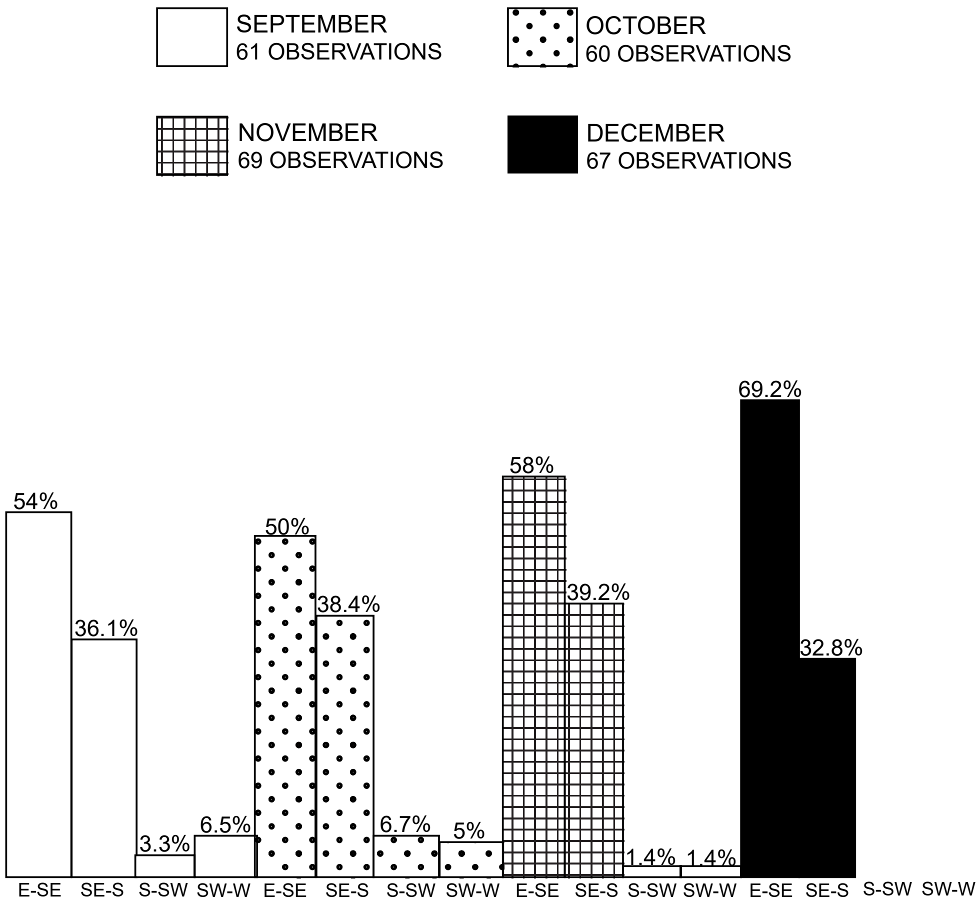


Figure 5. Distribution of southerly winds at the Peruvian Naval Academy, Callao: September - December 1939.

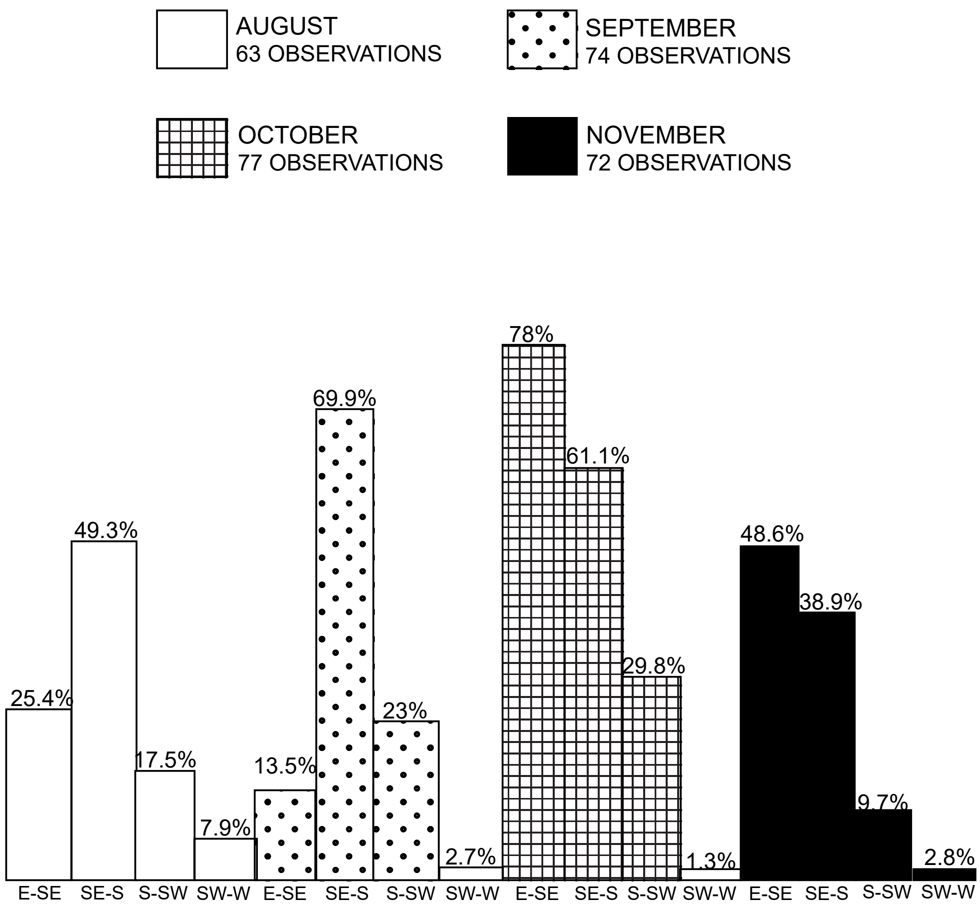


Figure 6. Distribution of southerly winds at the Peruvian Naval Academy, Callao: August - November 1940.

The direction of the wind is closely connected to local conditions and there is little uniformity from one place to another. In 1937 and 1938 for example, when the observatory of the Naval Academy at Callao recorded extensive westerly winds, El Alto had no reports of winds from the southwest.

Observations made on islands sufficiently far from the coast to escape convection winds are probably the most reliable keys to the general system of regional winds. The observations made on Chincha Norte showed little of the typical daily variation characteristic of the coast, which suggests the island's usefulness in monitoring winds affecting coastal waters. A series of observations on the guano islands would produce results of considerable value in understanding local meteorological, hydrographic, and biological conditions.

The south and southeast winds have been regarded as controlling the flow of the Humboldt Current and the upwelling along the Peruvian coast (Murphy 1936). A change in the winds, if one accepts this theory, would have serious consequences. Before discussing this possibility, however, it is necessary to summarize the oceanographic situation. The Peruvian coast, from Tacna almost to the Ecuadorian border, is bathed by water 10°C colder than normal in these latitudes (Murphy 1936). Movement of the water to the north is known as the Humboldt or Peruvian Current (I prefer the former since it is much better known, the area includes hundreds of miles of Chilean coast, and because the term "Peruvian" has no priority).

The movement of the water to the north is undoubtedly caused, in part, by the south and southeast winds of the region. It is also the result of the general circulation of the waters of the South Pacific. The winds originate from a high-pressure area, the Pacific Anticyclone, located several hundred miles off Valparaiso.

Whatever the origins of the Humboldt Current, it is clear that the waters are not of Antarctic origin, as has been erroneously stated by several authors. The current originates at the edge of the deep South Pacific and its waters derive from that region.

The low temperatures so important for human life and the lives of the coastal birds come from another source, a layer of deep water along the coast. This water has been little studied, but there is little doubt that it is the source of the low temperatures (Murphy 1936, Gunther 1936). These waters are raised to the surface by the phenomenon of upwelling.

Various causes have been cited for upwelling; all probably play some part. It has been said that the surface waters driven north are also moved offshore (Murphy 1936) and are replaced by cold waters from lower layers (Gunther 1936). Gunther (1936) explained upwelling as a process of "aspiration": southeast winds drive surface waters away from the coast and are in turn replaced by bottom waters so that the temperature decreases.

Bottom topography has also been cited in explanations of low temperatures (Murphy 1936). Since coastal waters flow toward the open ocean and are replaced by bottom waters, one could argue whether there is in fact a Humboldt Current. Perhaps it would be more exact to compare it to a conveyor belt, which winds around a cylinder whose axis is oriented along the coast from the island of Mocha (LaValle 1920) to Cabo Blanco. The cylinder moves counter-clockwise, raising deeper waters to the surface and pushing them offshore. At the same time, the whole system moves to the north. The extreme cleanliness of Peruvian beaches, in contrast to the beaches of the eastern shore of North America, supports the argument that most transport of water is offshore, rather than parallel to the coast. On the east coast of the United States, the beaches are littered by all sorts of flotsam, and the tideline is covered with refuse, wood, bottles, dead birds, and fish. In contrast, Peruvian beaches are spotless. Millions of birds die in the area each year and the beaches should be covered with feathers and bones. Birds that die at sea are swept offshore, as are those that die below the high-tide line.

The temperature of the sea, the biological implications of which will be discussed later, presents many anomalies, if one reviews the literature. According to Murphy (1936), the average temperature of surface water close to the Peru Coast is between 14.4 and 17.8 °C. Gunther (1936) noted sea surface temperatures within 20 miles of the shore fluctuating between 14.0 and 19.7 °C (these averaged 16.7 ± 0.231 °C with a standard deviation of 8.54 ± 0.98 º). Two hundred and fifty-eight temperature readings made on Isla Chincha North from 28 October 1940 to 3 September 1941 ranged from 14.9 to 24.0 °C with a mean of 18.9 ± 0.138 ° and a standard deviation of 11.75 ± 0.512 ° (Fig. 7). Thus, observations made by various investigators differed considerably.

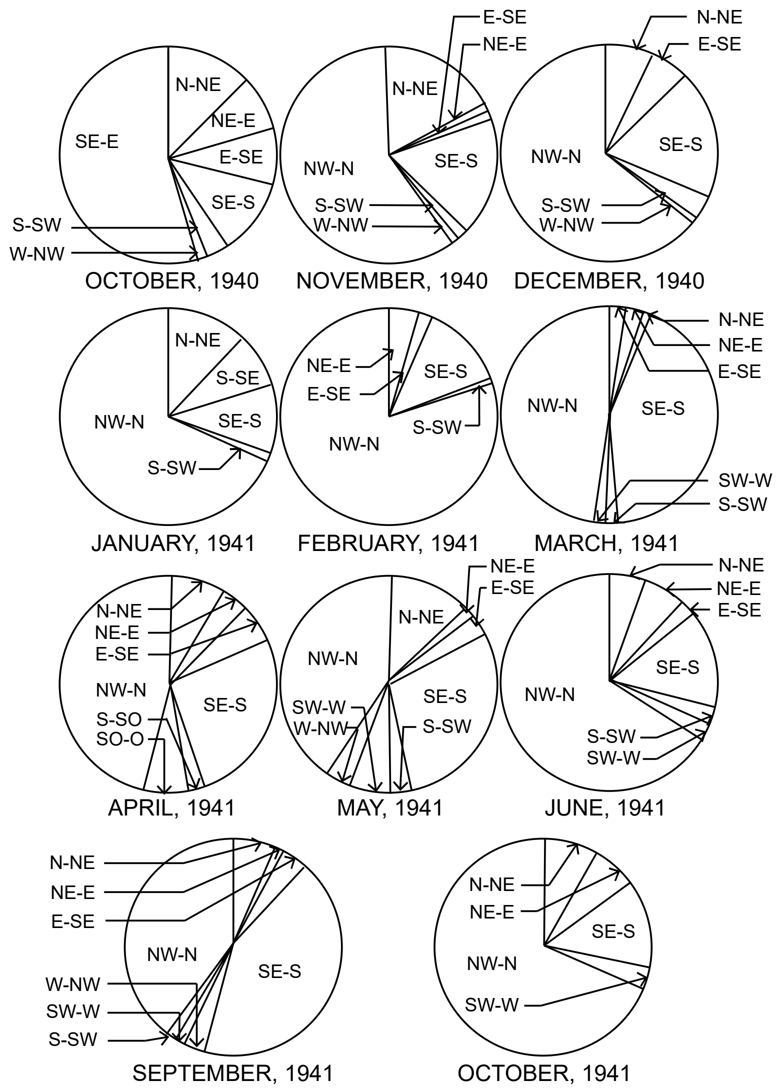


Figure 7. Surface current directions, Isla Chincha Norte: October 1940 - October 1941.

Conditions obviously change from one year to another. There may be periods of stability that last for considerable lengths of time, monitored by some studies, and then periods of instability observed by other workers. In addition, there are local variations that change from one year to another. Only intensive studies will clarify the situation. The problem is of great importance since it affects the abundance of birds and their food and, thus, the quantity of guano available for the prosperity of Peruvian farms.

These changes in temperature are accompanied by variations in salinity, nitrates, and phosphates. In some cases, the high temperature of the surface is simply the result of solar heating during periods of cessation of upwelling. This is probably what happened in the latter part of 1940 and at the beginning of 1941, at least in the Pisco region. At that time, we expected a thermocline (Sears 1941), but the temperature at 50 m reached 19° C. Another factor, which may have played a role during this warm-water period, was the incursion of warm water into the coastal waters from the north or the open ocean. This is a phenomenon known as El Niño.[1]

Much has been written in the scientific and popular literature about El Niño. There is the general impression that a marked increase in temperature along the coast of Peru is always clear evidence that El Niño is flowing to the south. However, my studies cast doubt on this. It seems probable that the warm water which reaches the central or south coast of Peru in years of marked climatic change such as 1851 (Bowman 1916, Murphy 1936) and 1925 (Murphy 1925, 1936) comes not from the region of Cabo Blanco but from the open sea.[2]

As noted previously (Vogt 1941), elevated temperatures in 1940 and in the first two months of 1941 were not accompanied in the Pisco region by significant southerly-flowing currents as would have been expected if the warm water came from the north. A current meter was installed on Isla Chincha North and daily measurements were made at 0600 h, 1200 h, and 1800 h. Observations from October 1940 to June 1941 (Fig. 7) clearly showed a northerly prevalence of the currents. However, there was a marked increase in the number of southerly currents during March, April and May. Figure 8 shows that sea temperature constantly increased during the preceding months, with southerly-flowing currents. During April and May when the currents came from the north, the temperature began to decrease. It is difficult to believe that El Niño, a current from the north, was responsible for the increase in the temperature. Gunther (1936) also suggested the possibility that the warm water has an oceanic origin. Figures 2 and 7 show a strong correspondence between wind and surface temperatures. During October to February, the proportion of winds from the east and adjacent quarters diminished while winds with a westerly component increased. Sea temperature also rose. In the middle of March, the temperature began to decrease (Fig. 8), and from March to June, there was a steady increase in the proportion of winds from the east. These winds would drive surface water away from the coast and augment upwelling. In view of these observations, it is impossible to accept a southward-flowing El Niño current as the explanation of the warm waters of 1940 - 1941. I am inclined to favor the incursion of oceanic waters as the cause, because sea-surface temperatures here are always higher in oceanic waters than in those closer to the shore.

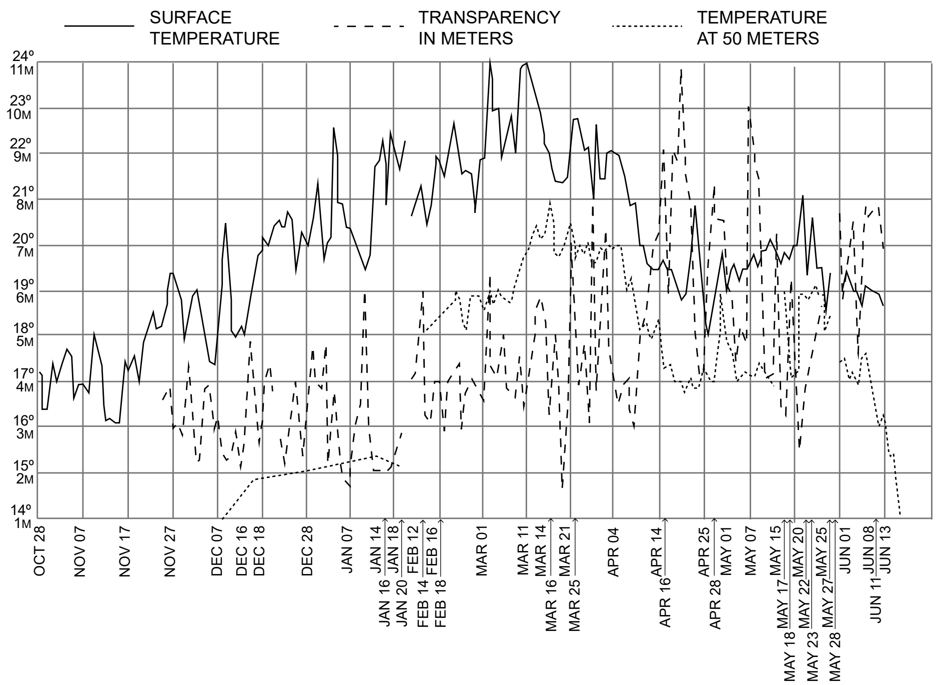


Figure 8. Sea temperatures at the surface and the 50 m and Secchi disc measurements of water transparency, Isla Chincha Norte: October 1940 - June 1941.

Currently, as I write this report, we are experiencing another regime of winds from the west (September and October 1941, Fig. 2) and sea temperatures are steadily increasing.

I had the luck, both good and bad, to have been in Peru during a period which has been almost completely "abnormal" (as I will explain later, this "abnormality" is a phenomenon that is repeated more or less regularly and ought to be considered as abnormal only in the sense that it occurs every seven years, on average). This has been a period of widespread nesting failure, food scarcity, the deaths of thousands of birds from hunger and disease, and a decrease in the quantity of guano harvested. The opportunity to study the phenomenon has been valuable; however, I still have not seen the normal conditions described by Murphy (1925, 1936) and Coker (1919, 1920, 1921, 1935) nor, even more important, have I had the opportunity to study the birds when they are at their maximum population or close to it. Therefore, it is extremely difficult to generalize, except for the period of my study, or to reach conclusions concerning an entire population cycle.

Environmental perturbations have been recorded in 1911, 1918, 1925, and 1932 (Murphy 1936). Less destructive perturbations took place between the larger events. The major events seem to occur approximately every seven years.[3]

In addition to these data, we should take special notice of the description of the Islas Chinchas and Ballestas in 1869, 70 years before the most recent perturbation. Dr. F.A. Lucas (in Murphy 1925) writes: "Birds were surprisingly few, not merely on, but about the islands. . . there were no birds occupying the tops of the Islands in 1869, none on little Blanca Islet, and none even on the Ballestas . . . Twice, a really large shark, ten or twelve feet in length, paid us a visit, and after nightfall ghostly rays could be seen gliding along in the depths, visible by the gleam of their own phosphorescence."

This has much in common with what occurred in the region of the Chinchas in 1939 (Vogt 1940). One of the enigmas of biological literature is the total lack of any mention of great numbers of birds along the Peruvian coast in the diary of Darwin.[4] He was too keen a naturalist to have missed the phenomenon of such numbers or to have failed to appreciate their significance. It seems highly probable that when Darwin visited the west coast of South America in 1835, the avian population had not yet recovered from a recent disaster. Presumably, based on the theory of seven-year cycles, the disaster of 1834 was very strong, perhaps comparable to that of 1891 or 1925.

By an extraordinary coincidence, Van Tschudi, Raimondi, Darwin, Lucas, Forbes, Bowman, Murphy and I worked on this coast in years, in accordance with the seven-year cycle, characterized by depressions in the bird population. Van Tschudi studied the islands in 1842, a year in which nesting failures ought to have taken place. Raimondi was in the islands in 1855, also probably a year of failure. It is possible that the seven-year cycle explains why von Tschudi, in the words of Murphy (1936), "failed to recognize the peerless position of the guanay," and why Raimondi wrote (quoted in Coker 1919), "It appears that cormorants do not contribute much to the production of guano." This same publication mentions an observation by Forbes that disagrees with current conditions: "In relation with the changes of the lives of the birds, it should be noted that there was an extraordinary disappearance of some of the main species in 1911." From his later observations, the birds appear to have returned before he concluded his observations along the coast.

One of the major problems of studies of animal populations is the lack of statistical data. A life insurance company would not be able to function without a vast accumulation of data on life and death expectancies of those wishing to be insured. To the naturalist, it is similarly impossible to reach valid conclusions without comparable data. The first step, in studying any animal population, consists of determining if possible how many individuals exist, what their growth rate is (their biotic potential) and an estimate of the mortality (the resistance of the environment). It is not by mere chance that the major steps in the study of the natural populations, as opposed to those of laboratories where populations are maintained under artificial conditions, have come from studies such as that of the long-term data of the Hudson Bay Company (Elton 1927). In Peru, we are fortunate to have data dating from 1909 (Anon 1941). These give satisfactory estimates of guano bird numbers for our purposes.[5]

Analysis of these data has certain disadvantages that have to be kept in mind. The data do not permit analysis by species. Over a long period of time, the guanay has provided more than 90% of the guano, so I have lumped all the birds as if they were guanays. This introduces what is probably a relatively small error, because the amount of guano varies in relation to the size of the bird. The second problem is that boobies nesting on cliffs are not included in the census because their guano is not harvested. For these reasons, the data refer only to guano-producing birds rather than the entire population. However, the second factor is probably also of little importance because of the preponderance of guanays.

These problems notwithstanding, the population figures (Fig. 9) are probably among the more reliable for any group of wild animals. The fluctuations can be accepted as an indication of changes in numbers from one year to the next. The population of birds was calculated in the following manner: 66 quadrants of 100 m^2 each were measured on various islands from Santa Rosa to Lobos de Tierra and the number of guanay nests in each was noted. The total number of nests in all the quadrants was 23,822. The average density of nests in each 100 m^2 was 313.9 ± 3.76.[6] This indicates the presence of 617.8 adults/100 m^2 at the start of the nesting season.

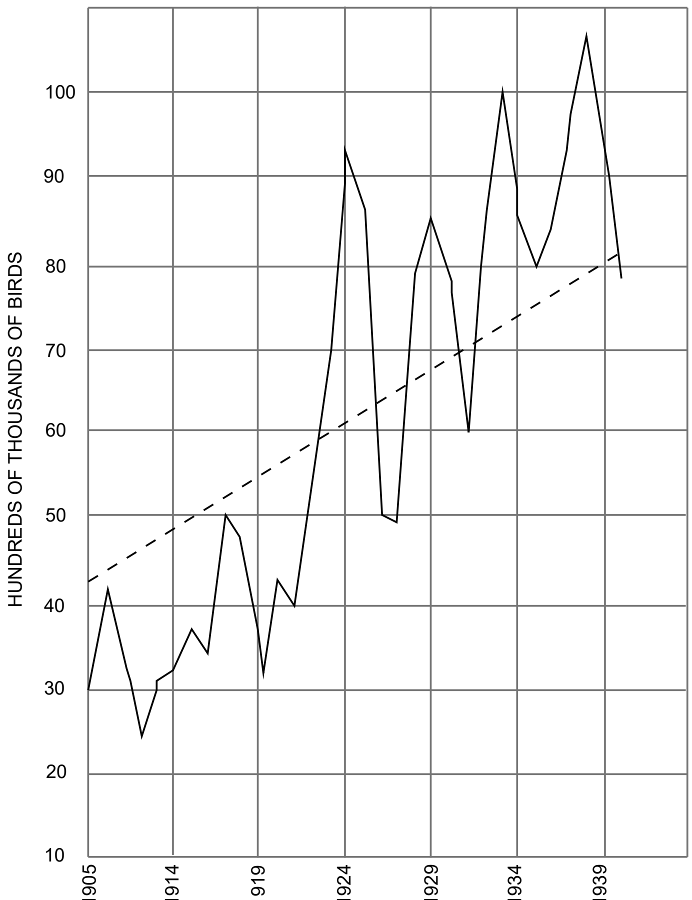


Figure 9. Estimated bird populations from 1909 - 1940, based on guano production.

To determine the number of birds, some period of the year has to be selected. It is customary that this period be the reproductive season. Two or three months after this, following the appearance of the young, the population approximately doubles. Since the food eaten by the young is brought by adults, the guano deposited by the young can reasonably be considered as guano deposited by adults. Before the next breeding season, there is a considerable mortality, when conditions are again similar for the estimation of the number of adults.

There is a major problem with this method. My work was done when the population was at a low point. It is possible that, when the population reaches its maximum, which will presumably occur in 1945 - 1946, the birds will exist at higher densities. However, if the standard error of the mean is considered, it is doubtful that, at the peak, the population will exceed the density measured. Even if we make the mean three times greater than at present, the increase in density would be less than three percent. In the Islas Ballestas, ten quadrants of 100 m^2 were set up and the guano carefully removed and weighed. The mean density of nests in the quadrant was 303.3 +5.57 nests/ m^2 (close to that calculated for the entire coast). Over two years, the 10 quadrants produced 19,293.1 kg/quadrant.[7] Each bird thus produced 15.8 kg/year of guano, so that 15,000 metric tons of guano would have been produced by 9,810,126 birds.

The bird population (Fig. 9) was determined by dividing the total harvest of guano in each year by 15.8. I do not know of a more precise manner to determine the population of the birds, except through annual aerial photographs. The present method also eliminates the difficulty presented by the biennial harvest of guano. All who have followed the progress of aerial photography during the current world war know that it provides a satisfactory means of estimating areas. This method would be equally satisfactory for nesting birds. This number could not be compared with the population estimates based on guano harvests because, during such periods as recently experienced, many birds did not nest.

Figure 9 demonstrates two outstanding phenomena. The figure indicates a steady increase in the average annual avian population, an increase of which the guano company can be proud. The rate of increase can be better seen by the smoothed curve (dotted line). It is doubtful whether any conservation organization elsewhere in the world has produced similar results in the same amount of time. This suggests that the methods adopted by the company in managing the birds are highly successful and that any change ought to be introduced only with great care.

The unsmoothed curve shows clearly, however, that despite the continued increase of the birds, there have been periods of population crashes. These, as I will show later, are probably inevitable. In my opinion, the problem has two aspects: first, how to maintain a constantly increasing population; and, secondly, how to reduce the magnitude of periodic setbacks. The unsmoothed curve shows that population decreases last for an average of two years. This is at least partially a result of the two-year delay in the statistics of the guano harvest. A decrease of the avian population and, consequently, of guano production, will be recorded in the harvests of two years because only half the islands are harvested in any one year. We know that the most recent nesting failure lasted two years but there are no data to indicate that this has occurred previously.

Most of the major drops in guano production, with only one exception, have occurred in the years of climatic perturbations already mentioned earlier: 1911, 1918, 1925, and 1939. In 1930, with a temporary change of the personnel of the guano company, the exploitation methods were altered. This was probably responsible for the anomaly in the curve. However, the seven-year cycle would predict a 1932 disaster. In that year (Murphy 1936), a large number of guanays appeared in the Gulf of Guayaquil, during a season of unusually intense rains, and thousands subsequently died.

These data suggest that the periodic catastrophic mortalities of the birds (Fig. 9) are connected with the cyclic fluctuation of the climate. The effect of these cycles on the birds will be discussed later, in the section on guanays, but certain climate phenomena, apparently common to all the cycles, ought to be mentioned at this point.

The years 1891 and 1925 (Murphy 1936: 285) were characterized by torrential and destructive rains.[8] Abnormal rainfall was also noted in 1911 (Bowman 1916), 1918 (Schott 1933), 1932 (Murphy 1936) and 1939, although rainfall was not as intense as in 1891 and 1925. High sea temperatures were registered in 1891 (Schott 1933), 1925 (Murphy 1936), and 1939 (Vogt 1940b). In fact, as Figure 7 shows, the high temperatures continued well into 1941. In recent months, temperatures as high as 26°C were encountered; these are much higher than noted by Schott in Pisco in 1891 and approximately the same as those recorded by Murphy in Mollendo in 1925.

A high proportion of the winds have been westerly during recent months, as mentioned earlier, and as noted by Bowman (1916).[9] Because of these, even with the few data available, we can suppose that these recurring periods are characterized by sea temperatures higher than normal, heavier rainfall in the north, and a greater proportion of westerly winds than normal. These periods occur at approximately seven-year intervals and we can expect them to continue. They seem always to have disastrous consequences for the birds. For this reason, we can expect a decrease in the guano bird population and in the guano produced. It is probably impossible to prevent this loss, but I believe it can be reduced. The biological results of the climatic cycle and the mode in which the birds are affected will be discussed later, as will methods for reducing damage.

Turning from the sea to the islands, we find ourselves concerned first with the aerodynamic problem. While this could perhaps best be examined by making a precise scale-model of each island and studying its aeolian characteristics using a wind tunnel, this method has not been practical, and we are limited to the data at hand.

It is obvious to anyone familiar with the islands that certain parts of them are suitable for birds while others are avoided. The area used in each case, divided by the total area of each island, can be taken as a coefficient of the efficiency of each island. If the data were available to determine these coefficients, and they can only be measured when the bird population is at its maximum, Santa Rosa and Macabi would probably show efficiencies greater than 90% while others such as Blanca and Tortuga would show efficiencies less than 50%. Some islands are almost completely suited for birds, so that they deposit guano over almost every square meter of available surface. Other islands are so hostile to the birds that the quantity of guano produced is small relative to the total surface area. This point is of considerable practical importance since it provides us with a means of improving various islands.

In theory, each island could be as productive in relation to its surface area as is Macabi at present. The form and size of the islands are so varied that one can encounter, on the same island, variation in wind velocity and in temperature that differ more than do coastal meteorological stations hundreds of kilometers from each other. Figure 10, which should be examined in conjunction with Figure 1, shows the maximum daily temperature recorded by thermometers placed on the ground without shading from the sun, at three stations on Isla Chincha Norte between 15 November 1940 and 6 January 1941, the most important nesting period of the birds. Station G was situated on the south side of the island, exposed to the south and southeast winds, but not their full force. Given that the readings were made during a period when the southeast winds were extraordinarily frequent (Fig. 2), temperatures at Station G may have been lower than in other years. This station was at least 100 m from Station K which was located on the side of a hill and was sheltered from the full force of southerly winds. Station L was on the north side of the island and was completely sheltered from southerly winds. While temperatures at Station G varied from 28 to 42.5 ^{0}C, with a median of 34.7 ^{0}C, the temperature at Station L fluctuated between 36.2 and 50.1 ^{0}C, with a median of 43 ^{0}C. As expected, Station K was intermediate between the other two stations, with a temperature between 30.1 and 44.8 ^{0}C, with a median of 37.6 ^{0}C. The effects of such temperatures on the birds will be discussed below.

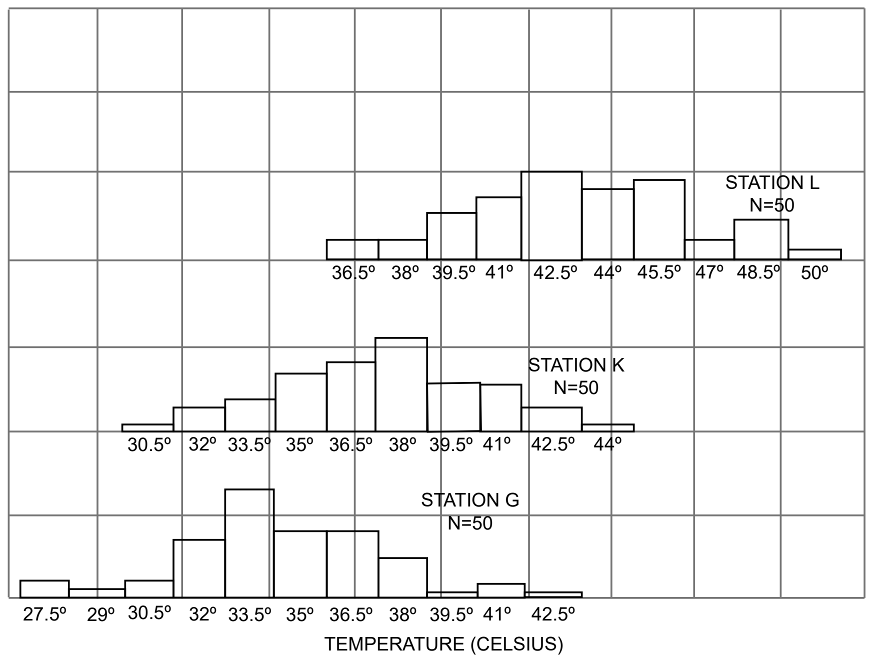


Figure 10. Maximum surface temperatures at three sites on Isla Chincha Norte: 15 November 1940 - 6 January 1941.

Flat islands such as Macabi and Santa Rosa present conditions over their entire surfaces comparable with conditions at Station G, while an island like Tortugas, with its ridgeline running east to west, has its northward-facing slope completely deprived of wind, with temperatures similar to those of Station L. San Gallan, which has a southward-facing cliff, should have temperatures similar to those of Station L over the rest of the island. All the temperatures mentioned above were taken from bedrock or guano. Temperatures on dark gravel were much higher, up to 7 ^{0}C. San Gallan and La Vieja islands, which are covered by such gravel, are not used for nesting by guano birds.

It is possible that temperatures on the islands change from one year to the next. When winds come from the south and southeast, the extreme eastern part of Isla Chincha Centro is very cool, but Chincha Sur blocks such winds from reaching the western part of Chincha Centro. In contrast, when the winds are from the southwest, the extreme western part of Chincha Centro is cool while there are high temperatures on the eastern part. An island such as Santa Rosa that is almost flat and level will be cooled by winds from any direction, except for a small area at the extreme southern tip of the island that is screened by a slight elevation.

THE BIRDS AND TIME

We do not know how long the three species of guano birds have existed on the Peruvian coast; however, it has probably been many thousands, perhaps hundreds of thousands, of years. Eggs buried in ancient guano at Mejillones (Chile) are believed to be those of Peruvian Boobies whereas others found at Taropoca came from Guanay Cormorants (Murphy 1936). A million years does not seem an excessive period for the community's existence. As Murphy has suggested, study of the Chilean nitrate caps would settle the issue.[10] However, for our purpose, the antiquity of the species is of academic interest. In considering how best to conserve the birds, it is sufficient to know that the birds have lived in Peru for hundreds of generations.

The birds, like all living organisms, are very much the products of their environment. Nature has, through its influence on genetic patterns, brought the birds to the condition in which we know them. Offspring that diverged from these patterns have died off. Those with the appropriate patterns, such as nesting in large groups, have survived and passed along their genes. If man does something that interferes seriously with these basic patterns, the birds would suffer the consequences and perhaps go extinct. This has occurred elsewhere in the world and even in Peru where such species as the Peruvian Diving-petrel (*Pelecanoides garnotii*), believed to have been an important guano-producer in the past, is now found in only small fractions of their former numbers.

Birds were probably nesting on the islands before man first reached the west coast of South America. The effect of man's arrival on the original biological equilibrium can never be known. Whatever the impact, the birds lived in association with the original inhabitants of the area for sufficient time to reach a new and favorable relationship before the arrival of the Europeans. Early Spanish writers reported that the birds were present in enormous numbers.

It would be of considerable interest to know the relationship that existed between the original human inhabitants and the birds. Guano has been harvested for centuries. The oldest evidence of this seems to be mummies covered in guano that have been encountered in Paracas. Whether the guano was used as a preservative or had some other use is unknown as far as I can gather. Guano birds made a great impression on the Inca and pre-Inca people, based on the numbers of cormorants, boobies and pelicans depicted on pottery and textiles. There is a huaco pot in Chiclín that shows a balsa raft next to a guano island, identifiable as such by the presence of characteristic nests.[11]

The oldest and most famous reference to guano, its use, and conservation is that of Garcilaso de la Vega: "On the marine coast from Arequipa to Tarapaca there are more than 200 leagues of coast on which they use no other fertilizer but that of seabirds, large and small, that travel in groups so large that they are not believable unless seen. They nest on uninhabited islands along that coast and so great is the guano that they produce that it is also unbelievable. From a distance the guano masses appear as peaks in some snow-covered mountain range. In the time of the Inca kings there was a strong policy of protecting the birds during the nesting season. No one was allowed to visit the islands under penalty of death so that the birds would not be frightened from their nests. It was also illegal to kill the birds at any time on or away from the islands, under the same threat of death as punishment" (Garcilaso de la Vega 1609, in Murphy 1936).

This passage has been frequently cited and, in my opinion, often misinterpreted. It is generally believed that the Incas had a highly developed conservation system; that coastal agriculture was based on the use of guano; that the Incas used all the guano deposited, and that, in consequence, the great deposit so wastefully collected and shipped in the 19th century was the guano accumulated only between the civil wars that preceded the destruction of Inca civilization by the Spanish and the beginning of guano mining.

It should be noted that, according to Garcilaso, the guano was used in the coastal sector between Arequipa and Tarapaca, a region that has not a single guano island of importance. If we take his narrative at face value, we must suppose that the guano had to be transported from the north in boats and that, as a consequence of the geographic limits he mentions, guano was not employed farther north. If it had been employed in the north, would there have been sufficient to transport to the south? Garcilaso refers to mountains of guano. If the Incas used guano to the extent that it is currently employed, then mountains of guano could hardly have accumulated.

Corroboration of Garcilaso's narrative comes from artifacts buried in the guano. Some of these artifacts, however, such as those in the possession of Mr. Francisco Ballén, are obviously of colonial origin. As far as I know, no artifact has been found deeper than the 10 m cited by Hutchinson (Murphy 1936: 292).[11]

If one considers the system of primitive exploitation of guano and compares this with practices at present, it seems likely that the Incas used only a small proportion of the guano deposited. The highly efficient operations of the present guano company are due in large part to the employment of a large fleet of tugboats, steamers, and motor vessels. Working with every possible machine, with modern means of transport, harvesting the islands with tractors, rakes and even railroads, the company can barely extract the annual increment of guano between successive breeding seasons.

The Incas were magnificent engineers and had one of the most highly developed social systems in human history. They achieved, given time, results that are almost unbelievable. But, especially in view of Garcilaso's comment that it was a capital offense to visit the islands during breeding, I cannot conceive how the Incas, with primitive rafts, however large, could have extracted all the guano deposited in a breeding season, especially when all the work would have to have been done in winter, a season of rough seas.

Some contemporary investigators have concluded that the Inca Empire depended on guano to the same extent that today's agriculture does, based on the necessity of frequent fertilization of cultivated soils to avoid their rapid impoverishment. However, it should be recalled that a new and very important factor in recent times in Peru has been the export of agricultural products. The Incas harvested guano only for their own consumption. The modern farmer produces with the aim of increasing his capital. Therefore, each hectare devoted to cotton, sugar cane, flax, or any other export product reduces the space available to satisfy the internal food needs of Peru. In addition, the Incas maintained their fields in much better condition than is usual in many parts of the country today. Presumably, also, a much greater proportion of food production occurred in the mountains. Without intensive cultivation for export, there was much less risk of ruining the soil, with a corresponding reduction in the need for fertilizers.

I am in general agreement with Murphy (1936): “It should be pointed out that it has never been possible to determine the age of guano strata on the Peruvian islands by the simple process of dividing the total depth of a deposit by the thickness of the yearly average increment. If Chincha guano had a depth of 50 m, and if the annual new layer amounted to five centimeters, only a thousand years could have passed since the beginning of the process. There are several imponderables here, however, of which the most important is the fact that the guano supply ages ago became heaped up on the islands until the slopes had reached the extreme angle of repose. The entire mass, therefore, lay characteristically in the form of a great lens upon the flatter parts of any given island—thick at its center, thin toward the edges where it crumbled and dropped away into the sea, with the result that the natural loss, from centrifugal pressure, wind erosion, and the constant treading, scratching, and wing-beating of numberless birds, fully balanced the gain.

"As for the guano-mining operations of the prehistoric Indians, who are estimated to have taken about three hundred tons a year from the Chinchas alone, it is possible that the total for the entire coast may have amounted to a thousand tons or more annually. The effect of such moderate and well-distributed withdrawals would, however, be negligible."

If one considers the quantity of guano in the 19th century as the result of an uninterrupted accumulation from the time of internal conflicts of the Inca Empire shortly before the Spanish conquest, it should be remembered that during much of the colonial period, guano extraction continued. Murphy cites references to this from the years 1716, 1748, 1804, and 1925. Dr. Basadre (1941: 250) pointed out that after 1840, "Guano was a commodity liberally extracted in Peru." Even these extractions left the island heavily covered, as 23 million tons were estimated to exist on the islands in 1847.[12]

At this stage, it would be useful to consider the state of the islands before exploitation began on a large scale. What were conditions like thousands of years ago when the birds reached their population limits for the first time, before man began to be a major factor in their lives? We know from geological evidence that there have been no large-scale changes in the climate of the coast for thousands of years. Consequently, the guano accumulated until it reached a critical slope angle, as suggested by Murphy, and the birds were able to breed relatively free of disturbance, generation after generation.

The islands were very different from what they are now. Instead of presenting rugged, steep slopes avoided by the birds (LaValle 1925), the islands were covered by thick caps of guano. These caps undoubtedly filled all the gullies, so that such areas did not exist as they do today, unusable by the cormorants because of excessive heat (see below). No bird had to lay its eggs on bare rock; there were always old nests with high rims that provided ample protection for the eggs and young. Nor was there a lack of feathers and other material for the construction of nests. The present-day problem of loss of eggs and young because of inadequate nests probably did not occur. Because the islands had the form of domes made of solid guano, they presented a natural aerodynamic profile that provided the birds with more extensive suitable nesting habitat than is available today.

The animal communities on the islands also differed greatly, both in relative abundances and in species-composition, from what we know today. Despite the obvious errors of Von Tschudi (1852) and Raimondi (1876), it is clear that burrowing avian species were much more abundant in the first part of the 19th century. There were vast numbers of the presently-scarce diving-petrels and penguins. The burrows of these probably covered the surface of the island, undoubtedly contributing to the erosion mentioned by Murphy.

The burrows also provided hiding places for the lizard (*Tropidurus peruvianus*) and since, as we shall show below, the lack of such refuges constitutes the principal factor limiting the abundance of these reptiles, lizards were probably much more abundant under pre-exploitation conditions. If the ectoparasites of the birds were the principal food of the lizards, then a greater population of lizards would have led to reduced populations of ticks, Mallophaga, and bird flies. The numbers of scorpions would also have been much higher. Whether the same can be said of spiders is debatable: they were probably less common where there were many birds because of their fragility and the small size of their refuge holes.

Gulls were probably much more numerous than they are today, as were sealions. There were no human attempts to control numbers of these species, but despite this, guano bird populations were sufficient to produce guano deposits of more than 50 m on the islands.

When we discuss predation, it would be useful to remember that, while conditions on the islands were probably much more favorable for the birds than they are today, the guanay, booby, and Peruvian Pelican may have experienced different feeding conditions. We have no direct data. Humboldt Penguins (*Spheniscus humboldti*), Inca Terns (*Larosterna inca*), Peruvian Diving-petrels, and perhaps other species, were so abundant that Raimondi (1876) listed them among the most important producers of guano. Competition for food may have been more intense than it is today. If this was the case and if the total avian population has subsequently decreased, an excess of food would be available for any increase in the numbers of guano birds.

On the other hand, it is possible that a new equilibrium has been reached in the past hundred years. The three species of guano birds have been increasing, apart from occasional setbacks, at an astonishing rate since the formation of the guano company (Fig. 9). The annual slaughter of tens of thousands of sealions has resulted in an alarming decrease of this species. Since a considerable portion of the diet of the sealion is bonito and other fish of similar size, the unrestricted slaughter of sealions may have resulted in an increase of bonito that feed primarily on Peruvian Anchoveta (*Engraulis ringens*).

Together with other changes in the environment caused by the arrival of Europeans, new diseases may have been introduced. This often occurs when Europeans come into contact with other human races and it is reasonable to assume the same for wildlife that are in contact with domestic animals.

Preceding the Spanish Conquest, it is likely that the guano birds were adapted to local avian diseases and had acquired a certain degree of immunity. The Spaniards brought with them Asiatic Jungle Fowl (*Gallus bankiva*) from Europe, as well as ducks, turkeys, and geese. These birds probably brought bacteria and other parasites with them. For years, domestic fowl have been kept on the islands and their diseases may have been one of the causes of the periodic sharp decreases in the curve in Figure 9. In other words, the introduction of these foreign birds increased the resistance of the environment without increasing the reproductive potential of the guano birds. With time, the guano birds may have developed a certain degree of immunity to such diseases; nevertheless, the guano industry should make every possible effort to avoid exposing guano birds to new sources of infection. This problem will be discussed in more detail below.

There is no doubt that, at times, as will be shown in the section on the guanay, birds starve by the tens of thousands, as do other species of the Humboldt Current. On the other hand, judging from the fishing methods of the guanay, there is generally an abundance of food. When feeding conditions are good, the birds can feed to excess, but we also know that conditions can change rapidly and, at times, catastrophically for the worse.

The fundamental reason for the abundance of burrowing birds in the past was, of course, the cap of guano into which to burrow. Today the cap is removed each year, and there is no place for penguins and diving-petrels to scrape their holes. The three guano species, the guanay, booby, and pelican, completely fill the islands when these species are at their upper population limits. In terms of guano production, it would not be an advantage to the guano company to increase the presently low populations of burrowing species.

The guano birds developed over a long period under conditions described above. The birds are not intelligent, but instinctive. If, to adapt to new conditions, they have to change their habits, the change will be insignificant. Since they are adapted to a previous environment in which they reached high densities, the previous environment is the one most suitable for the birds. Therefore, as the birds cannot change in response to new conditions, conditions should be changed, where possible, to those most appropriate for the birds. This will be discussed at greater length below.

To complete the history of the interactions of the birds and man, we should briefly review events from the first half of the 19th century. This history is too well-known to require details.[13] When the market for guano boomed, little or no attention was paid to the birds that produced the guano. Guano was supposedly unlimited, to the point that men were employed to scare off birds that tried to nest. The exploitation of guano by independent contractors placed the islands under the jurisdiction of men without any responsibility for the birds. The tragic outcome was inevitable. The guano was exhausted and birds were persecuted for so many years that, by the end of the 19th century, they had declined to their lowest point ever.

With the foundation of the Compañia Administradora del Guano, the guano company, the prospects of the birds changed for the better. Their populations began to increase and this trend has continued for over thirty years with the clear possibility of continuing. Time will confirm or invalidate my belief, but there is every reason to expect a continually-renewed guano resource for Peru in the future merely by maintaining or improving the present management of the guano islands.

THE GUANAY CORMORANT

The Guanay Cormorant has been called the most valuable bird in the world. If we were to give a price today to all the guano deposited by the guanay, it would surely exceed a billion dollars; however, assigning a definitive value is itself open to question. The guanay is the most important producer of guano in Peru and, therefore, a major source of national income. It is a resource different from minerals in that it is perpetually renewed. As such, it should be considered not only as a current resource but also as a resource for a century from now. The human population of Peru is increasing as is the demand for food. The protection and increase of a bird population which produces so many thousands of tons of fertilizer each year are important for the entire nation.

The life history of the guanay is complicated. Since the management of any species is never on completely firm grounds unless based on a thorough knowledge of its life history, I will discuss this topic at some length.

The guanay is one of the most gregarious of birds, often forming congregations of several million. These can be considered, within certain limits, as social groups. However, the cormorants are not social in the same sense as are some insects with different casts and division of labor. Nor are they comparable in terms of sociality with the megapodes of Australia in which a single bird cares for eggs laid by a. number of females. The sociability of the guanay is much more incidental. The responsibilities fall on all the birds and are not confined to one individual.

With occasional exceptions, guanays usually spend the night on land, on islands when these are available, or on points and coastal hills during irruptive flights. During this stage of their life, they are kept in groups by two factors: the relatively limited space on the islands and the shoaling habits of the anchoveta, which constitutes their food. Except during the breeding season, the guanay is a complete "hedonist," concerned only with its own well-being. The scarcity of nesting places forces guanays to form enormous groups when they are on land. This habit of aggregation holds great value for survival and will be discussed in detail in connection with the breeding cycle.

Guanays also feed in large groups, at times up to a million or more individuals. Some investigations claimed that foraging birds have developed a social sense of responsibility and that small bands sally forth in the early morning, locating the schools, and returning to the island to lead the flocks to the fish. I have paid special attention to this theory for two years and I have seen nothing which would confirm it. For example, I have observed that birds leave the Chincha Islands in the morning, when I could see clearly that the birds of the Ballestas Islands were feeding near the Ovillos (Isla Blanca) in Paracas Bay. Although the Ballestas flock could be seen with the naked eye and feeding activity was visible with binoculars, the guanays of the Chinchas paid no attention to the birds feeding near the Ovillos. Considering the general superiority of avian vision compared to that of man, flocks leaving the Chinchas must have been able to see those feeding near the Ovillos. However, the Chincha Island birds, instead of flying to join the feeding flocks, flew to the north, toward Cerro Azul. They did not return until well into the afternoon, indicating that food was either scarce or distant, or both.[14]

Feeding activity differs from one day to the next. One day the birds returned early, after having fed in one direction, indicating that they found sufficient food, but the next day, they left the island in a different direction and returned late. Food encounters seem to be a matter of chance. Guanays seem to have no memory from one day to the next of where they have found food. (Parenthetically, one ought to mention that when the birds return early to the island it is because they have found enough to eat. This is easily observable when birds are feeding near the island. The birds return to the island in less than an hour under these conditions.)

Additionally, the anthropocentric concept that the birds have leaders should be abandoned. This very old idea has been applied to a number of species, but it does not apply to the guanay.

Foraging groups of guanays are possible only because of the enormous schools of anchoveta. If it were not for these, the law of diminishing returns would operate. It would be so disadvantageous for birds to feed in large flocks that they would cease doing so and the flock would break up into smaller groups. In contrast, larger shoals make it advantageous for the birds to fish in larger flocks.

The birds descend on anchoveta schools in voracious hordes. Naturally, the birds in the front can feed most easily. Those at the back of the flock show a constant tendency to move forward. This gives the flock a circular movement and at the same time keeps the fish in a dense school. The action is very similar to a fishing net which is drawn ever tighter. This makes the food more available for the birds so that they can feed more rapidly and move on to another school. When such feeding takes place close to the shore, the anchoveta are frequently forced out of the water, so they become stranded on the shore. This does not mean necessarily that anchoveta are abundant; it indicates only that the anchoveta were attacked under unfavorable conditions for their survival.

Only once have I seen a possible social behavior, in the sense that the individual acts for the benefit of the group. In times of food scarcity, an adult occasionally returns with a certain amount of fish and is overwhelmed by such a number of young from other nests that it is forced to regurgitate part of its stomach contents onto the ground where it is immediately gathered by the nearest young. This behavior may act for the good of the species by making food available to the colony as a whole through the action of the most skillful or strongest adults.[15] Regurgitation by young birds may serve the same purpose.

Although in Peru the birds have no enemies on the islands (we will discuss this below), this is not true at all other locations and it is possible that birds of prey eat the prey regurgitated by the guano birds, instead of eating the birds themselves. This requires additional study.

At times, flocks of birds have arrived at the island late at night, suggesting that the birds are occasionally active at night. These flights were noted at or close to the full moon, suggesting that guanays can take advantage of the light to search for food. During night-ringing of adult guanays on Isla Chincha Norte in 1939, birds ran on the ground but did not take flight. Consequently, nocturnal flights appear the exception, rather than the rule.

In the months before breeding, the birds move continually. Where they spend the night depends on the food supply. If food is not available, there is no reason to remain on an island and the birds move on. This explains, in large part, why one island can be occupied and another abandoned in the space of a few hours, by hundreds of thousands of birds.

When food is found very near an island, a guanay can make more than one feeding trip per day. But normally, or at least during my studies, food was not so easy to acquire, and feeding normally occurred only once a day. Guanays left in the morning, more or less together, departing in one direction between 0600 and 1030 hours and returned between 1200 and 1800 hours.

Guanays normally breed once a year. I have no evidence that they breed more often. The peak of nesting can be seen very clearly in the reports of the guards on the islands (Fig. 11). Reproduction of the guanay takes at least four months: approximately one month in courtship, one month in incubation (including laying), and two months to raise the young. To have two clutches a year would make normal development of the young impossible, given the importance of October - December for egg laying.

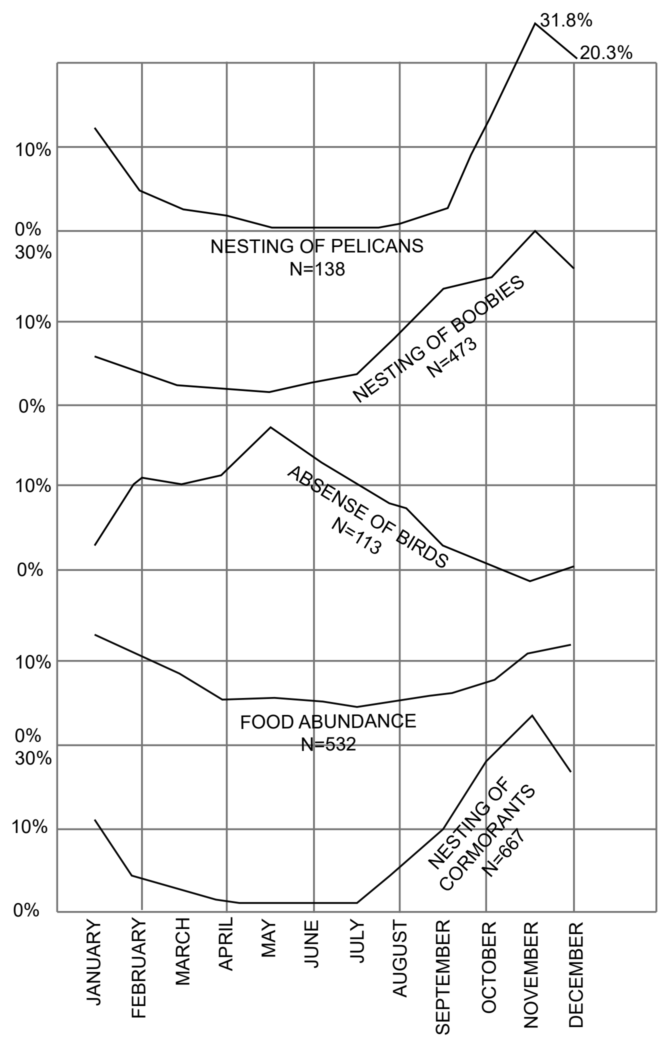


Figure 11. Monthly reports of nesting by Guanay Cormorants, Peruvian Boobies, and Peruvian Brown Pelicans in relation to reports of food abundance and absence of birds.

Guanays have nested during other months of the year but these may be birds which had been interrupted in their breeding at another location and were only completing their cycle. This appears to be the case when birds arrived at an island in great flocks and laid their eggs after only a few days, omitting the normal courtship period. Other egg-laying in the course of the year may include second clutches, but those are not typical or proven.

Outside the breeding season, birds do not associate in pairs or families. It is also doubtful whether a pair can recognize each other away from the nest site.

There has been a lengthy debate in the scientific literature over the last two decades concerning the periodicity of nesting of birds. As is well known, avian sexual organs shrink after the breeding season and grow as the next season approaches. The value of this is obvious; the egg-producing organs are so large and heavy in relation to the total weight of the female that gonadal reduction following the breeding season has a significant biological advantage: the females have less weight to carry. Various causes have been cited as responsible for these successive increases and decreases of sexual activity. In the northern hemisphere, changes have been connected with the increase and decrease of light and with day-length. Finally, in social species, they have been linked with sexual stimulation originating from intense courtship activity in large aggregations (Darling 1938).

During the year, there is so little variation in the duration of the day along the Peruvian coast that changes in activity periods probably play little role in regulating the size of the gonads. Whether variation in sunlight, determined by cloudiness in winter and clearer days in spring, plays a part cannot be determined without more experimentation than I have been able to do. However, the factor seems worth investigating, given the concentration of nesting in the months of intense radiation. Whatever the outcome, it is clear that the size of the gonads of the birds varies during the year.[16]

The nesting cycle, strictly speaking, begins with the choice of a nest site by the male. I use the term "territory" to designate a nest site even though it is not certain that the nest site of the cormorant fits the usual definition: the "territory" holder does not try to announce his ownership, contrary to the definition of territory by Mayr (1935). Additionally, while the adults may defend the territory, they are at times extremely tolerant of intrusions, in contrast to other birds with true territories.

The nesting site is chosen by the male. Criteria for selection of a site are not obvious if one excludes the ecological generalities mentioned below. The nesting flock grows outwards. The first males who feel the reproductive urge form a nucleus; additional birds establish themselves at the edges of the group. It is common to see hundreds of males, unpaired but ready to mate, at the edges of colonies. After a colony reaches a certain size, it is very rare to see a male without a mate within the colony. An unpaired male within the colony has less chance of securing a mate than one at the edge, since single birds which do wander into the colony are constantly attacked by territory-holders. Unpaired birds are rarely seen in the colony, except those returning to nest after feeding or collecting feathers for nests, or those awaiting the return of their mates.

Sexes in the guanay are relatively difficult to distinguish, except during the breeding season when the distinctions are obvious, contrary to what has been previously published. The male has a head and neck of almost chestnut color while the same parts of the female are more bronze-colored with a faint green tinge. The male may have some of this color but not to the extent of the female. During the nesting season, the tissues above the bill and eyes of the female become swollen so that they appear to be eyebrows. The forehead of the male remains relatively flat. Finally, the crest is more developed in the female than in the male; frequently the latter has only a trace of a crest.

After the male has chosen a nest site, he announces it, along with his own availability, to the neighboring birds by means of characteristic sounds and behavior. He stands on the site and attacks other males with his beak if they approach. At times, he pulls his neck back onto his back, with the throat facing the sky, until the head touches the base of the tail. After performing this, he emits a "quack" which reminds one of the sound of ducks. Although this display is undoubtedly stimulated by the presence of unpaired females, it must initially be motivated by an internal impulse, since he will perform even in the absence of potential mates. This activity is repeated with great frequency over a period of days. The male remains on his territory and defends it from other males except, of course, when he leaves to feed. I inferred that the same males returned to the same sites day after day because of the marked similarity of males at particular sites from one day to the next. There is enough variation between guanays so that it is possible to recognize individuals.

The display by the male continues until he is chosen by a female. Unpaired females roam the edges of the colony, approaching one male after another. When the female gets close to the male, she places her head next to his and bows. Often they do this together. Courting birds are so accustomed to close eye-contact that it seems likely that the green eyelids and red circumorbital edges are areas which attract the interest of the birds. This is something that can be resolved only by experimentation in the laboratory, but it presents a fascinating problem in the psychology of animals.[17]

As the female performs a bow with the male, her sexual impulses are clearly stimulated. She pecks at his head and neck, seizing his head in her beak, and at times attempts to mount him. However, the male is still not sufficiently advanced in the sexual cycle for copulation and, in hundreds of such encounters, I have never seen the male display the slightest inclination for sexual intercourse. Exactly how or when the female selects the male is still not clear. But, after the male has been displaying for several days, a female finds him to her satisfaction and remains with him; this constitutes what could be called “marriage.”

From this moment until the young are about a month old, the territory is normally not left unattended. When the female leaves to feed or to search for nesting material, the male protects the site and vice versa. Courtship continues for at least a month. At first the female takes the initiative. She initiates the bows and "ceremonies" to which the male responds almost like an automaton. When she lowers her head, he does the same as if they were bound together with invisible threads.

From the day they pair, the female solicits copulation, but in all the pairs I studied, the male showed no early interest in copulation. However, he seems very interested in "home-making," that is the construction of the nest. With his bill, he gathers pieces of guano, if the island has not recently been harvested. He leaves it to the female to arrange the stones, feathers, algae, rubbish, plants, or any other objects that could help protect the nest. The female also gathers material for the nest but her interest in nest construction is much less than the male's and her contribution is minor. Her basic interest is in courting the male and in copulation. She courts insistently and, as time goes on, with increased vigor. She reaches the extreme of bothering the male incessantly, making repeated bows with him, pecking, and mounting him. The scene is repeated incessantly but with no attempt by the male to make cloacal contact. Finally, the constant courtship of the female sufficiently excites the male to take an active part and the eggs are fertilized. The period between pair-bonding and the first copulation can last a month or only a few days. In the latter case, as already mentioned, the birds are probably those which have come from other islands after being disturbed. Such birds would have already gone through the initial stages of the cycle before taking up new territories.

Nesting material is a matter of considerable importance for the birds. They can be seen flying toward an island carrying feathers in their beaks, and on the nesting islands they use small objects to give strength to the guano of the nest. It is amusing and also a clear indication of the importance of such cohesive material to see a guanay walk 300 - 400 m towards a mound of vegetation, grab a piece, and then return to its nest. Nothing is too large if it can be moved, and many times I have seen guanays moving pieces of old guano sacks, stumbling over them and falling on their stomachs.

Nesting material seems more important than their eggs to the birds. I have frequently approached close enough to a nest that the bird incubating left it and did not return until I withdrew. But, at the same time, other guanays in search of nesting material approached the exposed nest to steal material. The impulse to protect the eggs was not strong enough to overcome the fear of man while the impulse to collect feathers, straw and pebbles was.

It was extremely difficult to obtain exact information on the laying of eggs. The birds did not tolerate repeated disturbance, despite my most careful efforts. In consequence, counting, marking, and weighing eggs daily invariably resulted in desertion. However, I can say the time between egg laying in a clutch is one - two days. The normal clutch based on a sample size of 89 is 3.13 ± .101. Incubation begins with the first egg and each egg requires 27 days to hatch. A nest of four eggs, laid at two-day intervals, requires seven days for laying and 33 days for incubation.

Both members of the pair share in incubation and the eggs are normally never left uncovered. A certain degree of courtship continues through incubation and what appear to be at least partial copulations continue daily until the young are three weeks old. Undoubtedly these relationships serve to maintain the pair bond, as has been noted by Huxley (1914) in his study of the Crested Grebe (*Podiceps cristatus*), and also perhaps to reinforce the bond with the nest site, at which copulation always occurs. Whatever the explanation, it is obvious that copulation serves a greater purpose than for the mere fertilization of eggs.

Guanays show no signs of group stimulation as described for Herring Gulls (*Larus argentatus*) by Darling (1938). Standing within a group of guanays and looking and listening to activity at neighboring nests, one encounters all phases of the sexual cycle. Generally, however, the intensity of activity increases from the center to the periphery of the colony. In other words, these manifestations are governed more by ecological than physiological conditions.

The first birds to nest on an island choose locations that are not only suitable for nesting but also have an abundance of wind (see Fig. 10). This first group will all be at approximately the same state of courtship. Owing to the method in which the colony grows, the birds which take up territories later will be birds that become ready for breeding later so that in the center of a large colony there may be nestlings, while at the edges unpaired males would be displaying.

The larger a colony of guanays, the greater the probability of nesting success, other factors being equal. The reason is simple. Figure 12 shows what can be called the curve of security of the guanays. This curve is nothing more than a representation of the values of a circumference of a circle and its area. The circumference increases proportionally more slowly than the area it encloses so that larger aggregations of nesting birds have proportionately smaller perimeters. This fact is important because nests at the edges of colonies will have lower nesting success.[18]

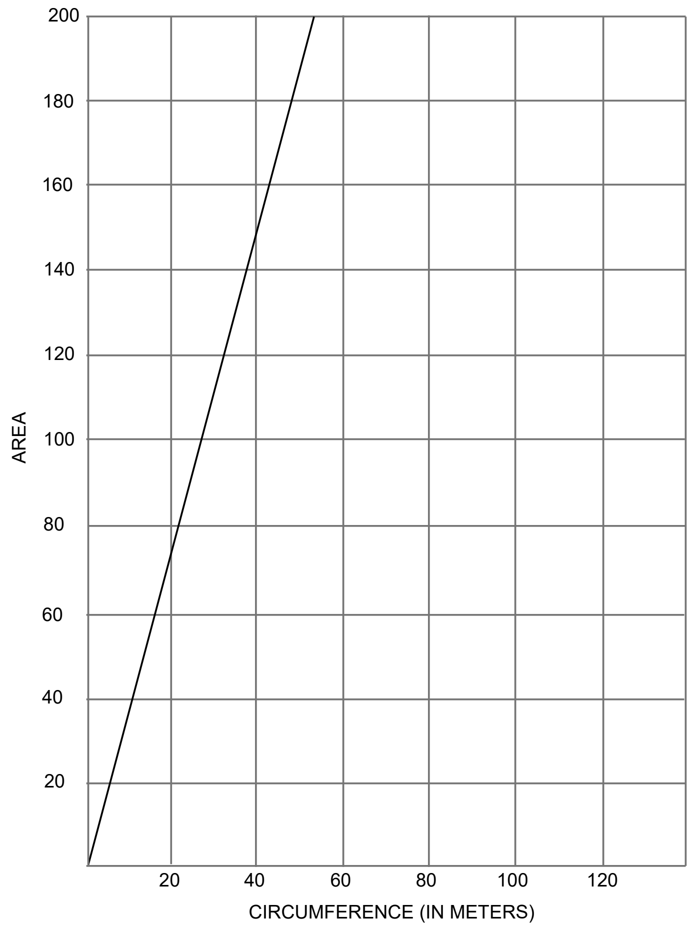


Figure 12. The relation between the perimeter and the area of a circle, illustrating that area grows much more rapidly than the perimeter.

Since groups grow from the center outwards and since birds occupy the most suitable places first, birds which arrive later may have less suitable territories at the edge of the colony. The borders of colonies are also the sites most accessible to predators such as Kelp Gulls (*Larus dominicanus*) and Turkey Vultures (*Cathartes aura*). As these approach the colony looking for eggs left uncovered, as occurs at times during territorial struggles, the predators are confronted by a multitude of beaks which wave menacingly, in the manner of bayonets. The possibility of landing and successfully robbing eggs among the defending birds is small. Nestlings are also much more secure within the colony than at its borders.

Nestlings occasionally reach the borders of their nests and wander away without the adults noticing. Additionally, when adults begin to leave them alone, while foraging, or during a period of food scarcity, the nestlings frequently crawl to the edge of the nest. Within a colony, a nestling attempting to leave its nest is immediately pecked by neighboring adults or nestlings and forced to return to the safety of its nest. In contrast, at the edge of the colony, where there are no birds to peck at adventurous young, these try to explore the world before a sense of home has developed and thousands of young are lost every year.

Finally, nests located at the edge of colonies are, for a large part of the nesting season, constantly under attack from adults seeking nesting material. Even when the owners of nest sites are present, feathers are constantly robbed. In the struggles which take place for nesting material, eggs and young are frequently ejected from nests and abandoned. So completely controlled is the guanay by its identification with its nest that its eggs or young can be twelve centimeters from the nest and the adult will make no attempt to rescue them. I have seen dozens of young, still not able to walk, abandoned, but I have never seen an adult recover its young. The sooner a nest becomes part of the interior of a colony, as the latter grows, the greater the probability that the nestlings it shelters will survive to fledge.

Group nesting has provided an advantage over thousands of years of nesting, selecting birds with the strongest impulse to nest in dense groups. This impulse, which may perhaps be called an instinct, can be seen every year when birds gather on an island, leaving adjacent islands vacant. This undoubtedly explains in great part why the Islas Ballestas, once the birds begin to nest on them, end up covered with birds while the Chinchas, which are so close, are barren of guanays. At other times, the reverse is true.

The seasonal distribution of nesting is extremely interesting (Fig. 11). This analysis is based on 667 reports of guanays with eggs and reports by guards on various isles since 1915. The distribution by months is shown in Table 1.

Table 1. Monthly percentages of reports of Guanay Cormorants nesting and reports by guards indicating that food was 'abundant.'

MONTH	GUANAY EGGS	ABUNDANT FOOD
July	1.9%	5.1
August	6.0	5.7
September	10.5	6.6
October	18.7	8.1
November	24.0	11.7
December	16.5	12.8
January	11.0	13.2
February	4.1	10.3
March	2.6	8.9
April	1.8	5.8
May	1.6	6.0
June	1.3	5.8

As expected, the flat curve indicating the absence of birds on the islands (based on 113 reports) is almost directly the inverse of the curve showing the presence of eggs. The strong correspondence between laying and reports of food abundance (based on 632 reports) is more surprising and probably of considerable significance.

The lag between food abundance and egg laying may be related to the time necessary for the incubation and development of the young. The greatest demand for food occurs when the young reach one month of age. The correlation will be discussed later, in relation to the environmental changes that occur during the year.

Laying slightly precedes the abundance of food. This correlation must have become established because of its great value in survival. The most difficult period of life for adults is, undoubtedly, the breeding season. During this time, the birds are attached to an island for some four months, in response to biological urges. They abandon the islands only under conditions of extreme stress and even, at times, as possibly in 1925, refuse to leave until too late and then die in large numbers (unfortunately the reports of island guards have been lost for 1925).

Outside the breeding season, the guanay can disperse, leaving one island for another when food becomes scarce. When they have young, the adults are confined to a certain flight radius of their nesting island, approximately one-half of what it might be, because one of each pair always has to be present to protect the nest. This restraint becomes less rigid after the young reach a month of age and both parents can leave to gather food, but, nevertheless, the adults must return to the same island, bringing food to the young, which have ever-increasing appetites. It would be strange if the peak of the breeding season did not correspond to the peak of food availability.[19]

Incubation is equally divided between the members of the pair. There is, however, a tendency for males to leave together to search for food and then for females to do the same; however, this is not an absolute relationship (a similar phenomenon has been encountered by Serventy [1939] in the Pied Cormorant (*Phalacrocorax varius*) of

Australia). Moreover, there is no diel rhythm as is found in some woodpeckers. Sometimes the female will incubate during the night and other times, the male.

The care of young, as of the eggs, is divided equally between members of a pair. Each brings food at least once a day, if available. If food is encountered very close to the island, feedings may be more frequent.

A few hours after leaving the egg, the nestling can lift its head and beg for food which it receives, semi-digested but still fairly whole, from one of its parents. From the first day of life, the nestling begins to exhibit an oscillating movement of the head which is characteristic of food-solicitation during the entire period of dependence on its parents. The neck muscles are still weak and the nestling has little control over them but its head shows a definite oscillation.

While this movement seems instinctive, in that it is done right out of the egg, the response of adults seems to depend to some degree on their experience. One female seemed not to know what to do with its recently-hatched young. When the small black head of the nestling stuck up below the adult, the parent turned its head more or less in the direction of the chick, but missed it repeatedly. The female bit the metacarpal articulation of its own wing and disgorged food into the nest before learning to feed its young. I concluded the female was very young and in her first breeding season.

The parents warm their young when the ambient temperature is low and shade the young during the hotter parts of the day. At times the adults fan the young with their wings to keep them cool.

The guanay is, according to Murphy (1936:100), a species derived from the Antarctic that probably reached the Peruvian coast by following the cold water of the Humboldt Current. High temperatures are undoubtedly one of the factors that limit its breeding range to the north, at the extreme southern tip of Isla Lobos de Tierra and adjacent islands. This is its geographical limit but there is also an ecological limit that restricts nesting of the guanay on all the islands of Peru. Every island along the coast includes areas that are as unsuitable for nesting as if the sites were many miles to the north of the Humboldt Current. These unsuitable areas represent an ecologically limiting factor that could, to a large extent, be eliminated by the guano company.

I have already indicated that microclimates, climates in small areas, show marked contrasts in their maximum temperatures on the islands. Guanays nest only in zones of low surface temperatures. At times, when an island is heavily populated, groups will try to nest in warmer areas but once the maximum temperatures of summer arrive, they desert their nests. Of the three zones mentioned earlier (Fig. 10), the birds used only those in the vicinity of Station G. They started to nest near Station K but the small size of the nests showed that they had been deserted after a few weeks. At Station L, they did not nest at all.

During the past autumn, I conducted a study on Isla Chincha Centro in which I marked out 10 quadrants. The density of nests per m^2 varied between 2.83 and 3.76. On eight clear and windy afternoons characteristic of the nesting season, I made observations in each of the 10 quadrants. Wind velocity was determined with a Fuess anemometer and the temperature of the guano was measured with a thermometer made by the Taylor Instrument Company designed to take human skin temperatures. The thermometer uses a thermocouple applied directly to the guano and is thus unaffected by sun or wind. It is so sensitive that even the slightest breath causes an oscillation. It shows the true temperature experienced by the feet of adult guanays or defenseless young.

Approximately three temperature readings were taken in each quadrant daily and their respective averages were correlated with the wind velocity at the surface, so that there were 80 mean temperatures and an equal number of wind velocities. Not unexpectedly, there was a negative correlation ($r = -.53$, $p < .01$) indicating that temperature decreased with an increase in wind velocity. It was not possible to determine if there was a direct correlation between nest-density and wind. Nevertheless, this seems very likely. As has been shown above, there is a marked difference in the surface temperatures, governed by the wind, between the areas where the birds usually nest (Station G); where they nest occasionally and later abandon nests, eggs or young (Station K); and where they never nest (Station L). The birds concentrate their nests in the most favorable parts of the islands where there is the most wind.

The exact manner in which heat affects the birds needs to be studied over a long period. Heat can limit the avian population through mortality of young. I have seen young fall from their nests many times after showing clear signs of heat stress: they lie, twisting on the ground, trying to crawl toward shade, and breathing with open beaks.

Lizards, as will be described below, cannot survive the direct force of the sun. It is difficult to believe that young guanays, featherless or with only partially-grown feathers and with thermoregulation still not well-developed, are much more resistant to extreme heat. To test this, I took a young guanay from its nest and placed it on the ground where it would receive the total force of the sun while sheltered from the wind. The surface temperature was more than 44.5 ^{0}C (the maximum temperature recorded has been 53 °C); the nestling died in a little over 20 minutes.

It is likely that the influence of microclimate upon the distribution of nesting birds depends on the effects microclimates have on eggs and embryos. Recently, an important study (Huggins 1941) examined the temperatures of eggs of wild birds under natural conditions by inserting thermocouples into incubated eggs and recording the temperatures with a potentiometer. Thirty-seven species of birds were studied in this manner, all of them belonging to more advanced orders than the Pelecaniformes. The average egg temperature was 34.0 ºC ± 2.38 º.

A decrease of 2.0 °C within a minute was caused by wind even when birds were incubating the eggs. There was a positive correlation between air temperature and the maximum temperature of the eggs overall: r = .4675 ± .0980; when birds were away from the nest, r = .4335 ± .09683; when birds were incubating, r = .6642 ± .0688; and for the average temperature of the eggs, r = .4934 ± .706. In other words, the temperature of the egg was clearly affected by air temperature, whether or not birds were incubating. If the same conditions occur on the guano islands, then guanays nest in windy areas (Station G) in order to protect their eggs against excessively high temperatures of the leeward areas (Station L).

This susceptibility of the birds to death from overheating reduces the available nesting space. Parts of almost all islands are unsuitable because they are windless or have sandy substrates that absorb more heat than do those of guano or rock. This thermal limit undoubtedly explains the frequent reports of nest abandonment on islands. Birds that during the spring are forced because of lack of space to nest where there is no wind abandon such nests when summer heat reaches its maximum.

It also seems very likely that, in years of abnormal winds, birds nest on north-facing slopes when atypical winds come from that direction, as happened recently on Isla Santa where the birds established territories and began to breed. When the wind reverted to its normal direction, the sites chosen for nesting were too hot and the birds abandoned them. The delay caused by renesting is unfortunate, since it causes the nesting season to extend into the part of the year when food is less abundant. Late-nesting pairs are also at a disadvantage compared to earlier-nesting pairs in which young are old enough so that both adults can forage, without one adult having to be present to defend the nest.

The high temperature of the substrate surface is undoubtedly the reason that a large island like San Gallan is not used by guanays. Its steep, south-facing cliffs impede the flow of wind so that temperatures on the island are too high for nesting. Isla Viejo, on the other hand, has windy surfaces but they are covered with black sand that results in high temperatures. It is not a matter of chance that two of the most productive guano islands, Macabi and Santa Rosa, are both almost flat and almost entirely exposed to wind. Heat is a limiting factor that falls within the possibilities of human manipulation so that a greater proportion of island surfaces could be improved and other islands made suitable for nesting as I will suggest below.

The feeding of nestlings depends above all on a strong territorial basis in that adults return to their nests with food and feed their young only at the nest. It appears that they do not recognize their own young. A guanay on a nest will peck at a nestling trying to enter the nest, until the nestling moves away. However, if a strange nestling is placed in the nest while the adults are absent, they do not seem to notice it upon their return.

Nestlings are also governed by territory limits until they are approximately one month old. If a nestling tries to leave the nest, unseen by its parents, or when adults are absent during a time of food scarcity, it is pecked by neighboring birds and forced to return to the nest. Nestlings older than three weeks also attack intruders and help defend nesting territories. At times, adults permit incursions by other birds with apparently complete tolerance, but it is impossible to determine when a trespasser will be severely pecked. The difference may be the result of a temporary weakening of the territorial impulse.

Nestlings are left alone at the nest by their parents when they are approximately one month of age and the territorial urge begins to decrease. The young slowly venture farther and farther from their nest. The biological justification for this is easy to see: the young begin to sense an almost irresistible urge to go to the sea; they begin to exercise their wings and to make the first attempts at flight. None of these activities could take place within the confines of the small nesting territory. The abandonment of the territory is gradual.

Nestlings begin to wander from nest to nest and, after a few days, form groups across the top of the island just as adults do before and after nesting. The entire appearance of the colony changes. Before, birds on nests were regularly distributed and the colony appeared gray from a distance. Large empty spaces appear in the colony and dense dark groups of nestlings appear from place to place.

The impulse to return to the nest is still strong and, even when the young wander some distance, they always return to their nests. This is most obvious during ringing operations when young, displaced some hundred meters from their nests, return to them within two hours (this was determined by close observation of marked birds).

Between six and seven weeks of age, the birds begin to wander in search of water, making long trips, up to one kilometer per trip on Isla Chincha Norte, to parts of the shore where they can bathe. They are not stopped by the need to scale cliffs that would be difficult for humans, as on Isla Don Martin.

On some islands where there is no natural access to the sea, hundreds if not thousands of birds die every year during these attempts to reach water. This is most noticeable on islands such as the Ballestas and Macabi. The birds throw themselves half-flying and half-falling from the cliff tops before they are fully able to fly and end up dying of cold and starvation when they can't return to their nest sites.

Although the need to bathe may be augmented by other factors, such as ectoparasites, there seems to be a clear relationship between the urge to bathe and the island's temperature. On Isla Ballestas, during the hottest hours of the morning before the trade winds have begun, birds gathered at the edge of the cliffs, trying to reach the sea and falling as I have already described. At the same time, younger nestlings, too small to make trips to the sea, were obviously suffering from heat and struggling to obtain whatever shade was available, even when they had to crowd under their neighbors. When the wind began, this activity ceased; the birds gathered at the cliff edge began to return to their nests. Within roughly an hour the interest in bathing vanished.

For some weeks following their first bathing trips, guanay nestlings continue to return to the nest to be fed. Some of them bathe only a short time each day; others, apparently the great majority, remain bathing until they see large groups of adults returning to the island. Then the nestlings precipitously leave the bathing area, a movement that almost suggests that the birds possess intelligence and memory.

Once the young are capable of flight, it is almost impossible to follow single individuals in the dense groups. The young are no longer linked to their nests by instinctive bonds and they begin to be as shy as their parents. When an observer approaches, young and adult guanays scatter and marked individuals are lost.

Young guanays take to the air or water before they are completely capable of flight and begin to feed as soon as they find food. Bathing young consume "muimui" (*Hippa* sp.) when available. Young birds with down still on their heads can be seen at times several miles from their natal islands.

The food and feeding habits of the guanay have provided one of the most important and fruitful fields for my investigation. There are few aspects of the life of the guanay so poorly understood. Many persons have supposed that there is always an abundance of food for the guanay and among laymen there is the general impression that guanays daily ingest more than eight times their body mass in food.

At times, the guanays exploit a wide variety of foods, but they depend almost entirely on the anchoveta for the simple reason that, in these waters, no other fish occurs in sufficient numbers to serve as their principal prey. When they exploit other species, it is an indication that anchoveta are not available in adequate numbers.

It is difficult to determine the quantity of anchoveta ingested daily. Two methods are possible. One would be to feed a sufficiently great number of captive guanays, enough to be statistically significant, during enough time to permit a study of the mass lost or gained. However, this test would be misleading, since it would be no more indicative of daily food intake than would the lavish meals of Maury or Bolivar during the War of Independence be representative of the daily food intake of the indigenous people of the highlands of Peru. The most elementary study of the birds in the field will show that there are periods during which they ingest more food than at others, when little food is available. I did not try this method because a sufficient supply of anchoveta was not available and, if I had used another species of fish with different nutritional values, the results might not have been applicable to anchoveta.

The other method consists of looking at stomach contents in the field. This method has the advantage of providing information concerning the normal extent of variation in the availability of food. On some days, birds fill their stomachs, while on others they must return hungry to the islands. This is not conjecture; it is based on birds that have been observed to abandon their nests for an entire day. The study of stomachs in the field has the disadvantage that it is impossible to determine the amount of digestion that has occurred before the stomachs were examined. I believe, however, that it is possible to introduce a correction for this factor which provides a useful approximation.

The ideal would be to kill a large number of birds and examine their stomachs throughout the year and during years of food abundance and scarcity. However, it would be wrong to kill such a valuable bird in large numbers, so I limited my collecting to 23 birds. The results were statistically sufficient for my purposes.

All the birds were shot when they returned to Isla Chincha Norte after having fed. I excluded the dozens of birds I observed dying of hunger on the island. If these had been included, the estimation of food intake would have been much lower. The average content of the 23 stomachs was 143.17 ± 22.5 g. This standard deviation of 22.5 could have been reduced if more stomachs had been collected, but I have already explained why this was not desirable.

In accordance with statistical theory, we can expect 99.7 % of all stomachs examined to fall within three standard deviations of the mean (Simpson and Roe 1938). In other words, if we take 99 birds out of 100, their stomach contents will have a mass between 75.67 and 210.67 g. This means that we can be sure that only one bird in 100 will have more food in its stomach than the value given.

To what extent do these values represent the daily food intake of the guanay? How much digestion takes place before birds have returned to an island? It is impossible to answer this categorically but there is considerable evidence that the digestive function in these birds is relatively slow. In the first place, many of the stomachs examined contained anchoveta that showed little or virtually no evidence of digestion. Some of the birds were shot when they were known to be feeding within three or four miles of the island. Finally, and this is perhaps most significant, I have observed a guanay that had been on its nest for over five hours attempt to feed its chick. The fish that was presented to the nestling was in pieces so large that the young was not able to consume them and I was able to extract the pieces from its throat. The food consisted of a large piece of anchoveta which had been so little affected by digestive juices after the adult's five hours on the nest that the color and scales were still clearly visible. I have also seen a Peruvian

Booby feed its nestling more than four hours after returning to the nest. More evidence that food remains for a long time in the stomach of the guanay is provided by pellets thrown up by birds that have passed the entire night on the nest.

If anchoveta can remain in good condition in stomachs for four or five hours, then stomach contents of birds returning to the islands are likely to be relatively unaffected by digestion and thus give a good indication of the quantity of fish ingested.[20] However, to be cautious, let us assume that the birds have ingested 50% more than we find in the stomachs of the collected birds. This would give us a daily food ingestion of 214.75 g. If we take three standard deviations above the mean, to obtain a 99.7% probability of including all stomachs, we have a daily consumption of 316.04 g. This quantity is biased toward fuller stomachs and includes an additional 50% to compensate for digestion. That the true daily intake is likely to be between the two figures is supported by the mathematical relationship between weight of food ingested and the mass of a bird species.

Twenty-seven guanays, all in apparently good health, had an average weight of 2072.3 ± 53.89 g. before removal of their stomach contents. In some zoological parks that use large cages and keep pelicans in good condition, the keepers feed them a quantity of food equal to 13% of body mass. For the guanay, which is closely related to the Peruvian Pelican, this amount would be 269.36 g, an amount intermediate between my two means. These quantities seem reasonable, based on other investigations.

Serventy (1938) wrote, "At present the only satisfactory data are those obtained from birds in captivity. These data ought to be used with caution, because if a bird is offered an unlimited amount of food, it will ingest much more than under natural conditions in which the energetic requirements of fishing restrict effort to a level at which hunger is satisfied. This is some quantity less than the saturation reached when a bird has every opportunity to gorge itself with food." In this regard, cormorants that have been examined after they have fed on fish extracted from fishing nets have much more food in their stomachs than is found in stomachs of birds that have fed naturally. Dr. Alexander Wetmore wrote concerning the food given to Double-crested Cormorants (*Phalacrocorax auritus*) kept in captivity in a flight cage at the National Zoological Park in Washington D.C., "The cormorants were in good physical condition and bred in captivity. Each bird received three-fourths of a pound of fish daily, given as one meal six days a week. . . averaging the weights of both sexes, these cormorants consumed almost 17% of their body weight per day. In comparison with what we know of other birds of a similar mass, this percentage is very high and one has to doubt whether cormorants in natural conditions can eat as much as those of the National Zoological Park."

Nice (1938) writes that, "In Europe, experiments have been conducted concerning the percentages of food ingested daily by birds in relation to the body weight of each bird, and through these experiments, two main conclusions were reached: first, the colder the weather, the greater the food consumption, second, the smaller the bird, the greater its proportional ingestion."

On the basis of weighing in the morning and night of 15 species which ranged in size between warblers and Mourning Doves trapped in Illinois, Taber concluded that the daily food consumption of birds in the wild ranged between 15 and 16% of body weight. This would be true for the sizes of birds considered. However, Table 2 shows a clear inverse relationship between species' body size and food as a relative percentage of body weight consumed per day. The smallest species has a greater relative surface area than does a larger bird and it follows that a smaller bird loses more heat than a larger one.

Table 2. Food ingested per day as a percentage of body mass.

SPECIES	MASS OF BIRD	FOOD/BIRD
Buteo buteo	855-900 g	4.5%
Falco tinnunculus	200	7.2
Gallus domesticus	1,800	3.2
Colinus virginianus	170	8.8
Vanellus vanellus	195	7.8
Pelidna alpina	114	8.5

It should be noted that careful calculation of density of nesting birds and the quantity of guano produced shows that each guanay produces 15.8 kg of guano per year. This is a smaller amount than that estimated by Coker (1919) of 22.7 kg/year but Coker had fewer data available than in the present study. He studied the birds in 1910, a year of presumed abundance, just before the population crash of 1911, and it is possible that the birds produce more guano when more food is available.

Using the mean mass of the stomach contents of the birds collected and adding 50% to allow for digestion, I estimated that each bird consumed 78.38 kg/year of fish. Dividing this quantity by 15.8 kg of guano that each bird deposits, each ton of guano deposited on an island requires the consumption of 4.95 tons of fish. Using an inflated value of three standard deviations above the mean and increasing this by 50% to allow for digestion, each bird would have consumed 115.35 kg of anchoveta/year and 7.3 kg of fish would have been required for each kg of guano deposited.[21]

Taking into account that the first figure is the lowest, the birds would require 711,903 metric tons of anchoveta to produce all the guano collected in 1940. If we use the second, higher value, the birds would have to consume 917,150 metric tons to produce the same quantity. These calculations of the relationship between food ingested and guano produced are based only on guano deposited on the islands. Only this guano is available for harvesting. If it were possible to determine the quantity of guano that falls in the sea, the ratio of guano produced to fish consumed would be smaller. Unfortunately, there is no method available to estimate the guano produced away from the islands. This guano is of benefit to the ecosystem since it enters the marine nitrogen cycle, as do the bodies of dead birds. These two may be important, if not indispensable, sources of fertilizer for the microscopic plants that form the basis for life in the Humboldt Current (Murphy 1936; Sears 1941).[22]

The importance of food as a limiting factor has been ignored for a long time in the belief that, because of the almost mythical richness of the Humboldt Current, there was no need to consider food shortages. However, my studies of the last two and a half years show that food shortages caused by the unavailability of anchoveta have been the primary cause of the death of thousands, if not millions, of birds. Given the climatic anomalies that have characterized other years with population crashes, it is reasonable to assume that previous years of failure have resulted, as has the present, from a shortage of anchoveta.

Before discussing the recent food shortage, it would be useful to consider the food chains that link the sun's energy with the birds and some of the conditions that affect the various links. In Figure 11, as already mentioned, there is a marked concentration of reports of birds with eggs during the summer. Before accepting these data, I should mention two points that affect their validity. My assistant made a careful analysis of the reports of guards from the islands from 1916 to the early months of 1942 (except 1925 because these reports are missing) for the islands Lobos de Tierra, Macabi, Guañape, Chincha Norte, Ballestas and Santa Rosa. There was a great variation in the consistency and apparent accuracy of the reports and some of the information seemed to be of dubious value. When, for example, the guards indicated food availability was "regular," this probably means that food was almost normal, but the majority of guards have no clear concept of normality. In any case, only a laborious statistical examination would be able to establish "normality," using data worth studying.

At the other extreme, as in the obvious abundance or total absence of food, we can probably accept the reports as being relatively accurate. (In passing, I should point out that the judgment of some guards can be accepted without discussion in almost all aspects. Some of them are very competent observers. However, it is impossible to distinguish on the basis of the reports those which are trustworthy and those that need to be used with much more caution. Finally, it is pleasing to note that the accuracy of the reports is improving).

According to the guards' reports, the period of food abundance begins in August, reaching its peak in January. This curve runs two months behind the pattern of egg-laying so that the period of food abundance occurs when the young are more or less a month old. After this, the young can be left alone in their nests while both parents forage. During the same period, there were 86 reports of total absence of birds and 33 reports of abandonment of eggs and young. The distribution of these reports shows that, at least in the opinion of the guards, there was no doubt of an association between food availability and egg laying (Table 3). This association is highly significant (χ^2= 13.3, p = 0.01). In other words, over 25 years, egg laying and food availability have been tightly linked. Both reach peaks during the summer. The 119 reports of absence of birds or desertions of eggs and young during the same period showed a strong relationship with food shortages, according to the reports of the guards. (The total number of cases in the table would have been much greater except for the fact that when an island has been abandoned by birds, the guards often did not fill in their monthly reports. The values reported here are based only on clear reports of absence.)

Table 3. Reports by guards on food abundance in relation to absence or colony abandonment by Guanay Cormorants. *The column is unlabeled in the original but is inferred to represent "rare."

BIRD BEHAVIOR	FOOD				
	ABSENT	VERY RARE	RARE*	NORMAL	ABUNDANT
Birds absent	7	58	13	6	2
Eggs and young abandoned	0	12	19	1	1

What is the reason for the relationships? Once more, we suffer from a lack of data. One obvious aspect is the need to investigate other aspects beside the birds; we need to look at the environment. We need data on the abundance or scarcity of anchoveta from year to year; meteorological data, not only from the coast but from distant locations; and data such as wind speed and direction, barometric pressure, and air temperature. From some coastal sites, it would be useful to have data on insolation and the quantity of infrared and ultra-violet radiation; and data on salinity, nitrogen and phosphate levels in the sea.

Even though the available data are far from complete, they provide much more information than has been previously published for the region, and they give a general idea of several important factors, at least during recent months. Figure 8 shows three curves: sea-surface temperature, since 28 October 1940; temperature at 50 m depth (taken daily since 27 February 1945); and sea-water transparency. Most of the measurements were made with improvised equipment. The surface temperatures were taken with a "Green" thermometer at the same time that we took plankton samples. The temperatures at 50 m were taken with a Six's maximum-minimum thermometer. The lowest temperature registered was taken as the temperature at that depth. An inverting thermometer would have been more precise but one was not available. If a layer of cold water overlaid the water at 50 m, the reading would have been erroneous, but this would be so unusual that it is unlikely that such events affected the results to any significant extent.

Sea-water transparency was measured with a Secchi disk that was lowered until it disappeared, then raised until it became visible again. The average of the two depths was taken as the transparency value. The disk was nothing more than a black and white painted metal circle of 20 cm diameter. "The limit of visibility is a measure of the transparency of the water and is not materially affected by light intensity at the surface, within broad limits. The disk becomes invisible at the depth at which the same fraction of light that enters the water is absorbed; in this manner, the depth of visibility obtained is a rough measure of the quantity of material in suspension. . . In the blue and very deep Sargasso Sea, the disk is visible to 66 m and in the blue waters of the ice fields of the Antarctic, to an average depth of 50 m." (Harvey 1928).

Observations were made at the same hour every morning in the region of the Bay of Pisco. The waters in which the study was conducted were oceanic rather than coastal, based on plankton collected and water color seen from the surface and from the air. Also, during the study, there was so little run-off from the Rio Pisco that it did not affect the waters around the islands. In other words, transparency of the water was determined primarily, if not totally, by natural organic material, especially by plankton.

A statistical analysis of the correlation between sea-surface temperature and transparency gave a very high value ($r = .81$). The Z was $1.1 \pm .08$, meaning that the correlation was highly significant: the warmer the water, the lower the transparency, and the greater the organic material. The temporal pattern of this increase is interesting and is shown by the mean monthly transparencies noted in the lower part of Figure 8. The density of organic material in the ocean increased from November to January, after which it began to decrease, reaching its lowest value in June. The two values correspond, to an extraordinary degree, with the reports from guards on islands concerning the amount of food. In other words, if the fluctuations of 1940 - 1941 were typical, then anchoveta are most available to birds when the sea is most productive.

The explanation is not, however, a simple correlation such that as temperatures increase, marine life becomes more common. A careful study of Figure 8 shows paradoxically that in many cases a decrease in temperature, indicating upwelling, was followed by a decrease in transparency. The explanation seems to be that upwelling, bringing nutrients to the surface where they become available to diatoms, permits these to multiply, decreasing the transparency of the water.

However, the main trend is as indicated previously and probably has nothing to do with temperature. The changing coefficients of variation provide a clue to this. They are high in November, fall in February, increase again in May, and fall again in June. December - February is the period when clear skies occur in the Pisco region, providing maximum sunlight. November is rather variable as are April and May. June has few clear days.

This information is valid only along general lines, since we do not have reliable data on solar radiation. Diatoms, probably the main cause of decreases in transparency, require sunlight for photosynthesis. We do not know how much they need or what degree of cloud cover inhibits photosynthesis. One can only suggest a very general and purely speculative relationship. In the spring, the diatoms increase and the coefficient of variation is high. In the summer, diatoms reach their maximum abundance with maximum sunlight and relatively stable conditions. At the end of summer, as solar radiation decreases, diatoms also become scarce and the coefficient of variation again becomes large. In June, with the arrival of dense clouds, there is less radiation but conditions remain stable and the variation is again low. This is the winter equilibrium. After this period, sea-surface temperature parallels insolation, and there is also a correlation between temperature and production of phytoplankton.

It is unfortunate that we do not have data over a number of years, to allow comparisons between years and to determine if the fluctuations recorded were typical. We know that sea-surface temperatures were abnormally high during the study period so that the diatoms sampled may have been different from those found in years with lower temperatures. The correlation of plankton (gathered with a planktometer) with sea-surface temperature was negative (r = -.28 with a deviation of .26 ± .008). The plankton measured indirectly with the Secchi dish consisted mostly of forms so small that they passed through the mesh of the planktometer. This is undoubtedly the reason that the diatoms and the planktometer gave results that were apparently contradictory. During much of the period, the main forms of zooplankton were those ordinarily associated with warm waters, as has already been mentioned. These probably came from the open ocean, along with the warm waters that elevated temperatures in this area.

Under more normal conditions, such as those described by Murphy, Gunther, etc., with smaller increases in temperature, the zooplankton of cold waters, principally copepods, would be as abundant as the phytoplankton. The plankton gathered with the planktometers probably hold less relevance to the problem which concerns us, since it is composed mostly of zooplankton while phytoplankton seem to be the main food of the anchoveta. In any event, the plankton collected will be studied by Dr. Sears. It is sufficient for our present purposes that the few data available indicate that guanay nestlings hatch before the period of maximum abundance of phytoplankton.

One hundred and fifty-seven plankton samples collected between 3 November and 13 June 1941 had a mean volume of 1.19 -11.0 cc/m^3. These plankton were taken only from the surface. Samples taken from the entire water column in the Gulf of Maine, U.S.A., had mean volumes of less than 0.5 cc/m^3 (Bigelow and Sears 1939). However, we should note that our samples for the Bahia de Pisco in the past year consisted in large part of ctenophores, siphonophores and chaetognathes: adult forms which contain 98% water. It is unlikely that the anchoveta eats these forms as they do not contain sufficient nutritional material (as indicated by Dr. Sears 1941) but, unfortunately, through a printing error, her statement says the opposite). The food of the anchoveta, at least for the period 3 November 1940 to 13 June 1941, probably will have to be determined through the study of phytoplankton. If the food of the anchoveta consists of diatoms, then there was probably sufficient food.[23]

There can be no doubt that during the nesting seasons of 1939 - 1940 and 1940 - 1941, there was a scarcity of anchoveta for the birds. There are several lines of evidence to support this. I made a careful study of the foraging success or failure of the birds. The times needed for foraging trips were recorded at a number of nests each day. I have already shown that during the nesting cycle, from courtship until the young are a month old, a period of three months, one of the pair is always present at the nest site. If the nest is left unattended, even for a moment, nesting material is stolen by other guanays which may also eject eggs and young from the nest, to die of hunger or exposure or, more probably, to be eaten by gulls or vultures.

Since one of the pair is always present at the nest, each bird has only a half-day to feed. No more than six hours are available to leave the island, find prey, catch it, and return. It is extremely easy to determine if there is sufficient food. If, by the middle of the day, half of the adults have not fed and returned to their nests, there is less than half a day for the remaining adults to feed. In other words, the foraging situation is unsatisfactory.

Figure 13 shows the results of several weeks of observation on the island Chincha Norte. The axes are the percentages of nests relieved and the hours at which observations ended. If there was sufficient food, all nests would have been relieved by 1200 hours: the male or female of each nest would have encountered sufficient food and returned. This occurred on only one day, 12 November 1940. On another day, 17 November, 90% of nests were relieved before midday. In other words, over this entire period, the most critical part of the life cycle, there was insufficient food. The result was the abandonment of tens of thousands of nests and a great loss of eggs and young.[24]

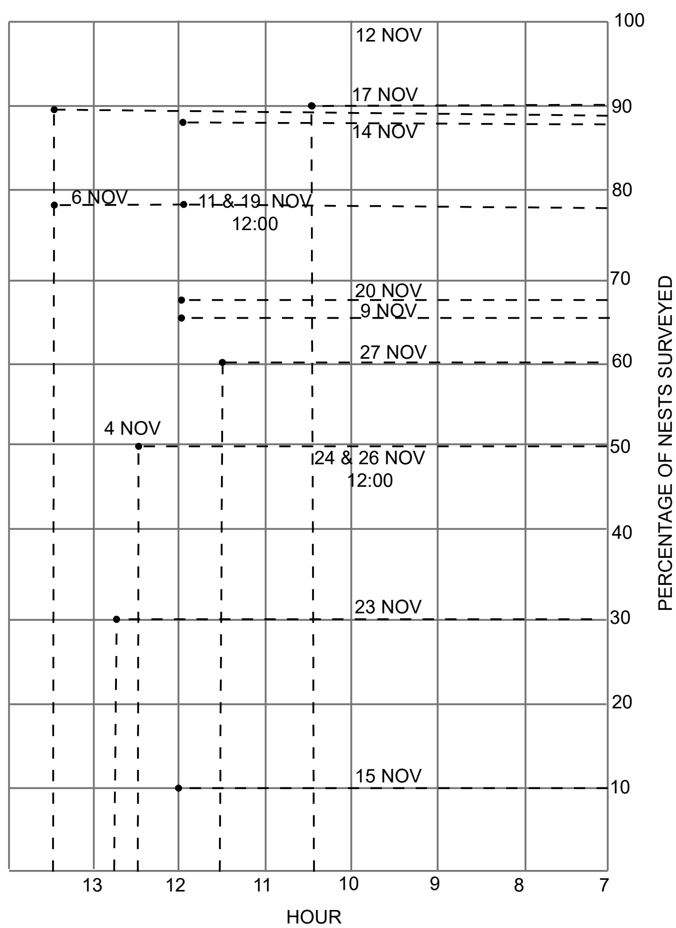


Figure 13. The percentage of nests where one bird had returned from foraging by the time observations ended on different days.

During the same period, I collected a large number of dying young and adults. Many had vegetable material such as algae and seeds of marine plants in their stomachs and intestines. These have yet to be identified. Such material is never gathered or fed to young except when other food is too scarce to support the birds.

Over most of the nesting season, the birds were obviously hungry. During the night, nestlings made a characteristic begging sound. Even the guards on the island commented on this desperate begging. When an adult returned to the colony late in the afternoon, it was swarmed by dozens of young, begging for food. Adults that could not escape regurgitated onto the ground.

In February 1941, tens of thousands of young pelicans were abandoned by their parents over a few days, as if it had become impossible to feed them. This began the second mortality since I started my studies in Peru. The birds literally died by the millions. This was especially impressive because the guanay, like certain other birds such as falcons and vultures, can survive several days without feeding. *The New York Times* reported that a guanay trapped in the hold of a ship on the coast of Peru survived until the ship reached New York where, according to Mr. Lee S. Crandall, in charge of birds at the New York Zoological Society, it lived for a period in the Zoological Park.

I arrived in Peru in January 1939 to begin my studies, but there were almost no guano birds along the Peruvian coast until June 1939. From Lobos de Tierra to Santa Rosa, the islands were almost completely deserted. Most of the birds appeared to have gone to Chile, from which we received reports of enormous groups of guanay birds. Some birds also dispersed to the north. Preliminary studies by Dr. Geiman showed absolutely no indication of any epidemic disease, but the birds did show extreme signs of starvation.

During July and August 1939, hundreds of thousands of birds of other species, especially the Sooty Shearwater (*Ardenna griseus*), died along the coast. The shearwater normally does not occur close to the coast (except to die) and it is virtually impossible to believe that a bird such as this, that has such an isolated life along the Peruvian coast, could be subject to an epidemic, especially an epidemic contacted from guano birds and in which the birds die principally of hunger. The shearwater feeds mainly on plankton and, during the period under discussion, there was almost no plankton in the waters I sampled along the Peruvian coast.[25]

In previous years of failure, shearwaters died by the tens of thousands together with guanays. Such a mortality, described by Sheppard (Murphy 1936), occurred during 1932 in the Gulf of Guayaquil and was attributed to a lack of food.

In 1941, the guanays I autopsied at the beginning of autumn showed no sign of epidemic disease. It was only when birds began to return from the south that I encountered diseased individuals. The pathology will be discussed below. However, there can be no doubt that during the past two years, the birds suffered severely from lack of food and that many thousands starved to death.

What happens to the food? This is matter of debate and can be settled only after more extensive studies. As is usually the case, we have more theories than data to explain the absence of the anchoveta. Until more information is available, most of the theories do not merit extensive discussion. It has been said that the anchoveta is always present in the waters off the coast of Peru but that during periods of food shortage fish move into deeper waters (by another typographic error [Sears 1941], the "probability" of such a vertical distribution was attributed to Dr. Sears even though she felt there was only the "possibility" of this).

We cannot test this assertion without collection of fish from deep waters. Even if a large number are collected at such depths, it does not necessarily show us what happens to the bulk of the population, the main source of food for the birds.

In support of the theory that the anchoveta descend to greater depths and are not actually absent, fish have been reported on the surface at night. Again there is an absence of documentation. How many anchoveta have in fact been collected at night on the surface during periods of food scarcity for the birds? Over what area are such surface schools distributed? Even if anchoveta are seen at the surface, this is not proof that all anchoveta schools occur on the surface at night. In fact, the reverse is shown by the fact that pelicans suffered severely from the recent food shortages even though they can feed equally well by day or by night. They are strong fliers and excellent at fishing. They can cover much greater distances at sea than can humans during an equal period of time. However, during the last two years, tens of thousands of pelican nestlings have died of starvation in addition to tens of thousands of adults that also perished from the same cause, lack of food.

Additionally, during this period of food shortage, many Pacific Bonitos (*Sarda chiliensis*) were caught in the Pisco region. These fish, that appear to feed exclusively on the anchoveta, had stomachs that were almost completely empty. In contrast, during the spring of 1941, when there was an abundance of anchoveta, almost all the bonitos examined had anchoveta in their stomachs.

Dr. Sears and I have recently begun a study of the anchoveta because the survival of the birds can be understood only when we understand the biology of this fish. It is too early to give definite results since we have yet to examine all the stomachs and gonads. We also are attempting to use scales to measure growth of anchoveta. We have measured more than 2,200 anchoveta and by December we will probably have measured 3,600. The stomachs, gonads and scales have been sent to Dr. Sears in the United States, to verify our earlier results.

Of course, such a small number of fish, collected over a short period of time, will not give more than a preliminary indication of eventual results but they ought to be sufficient to indicate goals for future investigation. We can, at this stage, say a few things about food, reproduction, growth rate, life expectancy and migration.

I have made a preliminary statistical analysis of the first 1,427 anchoveta collected during this spring. From the preliminary study of the year-classes, a very important fact has emerged. The commonest age-class seems to be three years old. This is very surprising. In the majority of populations that enjoy a more or less uniform reproductive rate, the one-year age-class is the most abundant. For example, in the case of the anchoveta, the youngest year-class would not have been subject to the same period of mortality as the older age-classes. Fish of one year of age ought to be more common than fish of two years and so on. However, from the study of anchoveta mentioned above, it is evident that the most numerous year-class is that of the three-year-olds, followed by the one-year-olds, with the two-year-olds being least abundant.

It should be kept in mind, in considering these proportions, that all the anchoveta were collected in the same area (Bahia de Pisco). If the anchoveta is migratory, one- and two-year-old fish may be in some other area. This could explain their absence during the past two years. The birds, as I will show below, reached the southern part of Chile. Thousands reached Valparaiso. It is very possible that they moved south following the anchoveta. There is a southerly movement of birds after each breeding season that may have the same cause. Moreover, if these anchoveta migrate, this is one indication that they are not in deep waters off the Peruvian coast, but instead are hundreds of miles away from the islands.

If the anchoveta is not a regular migrant, we can infer that the fish gathered in the Bay of Pisco are representative of the population, but only additional observations can settle the issue. If the fish are representative, then their age distribution is strong evidence of a reproductive failure of anchoveta in 1939 - 1940 and 1940 - 1941. Of course, it is possible that something happened to the eggs. If the anchoveta had merely deposited their eggs in especially deep water, this would not be a problem as the eggs are buoyant and would immediately rise to the surface. Something may have occurred that inhibited spawning.[26] In any event, since both summers were characterized by widespread mortality of the guano birds owing to starvation, it seems logical to assume that anchoveta were scarce along the Peruvian coast. As a result of this, the number of eggs spawned would have been very low so that we now find relatively few anchoveta of one or two years of age. The last intense breeding of the anchoveta may have occurred in the spring of 1938 - 1939 (it should be noted that anchoveta eggs are most abundant in November and December [Vogt 1940]), coinciding with one of the largest guano harvests recorded in the history of the guano company, despite the emigration and mortality of birds in the autumn of 1939.

An additional line of evidence that the anchoveta is migratory is supplied by the year-classes under study. Two samples of anchoveta were collected each week in the Pisco region. In October, anchoveta of four or five years of age were much more numerous while younger anchoveta were considerably scarcer. If these results are confirmed by future studies, which should be conducted over several years to be definitive, it means that anchoveta migrate from the Bay of Pisco and that younger anchoveta were replaced by older fish.[27]

All of these facts, taken together, leave little doubt that the shortage of anchoveta along the Peruvian coast was the main cause of the great mortality of guano birds and the resulting shortage of guano deposited on the islands during the recent period. Since the climatic conditions and sea surface temperatures during the past two years followed the patterns of previous years of population crashes, it seems very likely that the same cause (absence of anchoveta) has been responsible for previous years of population crashes.

It is very likely that this is not the first time birds have died of starvation, as LaValle (1925), reporting on the large-scale desertion of birds in 1923, notes: "Among the natural causes of desertion of nests by birds, the most important is the scarcity, within the birds' daily flight range, of the fish that serve as sustenance, of which the principal species is the Peruvian Anchoveta (*Engraulis ringens*), caused by changes in the physical, chemical, or biological conditions of the oceanic currents that occur in the area… Of the various major causes of desertion of islands by guano birds, food scarcity is the only one that can cause complete and successive migrations from all the islands affected by oceanic changes." The important report of LaValle, who reached similar conclusions in 1923 as he had in 1914, is worthwhile reading for anyone interested in recent events.

We still have to determine what happened to the anchoveta and why. I know of no reports of major die-offs of fish from any previous period. In fact, there has been a singular lack of reports of the red-tides that characterized the recent disturbances. It is very improbable that a widespread mortality of anchoveta would have taken place without being observed by the fishermen of the coast.

It is unlikely that the birds, having reached their annual maximum population in January and February 1939, exhausted their food supply owing to an increase in numbers. Desertions began in April in Lobos de Tierra; there was an intense mortality of birds in February on Macabi; and in May, most of the birds of the Peruvian coast reached the Chincha Islands on their emigration to Chile. The time available for the birds to destroy such vast quantities of anchoveta was much too short.

With all the data available and these, of course, are far from satisfactory, it seems likely that the anchoveta left Peruvian waters. We do not know at present if the fish went south or out to the open ocean, or both. Why they left, perhaps to avoid the high temperatures or in search of food, is unknown, but there can be little doubt that the absence of anchoveta caused the death of many thousands of birds.

The difference in mortality between years of good and poor food supplies can be seen in the number of bird-bands recovered on islands. In January of 1940, 3,000 nestling guanays were marked in Macabi. During that month and the following, food was "abundant" on Macabi according to the guards' reports. Only 21 or 0.7% of the 3,000 birds were found dead on the island, after a careful search for bands. This indicates not only that the birds were in good condition, but also that banding had no damaging effect on the birds. A mortality of less than one percent during banding is a very low figure, compared to studies of banding of other species under more favorable conditions.

During the nesting season of 1940 - 1941, 4,443 young guanays were ringed on Isla Chincha Norte. Of these, 122 or 2.5% were found dead on the island. This mortality was more than three times that on Macabi during a period of favorable conditions and occurred during a period of food shortage as already mentioned. These 122 recoveries did not represent the total mortality during the period in question. Many of the guanay young were already at sea, having fledged, and many of these must have died at sea.

Some employees of the guano company believe that banding is damaging for the birds. It is easy to understand this feeling among casual observers because, during banding, terrified groups of young run away and weeks later banded young are found dead. However, in considering this problem, it is necessary to remember that, banded or not, nestlings always die in large numbers. This is inevitable. The low percentage of banded nestlings found dead on Macabi is proof that banding is not damaging.

Young guanays should be banded when they are sufficiently strong to walk or run long distances from their nests to the bathing beaches, when they have already broken their territorial bonds and wander over the island. During this period, they struggle vigorously and, when hungry, can rapidly pursue their parents or other adults. The disturbance caused by banding does not have much effect. I observed, for example, a young banded guanay return to its nest minutes after being banded, despite the fact that its nest was some hundreds of meters away.

The idea that banding drives birds away from islands is refuted by what occurred on various islands along the length of the coast. The Ballestas Islands had two of their best years in history despite the fact that hundreds of birds were banded during each preceding nesting season. I saw Macabi almost overflowing with guanays after 3,000 nestlings were ringed the year before. The banding of 10,000 young on Santa Rosa was also followed by a dense nesting population and a good subsequent harvest of guano. Banding took place mostly during a period of food shortage, disease, and reduced population of birds so that some islands would be expected to be deserted; but banding played no part in the lack of birds.

It would be very useful to continue the banding program, if possible, for at least five more years. Inexpensive, portable cages could be constructed to capture some 300 - 500 guanays per morning, with a minimum of disturbance and effort.

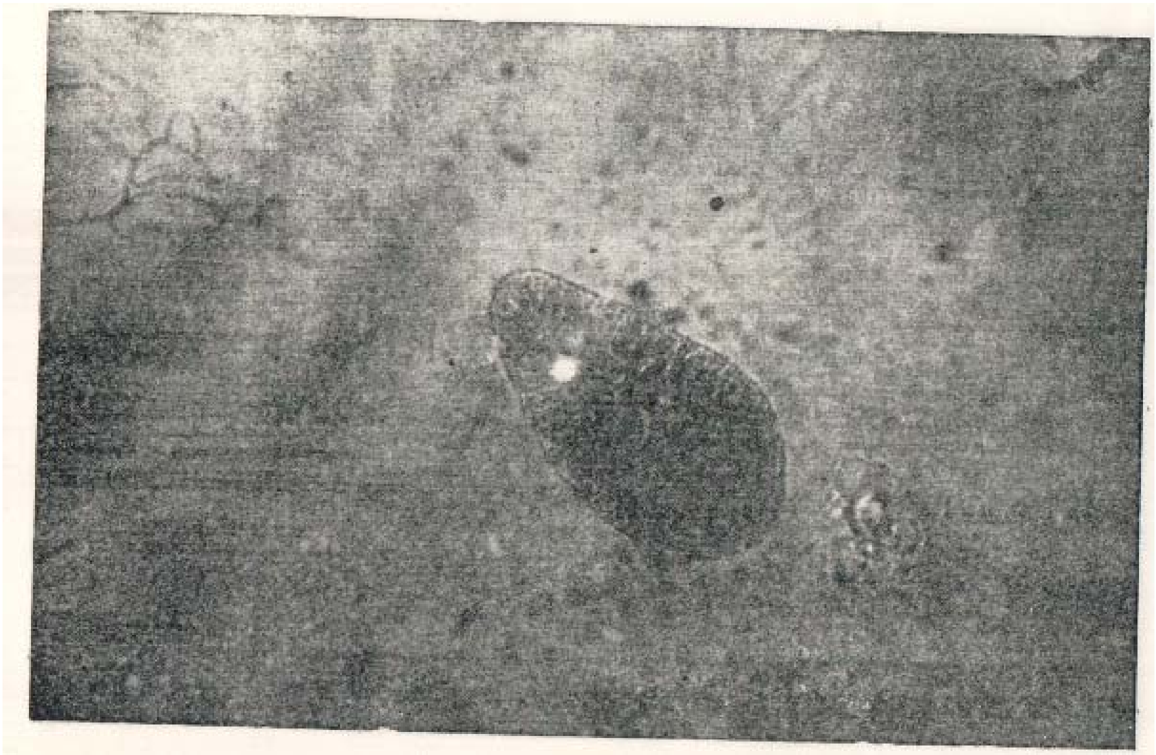
The data obtained from banding, such as movement of banded birds, mortality, distribution, and longevity cannot be obtained in any other way. These data will become even more valuable when supplemented with additional data from future years. In conclusion, if we desire an abundance of data for a statistical management of birds, banding is indispensable.

I will make only a few comments concerning parasites and diseases of birds. The problem is extremely complex and very little is known. As far as possible, I have studied all the avian diseases encountered on the islands. Dr. Quentin Geiman made an excellent start to this work before returning to Harvard Medical School. All the autopsy material subsequently has been sent to him. The tissues have been placed in Zencher's solution. I have taken numerous blood samples and during the last part of the study I cultivated blood samples in agar.

Relatively little progress has been made, in part, because I am not a parasitologist, microbiologist, or bacteriologist. An adequate field laboratory was not available, nor sufficient time to undertake studies of this type. Such an investigation should be undertaken, if we wish to completely understand all the factors controlling the abundance of guano birds. This requires a specialized investigation, over a good number of years. The study would require specialists with access to adequate reference collections and libraries. I have tried to gather all the information possible and have sent all the specimens to Dr. Geiman.[28]

Despite these limitations, it seems clear that diseases and parasites play an important role in the lives of the birds. Most guanays are infested by nematodes without apparent damage. Cestodes are common in the intestines and they are sometimes so common that they seem to kill infested birds. Flagellates, with the appearance of *Trichomona* of women, have been found in the cloaca of several birds but we do not know if they are pathological. There is no evidence of parasites of the blood; however, more observations should be made since blood-sucking ectoparasites are abundant in the colonies.

Image A. Photograph of a flagellate, many times augmented.



The mycosid infection known as aspergillosis is undoubtedly a cause of mortality among the birds and many of the deaths during years of collapse have been attributed to this disease. However, in the two and a half years past, I have encountered relatively few cases of aspergillosis in autopsied birds, suggesting it does not play a major role in mortality.

Avian cholera has been described as another disease of guano birds and, according to a letter that Dr. J. Garcia Suarez kindly sent us from Iquique, Chile, this disease was one of the causes of death of a great number of birds around Iquique in the autumn of 1941. Without bacteriological equipment, I have had to rely on symptoms of birds during autopsies to diagnose this disease, so that all the diagnoses must be tentative.

However, during the avian dispersal to the south, I did not encounter a single bird with symptoms of avian cholera. Later, when the birds returned from the south, several seemed to be dying of cholera. The birds may have been exposed to infection from domestic fowl during the dispersal. On the other hand, the lack of symptoms of cholera in birds moving south may simply have been coincidence. All the birds autopsied presented signs of extreme weakness and their intestines were full of bloody mucus. The other organs seemed to be normal.

When the birds returned north, there was another apparent cause of death known, because of the general appearance of the birds, as "pata pálida" (pale foot), characterized by a noticeable anemia. The feet of the birds (from which the popular name comes) are so pale that it is possible to spot a bird with the disease from a distance of 100 m with binoculars. The viscera are frequently extremely pale. It hardly seems necessary to say that starvation makes the birds more vulnerable to disease.

I made counts of red blood cells from blood samples of guanays. The blood was drawn from one of the veins of the wing and counted with a Bausch and Lamb hematocitometer, equipped with a Neubauer reticulation calibrated by the U.S. Bureau of Standards. The mean number of red blood cells per mm^3 in 28 birds was 1,807,250 ± 102.107. These counts included both sick and healthy guanays. I encountered considerable difficulty because of rapid coagulation of blood that made the extraction of blood from nestlings in the field extremely difficult. As a number of counts came from sick birds, it would be necessary to take a greater number of samples from healthy guanays in order to establish the normal number of red blood cells. However, it is probably significant that some of the counts that produced the lowest number of red blood cells, around 900,000, came from autopsied birds showing signs of "pata pálida." It seems likely that this disease, whatever its source, is characterized by an extreme anemia.

I began the extraction of blood samples at the suggestion of Dr. Geiman, who indicated that a very strong infection can produce an impoverishment of the blood that would cause serious damage to the birds. Even though further work is needed to confirm this, at present such a relationship seems very likely.

It is not at all extraordinary to see a nestling with its head covered with dozens of ticks engorged with blood.[29] If these drop off when satiated, then the number on a bird gives no idea of the total numbers of ticks involved. We do not know if the ticks are vectors for some disease, but such a possibility should be considered. Some ticks of this family are known to transmit diseases and even though the present species, *Ornithodoros amblus,* is not known to be a vector, this may simply be the result of lack of investigation.[30]

The Mallophaga or bird lice also occur in great numbers and irritate the birds, whether or not they cause other damage. The lice tend to concentrate in the throats of adult birds. This has given rise to a very interesting behavior of guanays. When a bird is incubating, before allowing its mate to take its place on the nest after returning from foraging, it generally opens its mouth so that the recently returned bird can clean the throat. The cleaning is done with the tip of the beak. As the bill of the guanay is very large for such delousing, it seems unlikely that the lice are killed but instead are probably dislodged so that the infested bird can swallow and destroy them with its digestive juices. The birds are much given to coughing and shaking their heads. I have dissected birds that were coughing without respite and have found nothing more to cause the coughing than the presence of lice in the throat.

The guanay has an interesting habit that may be associated with the presence of lice in the throat. In the morning, before leaving the nest, the guanay generally regurgitates a mass of undigested material: fish skin, scales, spines, and eye crystals of fish. To do this, the bird vigorously arches its head and neck. The material regurgitated sometimes has the form similar to the pellets regurgitated by owls. These pellets can sometimes be found on the islands. It seems likely that when pellets are regurgitated, they dislodge some of the lice from the throat.

The lice attack nestlings on the parts that have the most delicate skin: around the eyes, between the claws, and in the axillaries and inguinal areas. Even when one can see the adults pecking at their young as if removing the parasites, they do not seem to be completely successful, as dense patches of lice remain on the young after the preening.

Lice can bite human skin with sufficient strength to be annoying and there is no doubt that they bother the birds. There is some discussion of whether lice are enemies of the birds (Murphy 1925), and it seems likely to me that they are. They are able to pierce the delicate skin of the nestlings and it is very possible that, like ticks, they suck blood.

The third common ectoparasite of guanays is a hippoboscid fly about which we know absolutely nothing. Its interactions with the birds are also unknown, but there can be no doubt it annoys them. Guanays will pursue these flies among their feathers with obvious ferocity and at other times will avoid them as if dealing with frightening insects. At times, the hippoboscids are extremely numerous. I have seen such large quantities of them on the leeward side of Isla La Cruz that they blackened the ground. There were dozens of swallows feasting on them; it was the only time that I have seen these birds on the islands.

The guanay has few predators as adults. Eggs and small young are the stages most exposed to predation and even then primarily under unfavorable conditions.

The only mammal that I know as a predator of the guanay is the South American Sealion (*Otaria byronia flavescens*). Attempts to obtain stomach samples of sealions were unsuccessful so all my data are based on observations from a distance. A numerical evaluation of predation by sealions, the only sort of data worth believing, requires an examination of stomach contents. Such a study should run over several years. I have no evidence that sealions attack healthy guanays. I have frequently seen the two feeding together, with guanays showing no sign of fear. This habit is shared by other birds such as the Cape Petrel (*Daption capense*), the Giant Petrel (*Macronectes giganteus*), and the Inca Tern, species that seem to follow sealions to feed on scraps. When a sealion catches a fish or octopus too large to swallow whole, it scatters scraps of flesh as it shakes its prey, an action reminiscent of a fox-terrier shaking a rat. Pieces of food fall to the sea and the birds gather to feed. If sealions were frequent predators of birds, birds would recognize them as such and avoid them.

Sealions do kill some guanay nestlings. I have seen one shake a bird in the same mode as it would shake an octopus, but it did not seem to devour it. The behavior suggested play more than feeding, as a cat plays with a rat. That predation by sealions on nestling guanays is insignificant is shown by the fact that young guanays, like the adults, show little fear of sealions. I have seen hundreds of young standing around a sealion on the shore, at times almost resting on top of it. In the water, the young are also not afraid of sealions; however, when these approach within a few centimeters, the young swim away. This reaction may be a general response to any large approaching mass or it may be more specific reaction to a predator.

Predation on the part of the sealion may be, as happens with other mammals such as the brown bear, an individual habit. Some sealions attack guanays; others do not. Whatever the explanation, sealions probably kill only a small percentage of guanays so that there is no reason for humans to kill sealions. The presence of large numbers of sealions may have certain advantages for guanays, as I will discuss below.

Turkey Vultures and Black Vultures (*Coragyps atratus*), attack guano birds. The Black Vulture is rare on the islands. Turkey Vultures are about one hundred times more common but their predation is of little importance in predation on guanays. In fact, their predation can be beneficial. The vulture is timid and will never run the risk of an encounter with a adult guanay. When the guanay is at its nest, the vulture keeps a respectful distance. Since the guanay is always on its nest in normal conditions when it has eggs and young, the vulture has few opportunities to steal nest contents.

In periods of food shortage, such as the nesting seasons of 1939 - 1940 and 1940 - 1941, when the guanays abandoned their nests because of a lack of anchoveta, vultures took advantage of the absence of the adults to prey on the eggs and young. An egg without a brooding adult at the edge of a colony generally lasted only a few minutes. When a group of nests within a colony lacked adults to protect them, the vultures could feed with the greatest ease.

Two species of gull, Kelp and the Band-tailed or Belcher's (*Larus belcheri*), are the most active predators of eggs and young. It is said that the Grey Gull (*Larus modestus*) steals eggs, although I have never seen any evidence of this. The habits of the first two species are very similar to those of the Turkey Vulture in that, in order to steal an egg or chick, they have to wait until a nest is left unprotected. Gulls are more agile than Turkey Vultures and they are able to seize an egg in the middle of the colony where vultures cannot go because neighboring birds attack them.

The three species of gulls frequently roam the borders of a colony, feeding on pellets regurgitated by the birds. This can be misinterpreted by casual observers, or those with preconceptions, as attempts to rob eggs. It is likely that the bad reputations of the gulls spring from such misinterpretations.

A number of observers have reported that Andean Condors (*Vultur gryphus*) can displace guanays from their nests, to feed on their eggs and young. I have never observed this, but all the reports seem to agree that the condor is the only predator of the guanays that is definitely destructive.

In considering the problem of predation, it is important to remember that predators have co-existed with guano birds since well before Europeans first set foot on these shores. Some of the predators such as sealions previously existed in much greater numbers. Despite this predation, the birds have survived in great numbers for centuries. The predators have always been an integral part of the environment that produced the guano birds and, unless the numbers of predators have been increased by some change in the environment, they cannot be a serious danger to the guano birds.

The environment has evolved a dynamic equilibrium over thousands of years and man can alter this only at the risk of major damage to the entire structure. This has happened repeatedly and in completely unexpected and subtle manners. Undoubtedly, it would be possible to reduce the numbers of sealions, gulls, and vultures; but should we risk the consequences?

I have discussed the present state of sealions on the coast with a great number of people. All of them, with the exception of those interested in the harvest of sealions, agree that there has been a considerable reduction in their numbers. It is inconceivable, in view of the methods used in the harvest of sealions, that they will be able to maintain their numbers. Females and their young are killed during the breeding season and this reduces the reproductive rate. This system also probably produces a strong disequilibrium in the numbers of each sex, with an ever-increasing number of males. A similar process has happened in Alaska where similar harvesting methods have been used. The proportion of males has grown enormously, increasing competition between males for females so that thousands of young seals are crushed during fights every year. A similar method, killing females to leave an excess of males, has been deliberately employed to combat plagues of rats (Elton 1927).

With the reduction in the number of sealions (I have heard 80% mentioned), an important predator of the bonito has almost been annihilated. The sealion does not seem to eat small fish such as the anchoveta when larger fish are available. The bonito, judging from the few stomachs I have examined, seems to feed on anchoveta almost as much as does the guanay. The great reduction in the sealion population may have been followed by a corresponding increase in the number of bonito and a consequent reduction in the number of anchoveta. If the sealion acts as a protector of the food of the guanay, reducing predation by the bonito, then the guano company ought to protect the sealion from the harvest as currently practiced, at least until the bonito population is reduced to the level at which it was presumably maintained previously by sealions. If this supposition is correct, then the meager predation of the sealion on the guanay should be seen as an insignificant price to pay for the protection of its anchoveta food resource.

It ought to be obvious, even for a reader not accustomed to thinking along these lines, that we are dealing with extremely complex associations between plants and animals and that we have very few data on which to base an intelligent and constructive management. We should keep in mind that conditions as we know them, except for those derived from human interference, are the result of natural sources that have acted over innumerable years. We can do no less than respect the final results and agree that nature knows more about these matters.

The relationship between man and guanay has two aspects: competition and cooperation. In primitive conditions, as described earlier, the influence of man on guanays was probably not unfavorable. Any negative effects were probably minor. Except for fire, which can be very destructive, man has rarely caused damage to life in its natural state until the arrival of the twin forces of commerce and mechanization. Both have almost invariably produced disastrous results, as have been described so admirably by Ritchie (1920).

In the period between the discovery that guano was valuable and the founding of the guano company, the influence of man was mostly, if not totally, bad. That the efforts of the company have been beneficial is shown by Figure 11; however, we know that its influence has not been totally benign. For example, domestic fowl were only recently removed from the islands, where they were a potential source of disease for the guano birds. I will make new suggestions on how to improve the relationship between man and guano birds at the end of this report.

A constant watch should be kept for new dangers. Airplanes constitute a recent problem. An airplane passing over an island at a low altitude during incubation could cause the destruction of thousands of eggs. When a colony is surprised, the birds leave their nests so precipitously that eggs and young are kicked out of the nest without the possibility of their parents' retrieving them. Up to now, according to my observations, the danger of planes has been foreseen and strictly controlled so that planes rarely fly low or close to the islands. But a plane would be so destructive if it crossed an island at a low altitude that the government would be wise to impose heavy fines for infractions. At least 1,200 meters are needed to avoid dangers from single-engine planes.

The development of the fishing industry along the Peruvian coast should be carefully monitored for its effects on the birds. Unfortunately, this is another vast area of investigation where we lack basic information on the biology of the fish, such as migration, spawning, diet, life expectancy, and parasites. Elsewhere, the development of fisheries in the absence of such information, which can be gathered only over a number of years, has frequently been followed by collapses of exploited fish populations.

The New England fisheries, for example, earned more than 20 million dollars annually and, despite a great variety of conservation activities by the six states involved, there was no general plan to protect the fishery. Murphy (1941) states, "In 1934, the shad fishery landed 385,000 pounds compared to two million pounds landed only 50 years before. According to Ackerman (cited in Murphy), the annual fishery was much more than two million pounds at the beginning of the last century when the human population was only a fraction of what it is today.

"In 1889, Maine produced 25,000 pounds of lobster, a great proportion of which was sold to canneries at a price of 2.5 cents per pound. Since 1905, the fishery has rarely exceeded six million pounds, at a price of 25 cents per pound, at most, or ten times the earlier price. The sources of our lobsters are fishing grounds more and more distant. Modern means of transportation are only masking a collapse that is approaching. Before the current war, tens of thousands of spiny lobsters from South Africa were imported, frozen, to New York.

According to Murphy (1941), "Other fisheries have collapsed to the same degree. Perhaps the most spectacular has been the menhaden, which was almost inconceivably abundant during its summer migration to our waters in the north. The shoals were so dense and large that when they came to the surface, the agitated water had a rosy appearance owing to the opening and closing of thousands of gills. I have already mentioned this fish in connection with its use by Indians. The fish has also been a source of oil and fertilizer for the white man, before it was a source of food. In 1889, 173 million pounds of menhaden were landed by the fishermen of New England. However, after 1900, there was a continuous decline and, in 1933, only a million pounds were landed in our waters. The menhaden avoids cold waters but, despite this, even though the waters of the Gulf of Maine were abnormally warm, there were few of these fish, which had been exploited by the industry without thought of the future."

On the coast of California, the sardine, comparable to the anchoveta and menhaden in size and number, has been reduced to such an extent that catch per unit effort (C.P.U.E.) in 1937 - 1938 was something less than half the C.P.U.E. for 1932 - 1933. The reduction of the total fishery (currently an average of 500,000 tons per season in California waters) to half may provide the reduction necessary to avoid a further decline in the current population. To re-establish the population rapidly would require an even more drastic reduction, perhaps to one-third the present level (Clark 1939)!

I have already shown that the population of guanays depends on the supply of anchoveta and that, at least during some periods, the anchoveta is not available in sufficient amounts to support the birds. A certain amount of anchoveta can be harvested by man without any danger to the birds, at least in years when there is no scarcity of food for the birds; but, since we are almost completely ignorant of the biology of this important fish, it is impossible to determine what quantity of anchoveta can be taken without damage to the birds. Therefore, I cannot avoid concluding that a large-scale anchoveta fishery would become a danger to the guano harvest from the islands.[31]

On the other hand, the harvest of other species of fish may be beneficial for the guanay. If the principal food of the bonito is indeed the anchoveta, then a major fishery for the former on the coast of Peru could benefit the guano industry, by reducing competition for the anchoveta. However, given that we are again in possession of few data, such a possibility should be considered mere speculation.

The only aspect of the biology of the guanay remaining to be discussed is an important one: its movements along the coast. Migration has been defined as a movement which birds or other animals make "en masse" from the region where they breed to the area where they winter, and a return back to the former. In this light, it is not correct to define as migrations the periodic mass movements of the Arctic Lemming (*Lemmas lemmas*), the invasions of Europe by the Sand Grouse (*Pterocles* sp.), or the great flights of Monarch Butterflies (*Danaus archippus*). Nor, in all likelihood, should the mass movements of guanays to Colombian or southern Chilean waters be called migrations. This exodus of millions of birds occurs at intervals of several years and should more properly be termed an "irruption."

Every year, after the breeding season, a considerable number of guanays appear in the waters of northern Chile. Mr. A.W. Johnson of Santiago, one of the most active Chilean ornithologists, has generously sent me the following information: "I can assure you that the three species of guano bird are subject to a seasonal, relatively regular migration to the south. It is possible to observe birds along the length of the northern coast of Chile immediately after the breeding season. The number of birds varies enormously from one year to the next. In some years, there are truly millions and the bays, such as that at Iquique, are invaded by these birds which follow the shoals of fish and literally blacken the waters with their numbers…"[32]

The question as to whether they migrate is complicated by the fact that, while the guanay and the pelican never seem to have nested on the northern coast of Chile and the booby has done so only once, to the best of my knowledge; there can be no shadow of doubt that guanay and boobies nest on certain islands off the central and southern parts of the coast (between Valparaiso and Valdivia). The pelican has also nested in this region in years past, even though in small numbers.[33]

Up until the present, we have banded approximately 60,000 birds of the three species in the Peruvian islands (a final figure is not available because I am still awaiting the report of the guards of one island). Insights into the distribution of the birds and the regularity of their migration will be resolved as a result of band recoveries. There have been reports from Lima or Washington of more than 250 rings found, mostly on dead birds. In Washington D.C., the U.S. Fish and Wildlife Service keeps a record of such recoveries. The results have been very gratifying. Initially, we feared that few people would take the trouble to report bands, but the results have been quite different. People from four countries have co-operated in magnificent fashion. One bird, dead on a beach in central Chile, was reported by no less than eight different people.

One can gain some idea of the annual movement to the south by considering that the island Alacrán, off Arica, produces a harvest of some 3,500 tons of guano every four years, even though the guano birds do not nest on the island (Junius Byrd, pers. comm.). This annual movement might perhaps be considered a true migration but in my opinion the movements of the last two years should not be.

Banding of guanays began on a small scale at the end of the breeding season of 1938 - 1939, on Isla Chincha Norte. Only four recoveries were reported, two from north of the island and the others from the south, but all in Peru. In the months between the breeding season of 1939 - 1940 and 1940 - 1941, 48 reports were received of banded guanays along the coast. Of these, 25% came from the Peruvian coast north of Isla Chincha Norte, 33% from the mainland south of Chincha to the Chilean border, and 42% from Chile.

A total of 98 reports were received after the breeding season of 1940 - 1941. Of these, 15.2% were from points on the Peruvian coast north of the banding site, 4.1% from Ecuador, 33.6% from the Peruvian coast south of the banding site, and 47% from Chile.[34]

Except for 1,000 adults on Isla Chincha Norte, all the guanays were banded as young. Banding took place on the following islands: Santa Rosa, Ballestas, Chincha Norte, Don Martin, Isleta and Macabi. Young were banded at random so that the recoveries were probably a good indication of what happened to the birds in their dispersals during the past two years. In other words, if 42% of the reports came from Chile in 1940, we can suppose that 42% of the guanays of Peru, at least those of the same age, were in Chilean waters during this period. And if 47% of recoveries came from Chile during 1941, then 47% of guanays moved into Chile during this period. This movement provides a reason for the sharp decline in the amount of guano produced on the islands during this period. When something like 50% of the birds leave Peruvian waters, their guano is inevitably lost during this period.

While the geographic distribution of recoveries provides food for thought, it would be premature to reach definite conclusions. One of the most striking aspects of these movements is that they take place to both north and south. For example, the guards on Santa Rosa produced one of the better banding efforts along the coast, banding 10,000 guanays during the autumn of 1940. In the first year after banding, there were five reports of birds recovered in the north of Peru, seven in the south and 15 from Chile. In the second year after this banding, there was one report from the north of Peru, four from Ecuador, one from the south of Peru and 26 from Chile. In March of 1941, according to Dr. Murphy, guanays were seen flying upstream at Buenaventura, Colombia. It seems that the birds moved both north and south in great numbers. This does not fit into the general definition of migration. Also, it was evident that the flight of birds to Chile in the second year was even stronger than in the first.

We do not know what impels the birds to travel north as well as south, but in view of the food shortage along the Peruvian coast and the probability that the anchoveta is migratory, we should consider the possibility that the birds follow the fish. The majority of recoveries came from places to the south of the banding sites, showing that the birds had a tendency to fly south. We do not know if birds moving north are following some other fish species, are simply lost, or if the anchoveta disperses to both the north and south. However, there is no doubt that relatively few birds go north. The report by Mr. Johnson of large flocks fishing in Chilean waters is suggestive, as is his comment, that: "The general idea in Chile is that the birds die of starvation as a result of periodic failures of their food source, failures linked to variations in the Humboldt Current." This is not, of course, scientific evidence but it deserves attention, in view of the shortage of food supplies in Peruvian waters.

The total picture fits together to such an extent that the anchoveta appears very similar in its behavior to the California Sardine (*Sardinops sagax caerulea*). To compare the latter's life history with conditions in Peru, it is first necessary to invert the directions of the compass for the southern hemisphere and the months of the year (for February, read August, etc.). Spawning of the sardine takes place between February and July, reaching a maximum in April and May. The peak of anchoveta spawning, according to our observations, occurs between November and December (Vogt 1941). The main spawning area of the sardine is located off the southern coast of California, although a good number of eggs are found off Baja California. In some seasons, especially during warm years, the eggs have been found as far north as central California. In the Pisco area in Peru, anchoveta eggs were much more numerous in 1940, with its warm temperatures, than in 1941. The waters of the northern California coast are too cold; those to the south, too warm.

Larvae hatch after three days. This is also true for the California Anchovy (*Engraulis mordax*) (Bolin 1936) and probably for the Peruvian Anchoveta. There are few reports of sardine larvae off the northern part of California. During the first year, young sardines move several hundred miles. In each locality, smaller sardines are found close to the coast but move offshore when they grow larger. Anchoveta that Dr. Sears and I obtained in the region of Boqueron were longer than those in the Bay of Pisco. A small percentage of sardines may spawn at the end of the second year, approximately one-third spawn at the end of the third year, and all by the end of the fourth year.

Several facts indicate that sardines travel north in summer and south in autumn and winter. In waters off northern California, only large fish are common and then only during summer and the first months of autumn. According to the report of Dr. Johnson, cited above, the guanays move to northern Chile during their annual flights southward. During this period, they may well be following the anchoveta.

If there really is a parallel between the habits of the Peruvian Anchoveta and the California Sardine, then during years of population crashes, when warm waters are so frequently encountered, the anchoveta may range farther south than its normal limits. In other words, the anchoveta may move to Chilean waters in search of optimal sea temperatures when the sea temperatures between Mollendo and Pisco reach 26 ^{0}C (it should be kept in mind that we are discussing what happens to the main population of anchoveta, not to isolated shoals). If the anchoveta spawns in these waters, depositing its eggs under abnormal and perhaps unfavorable conditions, this would explain the apparent failure that has caused the scarcity of classes in the area under study.

It is possible that some anchoveta, while moving south, encounter patches of warm water and, through a negative thermotropism, return to the north. If these suppositions are correct, then we have an explanation of why, every seven years, there is a disastrous decrease in the number of guanays.

THE PERUVIAN BOOBY

The biology of the Peruvian Booby is so similar to that of the Guanay Cormorant that many of the comments made about the latter are applicable to the booby. Nevertheless, there are noticeable differences and management problems are, in some aspects, very different.

According to Murphy (1936), the booby was the commonest seabird on the coast of Peru in 1919. Today, in contrast, it occupies only second place behind the guanay, probably as a result of being displaced from its nesting areas by the guanay.[35] There is still a definite possibility of increasing booby numbers through better conservation. I estimate that the guano harvested from this species could be increased by roughly 10,000 to 25,000 tons per year. This will be discussed in the section on conservation.

The booby is far less gregarious than the guanay. It does not fly in large flocks like those of the guanay, and it is frequently found alone. Such behavior is so rare in the guanay that one assumes a solitary guanay to be infirm. While it is true that boobies nest in large groups, they also construct isolated nests on cliffs, in places far from others of their own species. For example, boobies nest on the south-facing cliffs of San Gallan even though the nearest colony of any size is on the Chincha Islands. Except during the nesting season, there does not seem to be any social organization. Boobies form pairs only at nest sites. Boobies may fly and feed in groups, but they do not seem to have any strongly developed impulse to stay together. At any moment, a member of a flying flock may break rank to fly and feed on its own. I have seen no indication of pair bonds or parent-offspring interactions away from the breeding ground.

The territory, which merits such a title more than the counterpart of the guanay, is chosen by the male. Presumably, the selection of a territory is caused by an internal impulse that increases as a result of hormonal secretions. The peak of nesting occurs in November, as it does for the guanay (Fig. 11). Nesting precedes the period of main food abundance by two months.

Generalizations concerning the booby are complicated by the fact that this species nests in flat areas and on cliffs, in windswept areas similar to those used by the guanay and on the hot plains of the Lobos Islands. During my only opportunity to undertake extensive studies of the Lobos Islands, in August 1939, there were no guano birds present. My study has concentrated on islands to the south of the Lobos group since the general ecology of the former appears to be uniform. Conclusions drawn from observations made on the Chincha Islands should be applicable to all the Peruvian Islands south of the Lobos group. It is possible that conclusions drawn from the other islands will have to be modified when the opportunity arises to study Lobos de Tierra.

The species holds two types of territories. One is on the flat parts of the islands; the other is on the steep cliffs. In neither case do boobies nest in concentrations as dense as those of the guanay. I measured several quadrants of booby nests and found a density of only 1.6 nests/m^2. However, these measurements were taken from a population close to its minimum so that densities are likely to be greater when the birds reestablish their numbers.[36]

I still do not know what factors govern nest-site selection by boobies. They nest on all sides of the islands in both cool and hot places, although they clearly avoid certain cliffs, perhaps because landings and taking-offs are too difficult. The male selects a site that will later become his nest and defends it with more vigor than does the guanay. While the guanay will occasionally tolerate an intruder, the booby invariably attacks other birds. Because of the difficulty of determining sex by appearance alone, it was impossible to determine if aggression was directed only at male intruders. Since male boobies are aggressive not only to all other boobies but also to any other species, it seems that the booby is completely intolerant of all intrusion. This aggression may spring from an inability to distinguish sexes, as occurs with some doves (Whitman 1919) in which males recognize females only on the basis of behavior.

The male booby announces his ownership of a site with displays and calls. This behavior, very like that of the Blue-footed Booby (*Sula nebouxii*), consists of a lateral compression of the body while raising the beak and the wings and lifting its feet, slowly and alternatively, as if mimicking the walk of a duck. When the display reaches its point of maximum tension, the male emits a panting whistle. This is repeated incessantly day after day, even after the male has acquired a mate. The same territorial behavior and calls are used to court the females.

In the spring of 1941, there was apparently a skewed sex-ratio, at least in the number of birds ready to mate. I observed males who remained unpaired after two months of display. The same behavior and calls are used to court the females. The territory is defended with a behavior used by both sexes. The defending booby moves its beak rapidly, tracing something like a figure "8," menacing its neighbor or intruder with the tip of its beak. The male accompanies this threat with a sound something like a neighing, while the female employs a repeated, sharp “honk,” like the cackling of geese.

The male is selected by the female and never the reverse. He is linked to the nest site once courtship has begun and seems to welcome, with a trumpeting note, any female that approaches him. He displays to her and if she does not depart, they are paired. If she does not find the encounter satisfactory, he resumes his wait. As in the guanay, the male booby shows more interest in the nest than does the female. He assiduously adds material, although rarely bringing things from any great distance as does the guanay. The male transports pebbles and pieces of guano, etc., up to several meters from the nest but does so without flying. I have never seen a booby flying toward a nest with nesting material, not even birds nesting on cliffs where there is only a few centimeters of space.

Courtship lasts about a month and, during this period, the nest is never deserted. Like the guanay, the booby has only a half day available to feed during territory-establishment, courtship, incubation, and the first few weeks after hatching, because one of the pair must always be present at the nest.

The sexes of the booby can be distinguished by voice. The female never produces the sharp whistle of the male. Once the pair has formed, the sexes can be separated by the feathers of the tail. Some birds have completely white central tail feathers; others have feathers that are completely maroon, with all possible intermediate tones occurring. I have never seen a pair of boobies where the two individuals could not be distinguished on the basis of their tail feathers, thus making it easy to follow their daily activities at the nest.

Before and during early courtship, the soft tissues of the male become reddish like the coloration of the head and beard of a sexually-stimulated male turkey. Before the male finds a mate, the gray, horny surface of his beak becomes pinkish. On certain occasions when I was able to closely observe a pair of boobies, I observed this color on the inner surfaces of the tarsus. This coloration may well be linked to the alternate raising and lowering of the feet, which is performed before the female.

Material does not seem to be important to the structure of the nest. Pebbles and guano may help to prevent eggs from falling out but the amount of material collected does not add to the nest structure as it obviously does for the guanay. However, the psychological effect of the nesting material is important. After egg-laying, the birds continue to bring small pebbles, with diameters of no more than two or three millimeters, which are deposited ceremoniously before the mate.

One recently-formed pair of boobies was especially amusing on Isla Chincha Norte. The male was very persistent in bringing pebbles to the nest. He deposited them in front of the female in the same way that a man would present a jewel to a woman. One ought never to attribute thoughts and emotions of human beings to lower animals but in this case it is impossible to resist. The male returned, composed himself, and deposited before the female, with great delicacy, and it appeared considerable excitement, the stone that he had brought in his beak. After this had happened several times, the female left the nest and her mate and returned with a pebble that she also placed before him. The male immediately showed intense excitement, contorting his neck and emitting a sharp whistle. I could only think that the female was like a young girl who cooks a special dessert for her boyfriend; the responses were so similar.

The eggs are laid at intervals of four or more days and incubation begins as soon as the first is laid. Incubation lasts forty-two days or 40% more time than does the incubation of the guanay. Both sexes incubate and, here again, the male shows more interest than does the female. Humans frequently think that incubation is tedious and boring for birds, but for the booby the opposite is true; incubation requires work. When the booby that has been feeding returns to its nest, there is always an interchange of calls, which seems to be initiated by the returning bird. The returning male produces a whistling call to which the female responds and vice-versa. A booby that has returned to its nest after foraging always cleans itself with great care. It arranges its feathers with its beak, spreading oil on them, the oil coming from its tail gland and perhaps providing Vitamin D. Afterwards, the bird passes the large feathers of the wings and tail through its beak, to clean and straighten them. Having done all this, the booby begins to care for its eggs.

This is generally preceded by a reciprocal preening that is begun by the returning bird. This preening consists of rapid and delicate adjustments by the beak to the small dense feathers of the partner's head and neck. After this has occurred for a while, the relieving bird bends forward, placing its neck across that of the incubating bird and occasionally picking up a pebble that it deposits in the nest. If the incubating bird is still not inclined to leave, it protests, with a weak whistle in the case of the male and a short squeaking honk if a female, and the newly-returned bird resumes preening. At times, the relieving bird has to wait up to three hours. This seems particularly annoying when it is the male who is trying to get onto the nest, and he will persist in trying to displace the female. At times she seems uncomfortable and may even threaten him with her beak. When a bird has been relieved, it may bring a few pebbles to the nest but it almost always leaves to bathe and forage shortly thereafter.

During the first days of life, the young are treated as carefully as if they were eggs. They are warmed during the cold periods and protected against the sun when it is hot. The nestling is fed from the time it is a day old. It begins to beg even earlier, raising and shaking its head weakly. I could not determine if it produces a sound or not at this age because I have not been close enough to the nest, but in view of what happens later, as with the guanay and Peruvian Pelican, it is likely that the young booby begins to use sound to beg shortly after it is born.

Adults typically respond to this begging by lowering their heads, opening their beaks, putting the head of the nestling into their mouths, then regurgitating the fish to the young in surprisingly large and relatively undigested pieces. Once a nestling has fed, it sleeps as, generally, does the adult. The period I have studied the birds was characterized by such a scarcity of food and a high percentage of abandoned nests that I have not been able to determine how long nestlings remain in the nest. All the nests where I made daily observations were abandoned. But, as I write this report, I am observing nests which will probably not be abandoned. The nestling period appears to last more than two months.[37]

During the first weeks of life, as in the case of the guanay, the booby nestling is strongly sedentary. If it tries to leave its nest, the neighboring birds, if any, attack it. If a nestling manages to leave the nest it soon dies because of the neighbors' jabbing. Here again we see the value of the surface-to-area law of colonies expressed in Figure 12: the larger the group, the smaller the proportion at the perimeter, so that fewer nestlings are exposed to such problems. This is probably the reason that large groups of boobies nest on the flat parts of the islands.

The territorial constraints on nestling boobies end in the second or third month of life, as in the case of the guanay, and for the same reason: the nestling booby begins to develop powers of flight and requires more space in which to practice than its territory can supply. When its wings become stronger, the nestling wanders over the island. Nestlings at cliff sites rise over their nests, much like the first airplanes. Eventually, a nestling will cover hundreds of meters by fits and starts.

The nestling leaves for sea, evidenced by guano being washed off the bands of marked nestlings, before the young are truly independent. It is common to see young returning to their nests in search of food when they are fully grown and capable of flight. At this stage there is a curious behavior. After having fed, the adult returns and perches at least 50 m from the nest. The young begins to beg for food and the adult walks to the nest, followed by the young. The parent feeds its young only at the nest. The survival rate of nestlings can be extremely high. In February and March 1939, we banded 1,009 young on Isla Chincha Norte. Only six of these died in the colony, based on a careful search for dead, banded birds. This indicates a nesting mortality of less than one percent. This rate is surprisingly low in any circumstances and is a clear indication that banding does not endanger nestlings.

When boobies nest on cliffs, nests are often widely separated so there is no social control of nestlings by neighboring birds. Many nests are precariously placed on small, rocky ledges where each nestling has no more space available than its own nest so that every year thousands of young fall to their deaths.[38]

This difference in mortality may provide an explanation for the change in booby nesting habits discussed by Coker (1935). He cited Von Tschudi and Raimondi as mentioning colonies of boobies on the flat parts of islands. Murphy (1925) also reported such nesting in 1919 and flat habitat is used today on the Lobos and Guañape Islands. However, when Coker was in Peru before the guano company began to protect the islands, he found no boobies nesting in flat areas. Murphy suggested they were displaced by pelicans, as also happened recently on Isla Chincha Norte. However, the guanay is probably a more important competitor of the booby than is the pelican, so that the increase in guanay numbers under the protection of the guano company has caused a decrease in the numbers of boobies. In 1919, Murphy recorded the booby as the commonest bird on the Peruvian coast. At present it occupies second place behind the guanay and nests mostly in places unsuited to the guanay.[35] This has occurred not only on the Lobos Islands where the boobies nest on flat areas but also on other islands. While studying the microclimates of nests on Isla Chincha Sur, I found booby nests at the extreme southern edge of the island, between the edge of the island and the main colony of guanays. At first sight, this seemed to be an exception to the rule, since the small colony of boobies appeared to be displacing the guanays, but I soon discovered that the winds striking the southward-facing cliffs were forced to rise, forming a windless pocket between the cliff edge and the line where the winds again reached the ground. Temperatures in the pocket were very high, making it totally inappropriate as a nesting site for the guanay but not for the booby, with its wider tolerance of temperatures.

Returning to the earlier discussion of the booby, it is possible, as already noted by Von Tsudi, that before the modern period of guano exploitation boobies preferred the flat areas of the islands where there was greater security. Boobies in these areas, rather than being an overflow, constituted the normal nesting population. Human activity has made flat areas less suitable for nesting boobies because the guanay is more tolerant of disturbance, so that the guanay population has expanded at the expense of the booby.

The exploitation of different niches by the guanay and booby is a matter of considerable practical importance. Some employees of the guano company have suggested that all the boobies should be killed since they compete with the guanays. This reasoning rests on the supposition that the extermination of boobies would be followed by a corresponding increase in guanays. This is, however, incorrect. Most of the guano harvested from boobies comes from parts of the islands where the guanay is unable to nest, because of lack of wind and the resulting high temperatures. If the boobies which occupy such areas were killed, the guanays would not be able to take advantage of the areas which would remain unoccupied.

If on the one hand the booby competes with the guanay for food, on the other hand it also deposits guano. In all probability, the booby is not as serious a competitor for the guanay as would be an equal number of guanays. The main food of the booby is the anchoveta, but it also takes other food and many of these are more solitary species. While it is rare to see a guanay feeding alone, unless it is in some manner incapacitated, solitary feeding is common among boobies. The booby dives from heights of at least 40 m, so it is likely that it can reach greater depths and velocities than the guanay, making it easier to fish. In addition, it suffers less during periods of food shortage than does the guanay and is not dependent, as is the guanay, on large shoals of anchoveta.

The booby probably suffers from the same diseases and parasites as does the guanay. It is unlikely that dispersed nesting on cliffs reduces the vulnerability of the boobies to these problems since ticks, lice, and flies are very mobile. It is common to see lizards feeding around booby nests twenty or thirty meters down a cliff. Boobies nesting on cliffs are probably less vulnerable to egg predation by Turkey Vultures than are guanays or boobies nesting on flat areas. However, as it is unusual to see eggs left uncovered, such predation is not likely to be a serious problem. Gulls undoubtedly can also take uncovered eggs. Since the booby generally does not enter the water until capable of flight, it does not suffer from predation by sealions to the same extent as does the guanay.

The booby has an enemy which does not bother other species. This is the Chilean Skua (*Catharacta chilensis*), a powerful gull-like bird which has developed the predatory habits of the Falconiformes, so that it can perhaps be called a marine falcon. The skua harries solitary boobies, forcing them to regurgitate their fish. Some observers report that skuas kill boobies, but I have never seen this. On the other hand, the skua does not always force the booby to disgorge. The booby may attack the skua or, once the more maneuverable skua forces it into the water, the booby may wait until the skua departs. I have never seen a skua attack a booby on the water.

The booby is obviously subject to the same natural laws as is the guanay. Although the booby feeds on various species, it is generally dependent on the anchoveta. The anchoveta eats plankton, mostly phytoplankton, and plankton is subject to variations in currents, upwelling, temperatures, and insolation along the coast. The factors are all, within broad limits, subject to the meteorological regime. These relationships have been discussed in the first part of this report and will not be repeated. Other general interrelationships, the synecology of the area, will be discussed below.

However, there is one aspect in which the booby seems to differ from the guanay: dispersal. We know nothing of the normal movements of these birds. Since they nest on various headlands along the coast, it is impossible to determine if boobies that one sees are local or have traveled even thousands of miles. To obtain reliable data concerning movements, banding is the only feasible method. Conditions have been very abnormal along the coast since the first boobies were banded in this study, so we have learned nothing of the normal movements of this species.

Mr. A. W. Johnson reports that the booby nests along the central and southern coasts of Chile.[33] This information was not available to Dr. Murphy when he wrote his book (1936). Murphy quotes Beck, who saw boobies near Ancud (1914), as saying: "To the north and to the south, there are never more than a few strays. I saw a single bird off Puna, Ecuador, on 25 February 1925 and Paessler reported one as far north as Manta, in November. In the periods of “peste” that follow the southward flow and the occurrence of El Niño, sick boobies enter the Gulf of Guayaquil in moderate numbers."[39]

The situation during the past three years has been very different. In 1939, 1,009 young boobies were banded on Isla Chincha Norte. Of these, only two have been recovered away from the island, one from Ecuador and the other from Chile. By the end of the breeding season of 1939 - 1940, the guards on Islas Guañape had ringed some 10,000 boobies. These islands were selected since they are the major nesting site of the booby south of Islas Lobos de Tierra and Lobos Afuera islands where banding effort was concentrated on pelicans.

There were only six reports of banded boobies recovered during the winter of 1940: two from Ecuador; two from Peruvian locations to the north of Islas Guañape; and two from Peruvian sites south of the islands. However, movement during the winter of 1941 produced 25 reports, with an interesting distribution: 4% from Colombia, 16% from Ecuador, 12% from Peru to the north of Islas Guañape, 27% from Peruvian points to the south, and 40% from Chile.[40]

Through the use of banding, we can determine where the guano was deposited during the past year. The report from Colombia came from Tumaco and the most southerly report came from Ancud, Chile, a range of some 4,000 km. With the general absence of guano birds along the Peruvian coast during the recent events, it seems reasonable to suggest that a considerable proportion of the booby population was distributed along the coast, to the north and south of the breeding sites. While there has undoubtedly been a large die off, so many birds have returned to breed that it appears that the majority of the boobies survived the exodus.

It would be premature to estimate annual mortality of boobies based on banding efforts up to now. With time and an increased number of boobies banded and recovered, it should eventually be possible to establish annual mortality and other important facts. I should provide a note of caution about the banding of boobies. As mentioned before, banding recoveries on the islands are very low, showing that banding itself produces little mortality. However, if the banding is done carelessly, mortality would be extremely high. Banding cannot be delayed, as in the case of the guanays, until the young are able to wander freely, because booby young become so active that they are almost impossible to catch.

Booby young can be banded as soon as their legs are sufficiently large to prevent the bands from slipping off. At this stage, they can be lifted from the nest without difficulty as they cannot escape. However, it is imperative that each nestling be returned to its own nest. If young are left to return on their own, they will be savagely attacked by surrounding adults and young. If there are very small young in the banding area, then the coolest times of day should be chosen, or banding should be done for only a few minutes at a time. When adults are scared off their nests, small young are exposed to the full heat of the sun and frequently die of overheating. However, if banding is done with care, it is completely safe and provides information that is not available in any other manner.

THE PERUVIAN PELICAN

Numerically the Peruvian Pelican is the least important of the guano birds and its guano is of lowest value since it is extensively mixed with other material. For these reasons, the pelican has been held in lower esteem than the Guanay Cormorant and

Peruvian Booby by some people. Some have even suggested that the pelican should be exterminated to conserve fish.

To judge the pelican only on the basis of the food it ingests and the quality of guano produced is to consider only two aspects of its enormously complex ecology. In the case of the pelican, as of the booby, its extermination would not result in an increase in the amount of guano produced by the guanay. The pelican, in contrast to the guanay, is of tropical origin. Some taxonomists consider it the same species that exists over large parts of northern South America, Central America, and north to British Columbia. Its centers of greatest abundance are the tropics and sub-tropics. Its tropical origin probably results in a tolerance of heat that allows it to inhabit all the guano islands, especially Islas Lobos de Tierra and Lobos de Afuera, where the guanay is not able to exist.

I have not had the opportunity to make a careful study of the pelican on these northern islands for reasons mentioned earlier. Therefore, I cannot present such detailed data as in the case of the guanay. Based on what we know of the microclimates of the southern islands, the pelican can probably nest in areas with high temperatures. The guanay, in the area of the Lobos Islands, nests only at the extreme southern tip of Lobos de Tierra and on small, neighboring islands. These areas are characterized by an abundance of wind. On Lobos de Tierra and on Lobos de Afuera, pelicans nest far from windswept areas and in deep gullies where temperatures are likely to equal those of Station K, if not those of Station L (see Fig. 10). Therefore, the pelican can nest without competing with the guanay for nesting space. Since nesting space is one of the principal limiting factors in the case of the guanay, the pelican does not aggravate the problem.[35]

The pelican does compete with the guanay for food but not to the extent that one pelican represents one less guanay. The pelican can eat much larger fish than can the guanay. The pelican, like the booby, does not fish in groups as large as those of the guanay and is, therefore, not as dependent on large shoals.[41] Pelicans often forage alone and often much farther offshore than do guanays. During voyages along the Peruvian coast, I have often seen pelicans in considerable numbers forty miles or more offshore, while the guanay generally forages close to the coast, at times just off the beaches.

To summarize the competition between the three species, we can say that each one has its own niche. The guanay nests only where the microclimate is not too hot and depends completely on the presence of large numbers of anchoveta. The booby nests in warmer and less windy areas than those needed by the guanay and it is not as dependent on the anchoveta as is the guanay. Additionally, the booby nests on cliffs where the guanay and pelican cannot. Finally, pelicans nest in areas where the heat would be unendurable for the guanay and perhaps for the booby. Pelicans are even less dependent on the anchoveta than are the other species.

It is likely that, under the conditions in which the islands are maintained by the guano company, pelicans have reached a relative equilibrium so that their extermination, or that of the booby, or the extermination of both, would not result in any significant increase in the number of guanays.

The pelican is the shyest of the three guano species and, therefore, the most difficult to study. Lobos de Tierra, with its large and well-established colonies, would probably be the best place to study the life-history of the pelican. I have been able to study only aspects of its biology on the southern islands. Pelicans are very prone to flight when a human approaches, and they desert eggs and recently-hatched young, leaving them to be attacked by gulls and vultures.

From the psychological point of view, the pelican is perhaps the most interesting of the three. I have not been able to identify the exterior differences in sex and, therefore, I have not been able to understand the courtship of the pelican.

Pairing seems to take place in groups. At the start of the breeding season, it is common to see groups of pelicans, perhaps 25, walking in a dense group near the colony and moving their beaks, one in front of the other. At times, one of the individuals appears to be the center of attention, but I could not tell if these were males or females. In contrast to the other species, the pair-bond is formed before a territory is established and pelicans continue their courtship while visiting different areas or even different islands.

Pelicans develop a prenuptial plumage that resembles a cascade of white feathers over the upper surface of the wings. These feathers reflect sunlight almost like tiny mirrors and they definitely play a stimulating role in the sexual process.

It is impossible to follow the behavior of a pair of pelicans within a colony for more than a few minutes, so I could not determine how long courtship lasts. Courtship consists of an exaggerated display of the white areas of the wings. The pair of pelicans ignore other pelicans, walking over the flats with their wings held high and half open to display their white feathers. The members of a pair do not follow each other tranquilly nor do they keep their wings open for long, without one bird's trying to get ahead of the other to display the white of its wings. The pair walk rapidly and generally take flight after a few minutes to continue the display of their white feathers in the air. One of the pair flies first, then the other, the first shaking its wings much as a housewife shakes a dusty cloth. When it does this, the white areas gleam in the sunlight.

I do not know how they choose their nest site or how long the interval is after forming a pair-bond, but they seem to select the site before the first copulation. In many hours of observation, I have never seen a copulation except on the nest. The role of the sexes in nesting is again unknown because I could not determine the external sexual characteristics. Both sexes incubate and both supply nesting material. Gathering material is done with the beak, filling the pouch of the lower mandible with dust, gravel, guano, ticks, feathers, and anything else transportable. It is not unusual to see pelicans carrying nesting material from one island to another.

Material is brought to the nest until the eggs hatch. A pelican returning to its nest with material generally tips its head over the shoulder of the incubating bird and dumps the material. The bird on the nest then arranges the material. There is a considerable variation in the density of nests. However, the density is not controlled by the length of the neck and beak (Murphy 1936). Studies of nest densities are almost impossible without unduly disturbing the pelicans since they trample the nests to such an extent that their borders are almost completely erased. Coker maintained that pelicans reach a density of two individuals per m^2, but eleven pairs recently nested on an observation hut that had a roof area of four m^2, giving a density of 2.75 per m^2. The density probably varies with the number of birds so that counts made at the peak of the population will differ from those made, as at present, during periods of low populations.[42]

Counts made by Coker and reported by Murphy (1936) give an average clutch of 2.41 ± 0.0799 eggs. Coker also encountered two nests that each contained eight eggs, but these may have been laid by more than one bird. These large clutches were, undoubtedly, as suggested by Coker himself, the result of disturbances by the observer.

Under normal conditions, the nests are as completely protected as those of the booby and guanay. I do not know the duration of incubation, but it must be more than one month. The young are dependent on their parents for at least three more months. Young banded on 19 March 1939, at an age of approximately one month, did not begin to fly until 15 - 16 May. This is of some practical interest since the length of this period means that pelicans remain on the islands and deposit guano longer than do the other species.

Feeding of the young begins a few hours after hatching. The young move their heads in a manner characteristic of the Pelecaniformes and, almost at the same time, produce a begging call. At first, adults cannot make their throats accessible to the young because of excessive lengths of their beaks but they keep them open and pointed downward. The nestling places its head, some four centimeters in length, in the tip of the beak, and the adult regurgitates. Chunks of fish slide down the beak like cargo sliding down into the hold of a ship.

When one month old, nestlings begin to wander and can be seen at times up to a kilometer from the nest. How do the nestlings know their parents, and the parents, their nestlings? No one knows. However, careful observation of color-banded young and their parents, which can be recognized to a considerable degree of certainty by speckling on their breasts and bellies, leads me to suggest that the same adults always feed the same young. As shown in Figure 11, the peak of egg-laying of the pelican, as in the guanay and booby, precedes the period of maximum food abundance by two months.

The pelican, unlike the other two, forages both by day and by night. During the nesting season, pelicans can be seen, on moonlit nights, coming and going through the night. However, nocturnal foraging was more intense during the recent period of food shortage than at present when there is an abundance of food. Despite being able to forage 24 hours a day, there has been an enormous die-off of pelicans in the past year caused by a lack of food. I have seen pelicans feeding on fish that live among rocks and on the "mulata" (possibly *Bodianus eclancheri*—Ed.) around the shores of the island as if food were everywhere insufficient.

I observed an unusual and abnormal foraging method during the period of food shortage. A shoal of fish of considerable size, perhaps some 30 centimeters, was discovered near the rocky intertidal zone of Isla Chincha Norte by hungry birds. The water was so shallow and full of obstructions that the pelicans could not plunge nor could they feed from the surface because of the surf. The shoal was discovered at the same time by guanays that congregated and dived for fish in the eddies, an unusual behavior for the guanay and an indication of the extreme state of these birds. The pelicans pursued the guanays. The fish were so large that the cormorants could not swallow them easily. When a cormorant caught a fish, it brought it to the surface to swallow, raising its head to do so. This was like a dinner bell for the pelicans that immediately beset the guanay holding the fish. At times, the guanay almost disappeared in the pile of pelicans, which frequently succeeded in stealing the prey. However, the guanays did not seem deterred since they continued diving for fish. Observing this parasitism, I wondered if the Chinese, by similar observations, had not been inspired to use cormorants for fishing.[43]

As mentioned previously, the starvation of nestling pelicans weakens the theory that anchoveta are always present but that they descend to greater depths during the day and ascend to the surface only at night. Pelicans were not able to encounter sufficient food, indicating that anchoveta were not available in the vicinity of nesting islands. More than 19,000 young pelicans were found dead on Isla Chincha Norte in February 1941 and more than two percent of the 2,551 nestlings banded on the island met the same fate. Undoubtedly the level of mortality would have been much higher if more bands had been recovered but the guards on the island were not yet aware of the need to collect and report all bands found. A good number of bands were later recovered from areas where the guards burned the dead birds. Dead young were apparently thrown onto the fire either without checking for bands or without bothering to remove them.

Pelicans are victims of predation by gulls and vultures on a larger scale than are guanays or boobies. Normally, pelicans do not leave their nests for long enough to permit predators to steal nest contents but, when pelicans are disturbed, they fly off for such long periods that gulls and vultures have sufficient time to take the eggs and young. This has been the main obstacle in the study of the pelicans.

In addition, gulls take eggs from beneath incubating pelicans. Pelicans see the gulls near them but apparently are not intelligent enough to scare them away. The Band-tailed Gull is the only species I have seen taking eggs. However, this habit cannot be an important limiting factor for pelicans.

Gulls were previously much more abundant along the Peruvian coast, when they were not hunted. It is unlikely that taking eggs is a new behavior. As the pelican has survived for many centuries on this coast, it is unlikely that gulls have any major effect on them.

Sealions seem to be a more important predator of pelicans than of the other species. It has been suggested that the sealions are more interested in the fish the pelicans have eaten than in the pelicans themselves. Most predation is on young pelicans. However, as in the case of the guanay, this predation is infrequent and I can show that sealions take less than one percent of the pelicans. As I have said earlier, our knowledge of the ecological role of the sealion is very limited and, as a consumer of bonito, the sealion may do more good than harm to the birds.

During the past thirty years or so, there has been a marked reduction in the number of pelicans. Coker observed 100,000 pelicans on Lobos de Tierra in 1907, but the reports of the last three years do not agree with Coker. It is interesting to note that Coker thought the pelicans had suffered a major decrease before his visit and that they had changed their nesting locations with the beginning of guano extraction. However, the largest nesting in the Pisco region during the past three years occurred during 1940 - 1941 in the Islas Chinchas, immediately after a period of guano removal.

It is very likely that feral cats on Lobos de Tierra prey on pelicans but it is not clear if they have played a significant role in the reduction of the pelican population. Whatever the case, the cats should be exterminated. This could be done in several ways: by trapping, poisoning, or by hiring hunters, equipped with powerful lights, to shoot them at night.

Pelicans are an interesting problem in themselves and, since they were formerly much more numerous, it would be useful to undertake a special study to determine the factors limiting their population. As the southern islands are well-populated by guanays and boobies when these are at their peak populations, the study should probably take place on Isla Lobos de Tierra where there is an abundance of nesting space not used by other birds and where pelicans are abundant.

Pelicans have the same parasites as booby and guanay, and they are probably subject to the same diseases. I have conducted several autopsies of pelicans but I await details from the report of Dr. Gelman.[44]

During periods of population decrease, judging from the last two years, the main danger to pelicans is lack of food. Most pelican mortality probably takes place at such times. Like the other guano birds, pelicans make large collective dispersals. Mr. A.W. Johnson reported large numbers, primarily of juveniles, in Chilean waters. Only banding can determine if these are regular annual movements and whether adults and young show the same behavior. Pelicans, like guanays and boobies, move both north and south. Murphy (1936) wrote, "We still lack trustworthy reports on whether this race is present in Ecuador," but banding has subsequently dispelled the uncertainty. Of the 25 recoveries of birds banded on Lobos de Tierra in the breeding season of 1938 - 1939, 4% came from Peruvian locations to the north of the island, 56% from Peruvian locations to the south and 4% from Ecuador. Twenty-two birds were recovered during the dispersal of the winter of 1940; all came from Peru.

During the winter of 1941, there were 32 recoveries. Of these, 31.2% were from northern Peru, 50% from southern Peru, 63% from Chile, and 12.5% from Ecuador.

Based on these initial recoveries, the pelican does not seem to disperse as much as the guanay and booby. The most distant report came from Perené. This seems so unlikely that it is difficult to believe there has not been a mistake. Unfortunately, the North American who sent in the report has not responded to our letters attempting to clarify this.[45]

In summary, before the beginning of banding, information on movements came only from the voyages of scientists. Through banding, we have the aid of fishermen, sailors, tourists, and a vast number of people interested in learning the origin of the bands they find. If banding continues, we will learn much about the three species of guano bird that we will not be able to learn in any other fashion.

Except for the considerable physical effort required, pelicans are the easiest birds to band. Because of their tendency to wander when young and their slow speed, banding a thousand takes relatively little time. There is only one danger and that is the disturbance of nestlings when still too young. They crowd together to such an extent that very small young can be trampled and asphyxiated. In contrast, if banding is done when all the nestlings can move freely over the island, there is nothing to fear.

SYNECOLOGY

It is obvious that the Guanay Cormorant, Peruvian Booby and Peruvian Pelican live in an environment of almost infinite complexity. An unknown number of factors play an important role in their lives, ranging from remote factors such as solar flares, which perhaps disrupt the equilibrium of earth's atmosphere, to more immediate factors. It is also obvious that, although we know a great deal about guano birds and their lives, there are many factors which we have only recently begun to understand and there are probably still others that have yet to be considered.

A discussion of the role of guano birds in their environment, or their relationships with plants and other animals, must be considered as only tentative and subject to correction as future studies reveal new facts. Additionally, any discussion of the environment should always include the question "when?", given the marked changes, both long- and short-term, that have taken place. Conditions in 1939 - 1941 were markedly different from those of 1937 - 1939 and it is virtually certain that the next two years will be different from those just past. Nevertheless, this section of my report is essential, in order to try and place the birds in the context of their environment, even though we must proceed with caution.

Even the list of the plants and animals that live with the birds is not complete. In this list, there are species that have not yet been shown to occur here. Future studies will probably uncover new species, especially among the plants and invertebrates. Most of the specimens collected have yet to be identified. This will require studies by taxonomic specialists. Therefore, the list that follows should be considered tentative.

PLANTS

Diatoms: *Nitzschia, Rhizosolenia, Guinardia, Coscinodiscus, Chaetoceros, Asterionella,* etc.

Algae: seeds of a marine plant not yet identified

INVERTEBRATES

Protozoa: Flagellates, Formanifera, Dinoflagellata, Radiolaria, Ciliata

Cestoda

Nematoda

Chaetognatha: *Sagitta* sp.

Crustaceans: Copepoda, Isopoda, Amphipoda, Decapoda

Insects: Hippoboscid flies, carrion flies, Mallophaga, beetles, termites

Arachnida: scorpions, spiders, ticks

Octopus, squid

Apendiculares (starfish)

VERTEBRATES

Anchovy, Pacific Bonito, Peruvian Silverside, Herring, “mulatas” (possibly *Bodianus* spp.)

Geckos

Guanay Cormorant, Peruvian Booby, Peruvian Pelican, Blue-footed Booby, Grey Gull, Band-tailed Gull, Kelp Gull, Swallow-tailed Gull, Franklin's Gull, Inca Tern, shorebirds (Ruddy Turnstone, Western Sandpiper, Black-bellied Plover), Neotropical Cormorant, Red-legged Cormorant, Peruvian Seaside Cinclodes, Black Vulture, Turkey Vulture, Humboldt Penguin, Peruvian Diving-petrel, Black Skimmer, Giant Petrel, Chilean Skua

Cat, rat species, South American Furseal, South American Sealion, whales, dolphins, bats

Of course, the food web begins with sunlight. This warms masses of air and water and establishes the circulatory movements which produce the Humboldt Current and its variations. These movements and the presence and shape of the South American continent result in the upwelling of water, a phenomenon which was discussed above. Upwelling brings to the surface nitrogen and the mineral salts used by plants. Plants can use only nutrients close to the surface where there is enough light for photosynthesis.

The food web can be most easily followed in Figure 14 which has been modified since its publication previously (Vogt 1941). This figure shows the movement of food in the directions indicated by the arrows. For example, the arrows show that humans consume dolphins, bonito, anchoveta, and use (although rarely eat) sealions. Humans are parasitized by ticks and cestodes and their excrement is eaten by flies. The food web is very simplified and includes some probable but still unproved relations.

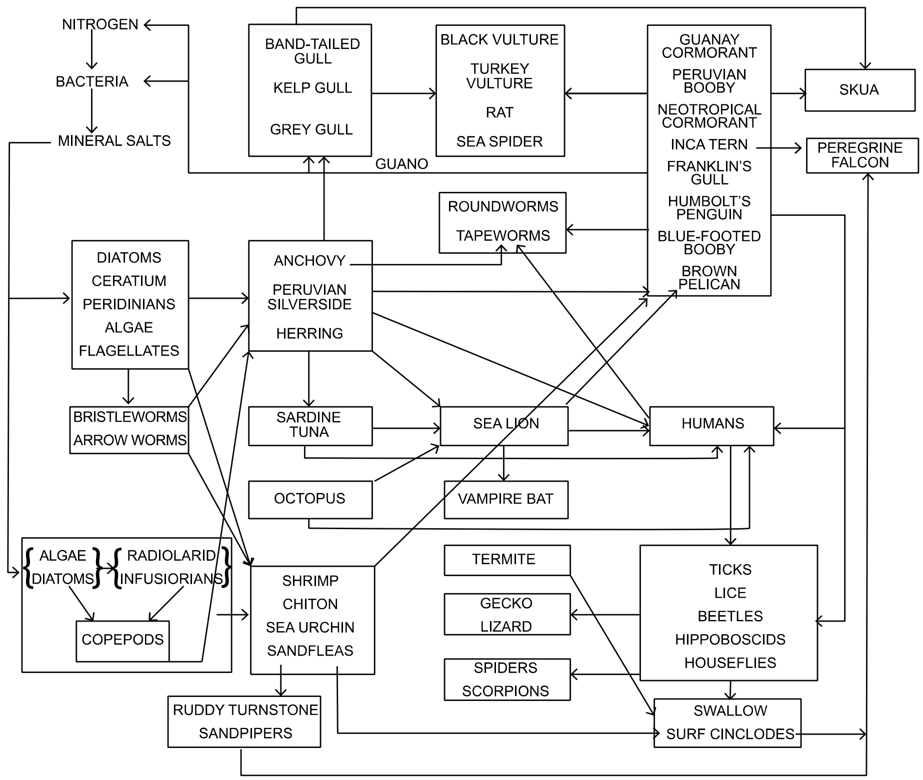


Figure 14. The food web of the Peruvian upwelling.

Mineral salts are used in the basic biological functions of all photosynthetic organisms. These require light which is probably the reason for the great abundance of photosynthetic organisms during summer (see Fig. 8) since this is the period of maximum sunlight. These photosynthetic forms include diatoms and other algae and protozoans such as *Ceratium, Peridinium*, and at least one flagellate which is at times incredibly abundant. During this spring, for example, there was a period when the sea was a yellow-green color, resulting from a super abundance of these organisms. For most of this period, no other plankton was available but anchoveta were nevertheless abundant. It seems that the fish fed exclusively on these flagellates even though each flagellate is only a fraction of a millimeter in length.

The food chain of the birds seems to be very short under normal conditions, with only three levels. The diatoms are the main diet of the anchoveta and these in turn feed the guanays.[23] However, as can be seen in the illustration of the food web, there are a larger number of factors which can play a part. A change in wind direction can affect upwelling which in turn affects the nutrients available to diatoms. This change in winds also results in a rise in sea temperature and is accompanied by unusual movements of anchoveta, either because of lack of food or some other cause, as in the case of the California Sardine. The result is the death of birds by starvation.

Since the nutrients derive in part from guano, we can consider guano birds as creatures which, to a certain degree, self-perpetuate their resources. The extermination of the birds in order to increase the supply of fish, as has been suggested by persons interested in the commercial exploitation of the anchoveta, might result in a considerable reduction in the anchoveta population because the marine "pastures" of this fish would be deprived of guano. Hentschel, according to Murphy (1936), reported that guano had a favorable effect on plankton and this is a factor that we must not neglect, at least until we can show (Sears 1941), beyond a shadow of a doubt, that guano is unimportant.[22]

The small plants are devoured, with some exceptions, by a great variety of fish, marine worms, and other invertebrates. In unusual conditions, the numbers of these will increase rapidly. For example, many more chaetognath worms were encountered in the spring of 1940 than at the beginning of the spring of 1941, and there was very likely competition for food with anchoveta.

The anchoveta appears to be almost as important for the bonito as it is for guano birds and it is also devoured by sealions. If the bonito has increased, as seems likely, because of the commercial exploitation of the sealion, then this increase could have a significant effect on the number of anchoveta. The exploitation of anchoveta by humans, especially when a destructive method like dynamite is used, has some effect on birds so that any immoderate fishery for anchoveta could be disastrous for the birds. I have no doubt that this would be the case if heavy fishing took place in a year of scarcity, such as those which have recently occurred. Even during the years of food abundance, we do not know if there is a sufficient quantity of anchoveta to support a large-scale fishery.

We are again ignorant of additional factors which limit the number of anchoveta, especially such agents as diseases and parasites. I have found and photographed cestodes in the intestines of anchoveta but cannot determine if these are an important limiting factor. Anchoveta are very likely to be the source of the cestodes which are harmful to the birds at times.

Something of the complexity of the problem of the anchoveta can be understood by looking at the situation of the California Sardine: after some fifteen years of study, its biology is still not understood. Meanwhile the overfishing of the sardine has been so excessive that the California Conservation Commission has recommended a reduction of 50 - 65% in the level of exploitation.

Other birds such as the Neotropical Cormorant (*Phalacrocorax brasilianus*), Inca Tern, Humboldt Penguin, etc., compete with the guano birds for food but their numbers are relatively insignificant.[46] Early investigators (Raimondi 1902) considered some of these species important producers of guano but at present their contribution is minor. It would be possible to augment their numbers but it is doubtful if this, given current conditions, would result in any considerable increase in guano.

The synecology of the islands themselves constitutes another problem which involves the number of animals present. The guanay is the most numerous and it owes its advantageous position to the management of the islands by the guano company. The guanay tolerates human disturbance better than do the booby or pelican. This is obvious during periods of guano extraction, when one can see guanays milling around, without taking flight, as a tractor or group of workers passes. It is not unusual for a man to have to walk in front of a tractor to prevent the guanays from being run over. The booby and pelican do not tolerate such human activity, so the guanay has an advantage over them.

The constant increase in the avian population, based on guano harvests, shows that management by the guano company has been beneficial (Fig. 9). The human factor has not been totally favorable, however. Until recently, barnyard fowl were kept on the islands, providing a potential source of avian diseases. Cats were kept which fed more on beneficial lizards than on the rats also introduced by man.

The unfounded belief, common among workers on the islands, that the small gecko is venomous has resulted in its being killed wherever encountered. This may be the reason that geckos are not found at present on many islands. The lack of shelter on the islands has, as explained before, resulted in conditions much less favorable for lizards and has undoubtedly led to a reduction in their numbers. Each lizard represents money to the guano company and should be protected as much as possible.

The sanitary habits of man on the islands leave much to be desired. No relationship has been demonstrated between these habits and the diseases of the birds, but such a possibility cannot be ignored. The workers have the habit of defecating anywhere on an island. The feces are feeding and breeding places for flies and beetles. If it were not for the feces, the number of these insects would be considerably reduced.

Under present conditions, these insects serve as food for the lizards and geckos. If these copraphagous insects are removed, the lizards would have to feed on ticks, Mallophaga and hippoboscid flies, resulting in a decrease in these parasites. In other words, the insect population is increased by filth serves as a buffer against normal predation on the parasites and probably even favors increases of these pests.

In another sense, humans have been too tidy on the islands and have created conditions unfavorable for the birds. The practice of throwing all refuse such as rocks, feathers, etc., into the sea while shipping off the guano, has deprived the birds of a large amount of nesting material and probably increased nesting failures. Under natural conditions, the islands were covered with a thick cap of guano and nests were not destroyed each year. Birds starting to breed could occupy existing nests, which had high rims owing to the larger accumulations of guano. Additionally, the guanays could "scrape," a behavior which rarely occurs at present.

If a human had to carry four or five eggs, it would be much easier to use a bowl than a flat plate, as there is much less danger of the eggs rolling out. Exactly the same reasoning applies to birds' nests. If, after the extraction of guano, the birds must deposit their eggs on bare rock, it is much more likely that one or more eggs or chicks will fall from the nest. Once out of the nest, they inevitably die. This is especially true on steep islands like Mazorca or Pachacamac. In contrast, when the birds can deposit their eggs in old nests lined with feathers, the adults can protect their eggs and young from inclement weather and reduce the chance of ejection. The guano company cannot cease the exploitation of guano, but it can stop the collection of nesting material. The most elementary of examinations shows that nests with an abundance of feathers are built more rapidly, provide a deeper cavity, and appear more comfortable.[47] Additionally, if nesting material were available, birds nesting at the edges of colonies would be less bothered by others collecting nesting material, and nesting success at such peripheral locations would be improved.

It is likely that microclimates on the islands affect the ectoparasites of the birds. To determine this would require meticulous censuses of the parasites. I have tried various methods, but without satisfactory results. I placed flypaper in different parts of the islands, but dust and guano reduced the stickiness of the paper. I then tried to count parasites on collected birds, but this took so much time that the birds were unsuitable for other studies and it did not seem worthwhile to kill enough birds merely to obtain a statistically-significant sample. This would be different if I had undertaken an intensive study of the problem. Counts of parasites collected from my body after working with the birds showed large variations and many small ticks escaped counting until they appeared hours later, under my skin.

I have noticed that, once the wind begins to blow each day, ticks immediately become less active and the guards on the islands complain that large numbers of small ticks are blown onto their houses. Wind may be one of the factors affecting the distribution of parasites because windy areas appear to have fewer parasites. The lower the temperature, the more suitable areas are for the nesting birds.[48]

The complete life cycle of Mallophaga appears to take place on the bodies of their avian hosts. Even though these insects are found crawling over the island and on people, they presumably have no need to abandon their normal hosts, the birds. Any means of controlling these parasites would be less effective than those used against other parasites.

I have learned nothing, because of a lack of time for an intensive study, of the life history of the hippoboscids, although I have seen them eaten with enthusiasm by lizards and swallows.

The ticks spend only a brief part of their lives on the birds. Their life history (for which I am indebted to Dr. Marshall Hertig, National Institute of Health and Public Safety) seems to be the following: the female tick lays her eggs in the soil, frequently under the edges or in cracks of the guano cap or under any object left abandoned on the island. Sandy soils seem to provide the best conditions for egg-laying. If one places two bricks on the surface, one on guano and the other on sand, the sandy one will shelter a much larger number of ticks.

Two female ticks in captivity laid eggs which hatched in 18 days. One clutch contained 605 eggs. Larvae with six feet hatched from the eggs. It would probably be relatively simple to determine how many times the larvae feed and how many metamorphoses they undergo, if artificial sources of food were available, but this has not been not possible.[49] The principal "preoccupation" of the larval tick seems to be eating and it is likely, at least if ticks transmit some disease, that this is the stage at which they do the most damage. When larval ticks hatch, it is common to see young guanays that seem to have their heads, breasts, axillaries and inguinal areas covered with rubies, the rubies being larval ticks engorged with blood. I do not know how much blood ticks ingest, but it must be a considerable quantity during periods of heavy infestation and possibly even a cause of nestling mortality.[29]

I have encountered so few ticks on birds in the period between the fledging of the young and the beginning of the next nesting season that it seems likely that, after their final metamorphosis, the eight-legged adult ticks hibernate for several months or at least enter into a state of torpor during which they don't need much food. It is at this time, after the guano has been removed, that tick control would be most feasible.

Spiders, of which there are a good number of species, and scorpions presumably feed on the parasites of the birds. In earlier times, when the islands were honeycombed with the burrows of Inca Terns, Peruvian Diving-petrels, etc., arachnids were probably much more abundant. At present, the surface of an island is a flat plane of guano, without hiding places, so that neither spiders nor scorpions can survive the treads of the birds. Arachnids are common only on the parts of islands not suitable for birds, such as the leeward sides. Spiders and scorpions are beneficial to the birds and should not be killed. I doubt, however, if they are an effective control of ectoparasites.

Based on my observations, the most important enemy of ticks, Mallophaga and hippoboscid flies are the reptiles: the lizards and geckos. I have already commented on their food (Vogt 1939).[50] After hundreds of hours of additional investigation, it is even more obvious that these reptiles play a major role in the sanitation of the islands. Murphy (1925) found 100 flies in the stomach of one gecko. When the islands are free of human feces and dead birds, the reptiles have little food except ectoparasites which they consequently devour with enthusiasm. The warm months, the period of major activity of the lizards, coincide precisely with the period of greatest activity of the parasites.[51]

Human activities on the islands have been unfavorable for the lizards and probably also for the geckos. My studies, still in progress, seem to indicate two important limiting factors for the lizards. One of these is the lack of refuges from overheating. Many people not conversant with these subjects, including many biologists, suppose that reptiles such as snakes and lizards, or the many other forms which live in the desert, thrive under intense heat and isolation. In reality, as shown by Buxton (1925), desert animals have many adaptations to protect themselves against intense heat. Many desert animals are nocturnal, others have developed special mechanisms that lower their body-temperatures, and many other desert species run rapidly from one patch of shade to another. The gecko belongs to the first group. Its skin is smooth and almost as delicate as that of a salamander, thus it is less suited than the lizard to survive exposure to the tropical midday sun. The lizard survives excessive heat by hiding.

As already reported (Vogt 1940), the inability of the lizard to survive high temperatures was established experimentally. Three lizards were tied out in the full force of the sun and three others were tied near the others but in such a manner that they could shelter from the sun in artificial shelters. Of the three lizards unable to avoid the sun, two died within twenty minutes after showing clear signs of extreme suffering. The other, also at the point of death, was released. In contrast, the three lizards which could take shelter showed no apparent signs of distress. That the traps provide sufficient protection is demonstrated by the fact that more than 500 lizards have been caught without a single mortality.

The limiting effect of high temperatures on lizards can be shown by examining their distribution on the islands. When one walks over an unbroken stretch of guano, there are no lizards even though there may be an abundance of ectoparasites. Lizards are not present because there are no refuges from the sun. Things are completely different if one goes to an area where there are crevices and small holes in the rocks or hollows under the guano. One can be almost certain to find lizards. Lizards cannot survive within a colony unless there is such an area in the center. When the nesting season is over, the lizards disperse over the island but always select places with shelter.

The other important limiting factor for lizards seems to be the lack of nesting places. Lizards lay their eggs in crevices among rocks and probably in sand. It is obvious that lizards cannot breed if they do not have suitable places to do so. Nor are such locations as frequent as shelters against the sun. Marked lizards have been found to have traveled over a kilometer, presumably in search of nesting places. Since the lizards are forced out of large portions of each island during the birds' nesting season which coincides with the main laying-season of the lizards, they are probably forced to use sites at the edges of the colonies.

The cat is an important predator of the lizards and perhaps of the geckos. It would be highly desirable to remove feral cats from the Lobos Islands where they thrive on lizards. The rule that guards may not keep cats on the islands should also be strictly enforced.

The rat is also, in all probability, an enemy of the lizard although I have no definite proof of this. Since both rats and lizards live in the same kind of hiding places, rats probably displace lizards from shelter and eat them and their eggs. It is not clear if the rat is an effective enemy of the birds. Rats live mostly on plants and animals washed up on the tide line, on carrion, human garbage, and feces. However, since they are likely to transmit diseases, destroy property, and because of their likely effect on lizards, all possible means should be employed to ensure that rats do not colonize additional islands.

Exterminating rats from islands will be difficult. It may even be impossible, without a major financial commitment. Rats seem to be immune to certain poisons; some of them consume substantial amounts of rice laced with strychnine without dying. Attempts to poison them with special fish pastes or using pellets such as employed in similar circumstances by the Pan-American Sanitary Bureau have been ineffective. Some rats die but others are immune to poisons or do not ingest baits.

Attempts to exterminate rats using fumigation have also been ineffective because of the numerous holes and vents which occur in the tunnels where they live. I would suggest two possibilities. One would be to institute a complete extermination campaign during the next population crash of the guano birds. When the birds have left the islands and food resources are sharply reduced, the rats may be forced to eat the poisoned pastes and pellets.

Extermination efforts should be conducted during winter. The poisoning should be done in such a way that the lizards do not suffer the same consequences as the rats. Lizards can ingest the poisons set out for the rats as happened during a recent campaign on the Chincha Islands. More damage than good may have been done, based on the large number of lizards killed.

The only way to avoid this is to set out a certain number of plates of poison each night when the lizards are in their shelters and to collect the plates each morning before the lizards are active. It should be obvious that such efforts should not be attempted when guano is being extracted, thus ensuring that only poisoned food is available to the rats.

Another promising method which has yet to be tried on the islands as far as I know is the use of ferrets. Managed by an expert, these could exterminate rats on Chincha Norte in a short time. Extreme care must be taken, however, to avoid the permanent introduction of ferrets to the islands. Only a single sex should be employed on an island.

Rats seem to be subject to marked cycles of abundance and scarcity. During the summers of 1940 and 1941, rats were very abundant on Chincha Norte, but there were only a few during the spring of 1941. The causes of such cycles can be determined only through careful study. Such investigation may be the key to the extermination of the rats as described by Huxley (Elton 1927).

We ought to consider another factor in the economy of the islands, the presence of avian species other than those that produce guano.[52] These birds are not numerous but they certainly play a role in the insular ecosystems. Vagrants from the continent visit from time to time. One of these, the Seaside Cinclodes (*Cinclodes nigrofumosus*), has taken up permanent residence on the island. In addition, a good number of shorebirds visit the islands throughout the year. These feed on the higher parts of the island where there is little food, except the ectoparasites of the guano birds. These birds should be protected. Indeed, the guards on the islands should be instructed that no species should be killed, except perhaps the Andean Condor.

I have already suggested that the vultures and the gulls are beneficial for the guano birds, based on the following reasoning: during the summer of 1939 - 1940, a considerable number of birds deserted their nests on the Ballestas Islands because of food shortages. At one nest, the male left first, followed several hours later by the female, leaving the eggs uncovered.

These naturally were eaten by scavengers. Forty-eight hours later, the female returned and began defending the nest against other guanays (females do not defend nests unless already paired with a male). As reported above, in courtship, the male guanay takes possession of the nest site and is then chosen by the female. In other words, the female guanay is not territorial, until paired). Therefore, it seems likely that the female returning to defend the nest after forty-eight hours was probably the female that laid the original eggs rather than a new bird, establishing a territory. If the eggs had not been devoured by gulls or vultures, the female would probably have resumed incubation. After two cold nights, the embryos would probably have already been dead so that further incubation would have been a waste. Fortunately, however, the gulls and vultures took the eggs, releasing the female guanay from her nest. Considering the length of the nesting season (Fig. 11), it is likely that she sought another mate and, if food conditions were favorable, laid a second clutch. Therefore the destruction of the first clutch is actually an advantage to the guanay.

This discussion of the synecology of the guano birds could be extended to book length, despite the shortage of information. However, we would gain little from this. We lack data, leaving us to make a series of suppositions. In addition, many of the ecological relations (Fig. 14) have little importance for the guano birds.

The most important lesson of this consideration of synecology is that the birds do not live in a vacuum. They are an integral part of their environment; they are profoundly affected by many factors in this environment. Any perturbation of environmental conditions could affect the entire community structure and produce serious repercussions for the guano birds.

MANAGEMENT RECOMMENDATIONS

As already mentioned, the main purpose of these studies has been to determine, as far as possible, which factors limit the numbers of birds. If some of these are susceptible to human management, they should be managed so that the avian population will increase. The second purpose has been to determine, if possible, methods to allow increased guano harvests.

With respect to the birds themselves, there are certain factors which obviously can not be altered. Nothing can make them nest more frequently than their natural nesting cycle. Nothing can increase the density of nests of the Guanay Cormorant above roughly 400 per 100 m^2. Therefore, in making management suggestions, certain factors simply cannot be considered. In addition, to avoid repetition, I will omit the reasons behind my recommendations as much as possible, since these have been expressed earlier in the text.

The recommendations should, therefore, be read after a careful examination of the rest of this report.

The first problem, concerning the number of birds, can be divided for convenience into two parts. I have already mentioned that the principal factor controlling the number of birds is the periodic mass mortality which takes place roughly every seven years. Since this seems to result from a decrease in the availability of anchoveta, it probably cannot be stopped. But perhaps there are ways to reduce its severity. The second phase of the problem, once we accept the inevitability of the periodic decreases in the guano bird population, would be to identify means to be taken to reestablish the population, after a die-off, as rapidly as possible and to ever higher limits.

As the principal cause of the mortality is lack of food, protection of the food supply is the best method to combat mortality. As mentioned above, virtually nothing is known of the biology of the main prey species, the anchoveta. A careful, scientific study of this species is required as soon as possible. Such a study should be conducted over at least eight years. Preliminary results of work by Dr. Sears and myself show clearly that such a study is practical and would yield valuable results. When we have studied our data more carefully, a special report will be published in this bulletin.

The anchoveta is the basis of the guano industry, one of the strongest parts of the Peruvian economy. It brings in millions of soles annually and is the main source of fertilizer for national agriculture. In view of its enormous importance and value, the cost of an adequate investigation of the anchoveta, to place its exploitation on a biological basis, would be a most necessary expense. Such an investigation should be linked, as much as possible, with other factors such as oceanography, meteorology, planktology, ecology, and studies of fish species from a commercial point of view.

Until this study is completed, we will have to rely on practical experience. Since the anchoveta is essential for the birds, it is obvious that it has to be protected against any possibility of an excessive reduction in its numbers. This does not mean that the anchoveta cannot be exploited by man, but that, until we know much more about it, its exploitation should be rigorously limited by the Peruvian government, to avoid any risk of losing the guano birds. If the anchoveta were exploited to the same extent as the California Sardine or New England Shad, both of which have suffered the consequences of overfishing for the production of fish meal, the guano birds of Peru would be seriously affected. I base this conclusion on three years of careful study.

The present anchoveta fishery, done by hundreds of small boats, should be investigated to determine how many tons of anchoveta are landed annually. It would perhaps be desirable, during periods of great scarcity, to limit the fishery to these small boats. The use of dynamite for fishing, which is believed to be very common, should be combated vigorously.

In years when the population crashes, the most important cause of mortality, after starvation, seems to be disease. This undoubtedly comes in large part from weakness promoted by hunger. Only investigations of avian pathology can determine which diseases are involved, and how they are contracted and spread. Raising domestic fowls on the islands should be stopped. There is no justification, under any circumstances, for running the risk of unleashing an epidemic among the guano birds because of diseases brought to the islands by such fowls.

The same reasoning applies to the personal habits of the workers. We do not know if human feces are a source of avian disease but caution should be exercised until all doubts are removed. Simple toilets, like those constructed for the guards, should be provided for the workers who should be compelled to use them. Needless to say, if the latrines are clean and comfortable, the education process will be easier.

Despite such efforts to prevent diseases, they can be expected to occur to a certain extent. But they can be reduced to a large extent by the disinfection of the islands after each period of guano extraction. After considering a large number of methods, I have come to the conclusion that the cheapest, most practical, and probably most effective disinfectant is fire. Flame-throwers are commonly used both in Peru and elsewhere to control a variety of pests. With these, as outlined in earlier reports, the disinfection of all the islands except the Lobos (which are probably too large) would be feasible.

The flame-throwers are supposed to produce a heat of over 1,000 ^{O}C, which should kill any tick, Mallophaga, or fly. In addition, the flame also destroys bacteria and the spores of *Aspergillus*. A systematic and complete burning of the islands, once they are cleared of guano, would improve conditions considerably.

One warning about the use of flame-throwers: the flame should not be used in holes and crevices which serve as refuges for the lizards. Flames should be applied only to the surface of the island or to crevices too small for the lizards, to avoid burning them. This method will not prevent all diseases but, together with other recommendations, will reduce disease considerably.

If the food supply is protected, wherever possible, and steps are taken to prevent disease, it is unlikely that man can do anything more to reduce the effects of years of population crashes with one exception, the reconditioning of the islands to make them more aerodynamic.

Such changes would benefit birds during both normal and abnormal conditions. In periods of abnormal winds, the birds would not be forced to abandon their nests as they seem to have done during the past two years (Vogt 1941). Improved windflow over the islands would increase nesting space for the birds when populations reach their upper limits, so that the population would be greater than at present.

Improving the aerodynamics of the islands is similar to changing the wings of an airplane. There are two ways to go about such improvements. The first would be to dynamite the obstacles which impede the flow of air over the surface of each island. There are many islands where this would be required on only a small scale as, for example, the southern part of Isla Santa Rosa; but there are others which would require the dynamiting of enormous rock masses. I am confident that Los Ovillos and San Gallán could be added to the chain of productive guano islands by this means. It would also be possible to make more platforms like those on Chincha Norte, using dynamited rock.

Work on such a great scale would be costly. However, improvements would be permanent and the costs would be recouped as long as the new areas continued to produce guano. When the present war ends, many governments will need to dispose of enormous quantities of explosives; Peru could then obtain explosives inexpensively for improvements to the islands.

In addition to dynamiting obstacles, the same purpose could be obtained by filling gullies. On many islands, the leeward sides and the bottoms of gullies are completely useless for nesting. If crevices were filled until they presented a smooth surface to the wind, nesting area would be increased. Many such gullies are quite small and could, in some cases, even be filled with local material. Waste materials such as rocks, which are separated from the guano when it is extracted, should be thrown into the gullies rather than the sea. If cheap explosives are available to dynamite obstacles, then the resulting rubble can also be used. Finally, such work should be supervised by engineers, if possible, in consultation with aerodynamics experts.

Many islands possess "dead areas" of sand that, although excellently located, are unsuitable for the birds. Sand absorbs more heat than rock so temperatures are too high for the birds. Such areas should be covered with cement or with some similarly-colored material, such as saltpeter. This would not only increase nesting space but would also remove the present gaps in the colonies. Such gaps, by increasing the surface areas of the colonies, increase the number of nests which experience the problems peculiar to such sites. If this method is used, birds might be induced to nest on Isla La Vieja which has been avoided up to now.

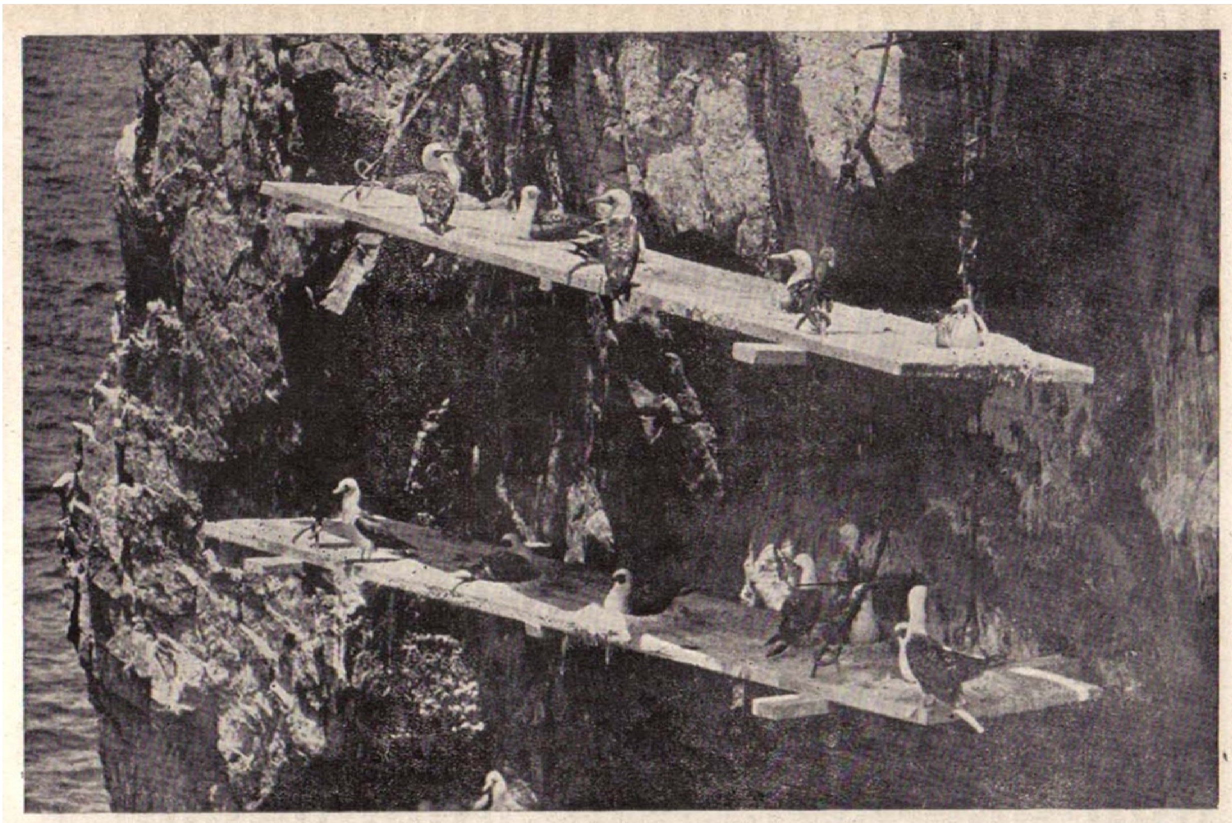
As already mentioned, it seems that Peruvian Booby numbers have been reduced by competition with the guanay and Peruvian Pelican. Whether by necessity or choice, the boobies nest in large numbers on the ledges of cliffs. Nestling mortality caused by birds falling into the sea has been mentioned by earlier workers. Most of the guano from cliff-nesting birds is not available to the guano company. It should be possible to improve the nesting conditions of the booby and assure a greater guano harvest from this species.

This could be done by constructing a type of nesting-shelf. Boobies readily accept these shelves which are much more secure for the nestlings and collect a good proportion of the resulting guano.

While this project would be very expensive at present, it should be considered when world conditions have changed, especially if the future industrial development of Peru reduces the cost of the raw materials. Capital investment is the only impediment for the gathering of thousands of additional tons of guano each year. The expense would be paid off over as many years as the nests on the planks continued to supply guano.

Boobies nest freely on the wooden platforms on the islands, on the roofs of houses, and also on artificial shelves on Isla Chincha Norte, despite the fact that their population is greatly diminished and competition for space appears to be reduced. On natural ledges, there are great gaps which would be full of nesting boobies in normal circumstances. Evidently the flat, clean, artificial sites are preferred as nesting habitat. By taking advantage of this preference, the guano company could considerably increase the guano harvest. In some cases, it would be possible to cut shelves in the rock itself. In other cases, it would be necessary to construct artificial shelves. Wooden platforms last approximately 20 years according to the guards. There is no reason to believe that the wooden shelves would not last as long. If they were made of asphalt or some other material more resistant than wood, they would last indefinitely.

Image B. Wooden shelves placed on the western side of Isla Chincha Norte where, as you can see, boobies are nesting.



During the present world war, when construction costs are too high for large-scale building, different types of platforms could be constructed as experiments and located in different places, to determine the most suitable methods. When economic conditions improve, the guano company would be ready to construct such platforms on a grand scale.

I have mentioned lack of nesting material as one of the factors limiting the population of guanays. This problem has been partially solved by removing guano every other year. Extraction should never be done more frequently. In addition, the company should cease throwing away feathers, stones, and marine plants sifted from the guano and save these for the birds to construct their nests. Although this supply will increase rapidly, it would be good to supplement this with an artificial supply of hay and straw.

If the islands are to be disinfected with fire, the nesting material should also be cleaned. This could be done using very volatile solvents or, lacking these, by placing the material briefly in boiling water in adequate tanks installed on each island.

Guano extraction campaigns should be as brief as possible, even shorter than at present, if possible. The decrease in the number of pelicans on the Lobos Islands may have been caused by the guano campaign, which extends until September when pelicans normally begin their courtship.

The present efforts at predator control are a waste of money and, in some cases, do more harm than good. I would recommend that, unless practices change drastically, the control of gulls and vultures be suspended. Sealions should be rigorously protected on the islands and their culling should cease, in view of their great value and reduced number. The few birds killed by the sealion are probably a small price to pay for all the good they do. Sealions have both biological and economic value. I would suggest only limited harvesting and then, as in the case of guano, on a rotating basis along the coast. The best results might come from dividing the coast in three and allowing harvesting in only one zone each year.

Hunting of the condor should also be limited. This bird is one of the most majestic in Peru and is linked to a national culture which has its roots in times going back well before the arrival of the Conquistadors. Fortunately, a considerable number still “spread their wings" over the countryside. In North America, large amounts are spent annually to save the few surviving condors. Killing of condors on the islands should be limited to those birds actually found causing damage in the colonies, at least until all condors at the islands have been proved to be destructive.[53]

Introductions of cats onto islands should be prohibited. Where they have become established, they should be exterminated. The same should be done with rats, even though their eradication may be more difficult or, at times, even impossible.

Thousands of young guano birds die annually, as mentioned, because they fall from the island before they can fly. This could be avoided at relatively little cost, by constructing ramps which lead to the water. On islands such as Ballestas Norte, a route to the sea could easily be constructed using dynamite. On islands like Macabi, steps of wood or other material would need to be constructed. There is no doubt that the birds would use them. The disinfection of the islands with fire would protect the birds all the time, in both normal and abnormal years.

The lizards and geckos are perhaps the best control of avian parasites and ought to be protected for this reason. Their only enemies seem to be cats and rats. The main factor limiting lizard populations is the lack of shelter against the sun. Artificial shelters could easily be supplied. The shelter-traps used on Isla Chincha Norte have proved a great success. They are simple wooden platforms of 1 x 1 x 0.25 m which are raised four cm over the ground by wooden strips. These shelters should be distributed over the island wherever there are no natural shelters. Eight per hectare would not be excessive. A cheaper type of shelter might prove even better, such as flattened or tubular bricks or even slabs of rock slightly elevated above ground.

Most islands probably have suitable nesting areas for lizards around their edges. If this is not the case, gravel layers could be placed in gullies on the leeward side of the islands.

When an island does not have lizards, it would be useful to introduce several dozen, with a ratio of one male to each four or five females. Although we know very little about the gecko, it also could probably survive transplantation. It would probably be better to introduce reptiles from the other islands, rather than from the coast. I have examined hundreds of lizards on the islands without encountering a single tick, in contrast to mainland specimens. Of course, we do not know if these ticks are dangerous but it is better to avoid problems. Lizards for introduction could easily be collected on Isla Chincha Norte.

When birds are ready to fly, a small number of them crash against cables, poles, and other obstacles. These poles are to a certain extent necessary on the islands since they are used for the extraction of guano, but their number should be kept to a minimum and, where possible, they should be removed at the end of a guano extraction. On the other hand, large structures such as buildings do not seem to pose any problem for the birds.

Guano birds are hunted in Peru, but only to a minimal extent. Reports from neighboring countries suggest that hunting is much more common. Treaties protecting guano birds should be negotiated with all the countries on the west coast of South America and these should be encouraged to pass laws implementing the treaties. Hunting is a problem which will not be solved over a few months. Above all, it requires education. The importance of the protection of birds, be they insectivorous, falcons, owls or guano-producing, should be taught in all primary schools as part of the curriculum. If this is done, the youth of Peru would begin to realize that guano birds are among the most valuable patrimonies of their country.

This combination of changes applied to the birds is almost certain to result in a major improvement for the birds, a reduction in mortality and an increase in the rate of population expansion. In other words, the guano company has the means to reduce the resistance of the environment and to produce more guano. It could also gather a greater proportion of the guano already produced. Using the nesting platforms already described, it could obtain another 10,000 to 25,000 additional tons of booby guano per year, and perhaps even more. The company could also obtain a certain amount of guano by destroying the loafing places of the birds away from the islands. Many of these sites are small, inaccessible rocks. If these were destroyed, the birds would be forced to rest on the islands themselves and their guano would be available.

As I have repeated over and over in this report, the overall problem of the production of guano is enormously complex. No one is in a position to give the last word about the ecology of the birds but, the more we know of them, the more effective will be the suggestions which are made to improve their condition and increase their numbers.

Every effort should be made to increase this knowledge, both through intensive investigations in the various fields involved and through cooperation with visiting scientists. The latter has been very beneficial from the time of Dr. Murphy to the recent visit of Dr. Sears; the guano company should make every effort to continue this symbiosis.

This is not the place to outline a program of future investigations, but I would like to suggest certain changes of procedure that would be of considerable benefit when future studies are carried out. In my opinion, it would be possible to obtain greater efficiency from the guards on the islands. These include a good number of capable individuals who could be even more productive than they are at present. To obtain this would require a reeducation of personnel, to a new point of view.

The guards have to be made to understand that their fundamental mission is to ensure that the birds are not disturbed. They are an important part of a great Peruvian institution, an institution which has received world-wide admiration for its achievements in conservation. A large part of this credit should be shared with the field workers on the islands.

I have lived and worked with the guards and have learned to recognize the importance and ability of these men. If their contribution is recognized, more and better work can be asked of them. Naturally, this can be done only through education.

I believe that it would help to have a "Section for Guards" in the bulletin of the guano company that would publish information for their use, report on their activities, and provide words of motivation or praise for their work. It would also be useful to create a “school” for the guards in Lima. Half of them would come to the school for one or two weeks every year with the guano company covering costs.

Each session of the school would go over the results of the past year in simple terms understandable by the guards, set new directions, or provide instruction of a general nature. This type of school is run by conservation commissions in the United

States and the participants are at a comparable cultural level to the guards of the island. The results have been productive and excellent.

If a similar effort were made here, the results should be equally satisfactory. This school would give administrators, heads of technical sections, and investigators an opportunity to instruct the guards concerning problems with which they should be familiar, and to show them the routes to be followed to greater efficiency and usefulness. If, during the school, prizes could be awarded and recognition given to certain guards for their outstanding efforts, the morale of the guards would be restored after its inevitable decline during the months of isolation on the islands.

Advantage should also be taken of the enthusiasm of many guards for reading, despite the scarcity of books. If they were given elementary texts related to their work, I have no doubt that some of them would be read and absorb the contents. Eventually, it would be useful to prepare a "Manual for Guards" and to require them to become familiar with the contents. Earlier, I submitted detailed suggestions for new instructions for guards. I will, therefore, give only a summary to indicate how I think the work of the guards can be improved.

The relation between humans and birds should be made clear and the guards should be trained in the management of the various species under different conditions. It seems strange but many of them do not understand the concept of management. They should be informed about diseases and methods to decrease these. They should learn the basics of natural history so that they can be more exact in their reports of the causes of mortality (i.e. disease, high temperature, lack of food, etc.).

They should be informed of the relationships of other birds with the guano birds and with the methods used by the guano company to control predators. If banding continues, as I hope it will, the reasons for banding should be explained, as well as the best methods for banding and for recording information. The majority of the guards could improve the quality of their reports. This should be considered individually for each guard. They should be instructed to look for bands and to report those encountered.

The company should insist on careful bimonthly reports of all birds of any species found dead. Guards should continue their observations during guano extractions. Each I5-day period should be summarized with a report so that gaps will not exist in the records of the guano company. Guards should be taught that the presence or absence of birds from islands can be caused by such a wide variety of factors that they are not to blame for the absence of birds. All this will result in much more accurate reporting.

I am not suggesting that the guards can be turned into scientists. However, with training, their observations can be of increased scientific value. In addition, wherever possible, the guards should be provided with instruments of the best quality available. Data, such as sea and air temperature, speeds and velocities of winds and current, are so essential for oceanographic, ecological, ornithological, meteorological and ichthyological studies that it would make sense for the company to install instruments to measure these phenomena on three or four islands along the length of the coast (at present, inexpensive but accurate scientific instruments are not available). Many observations cannot currently be interpreted because of a scarcity of such data. If the company accumulated data using such instruments, the results would be economically beneficial in the long-term.

Finally, it would be useful to make a complete and accurate inventory of all the records of the company, as I have done for seven islands and three headlands. The guano company has a tremendous amount of valuable data in its archives concerning the birds and the ecological phenomena related to them. Until these data have been properly organized, they are virtually useless. If the data could be tabulated and published, it would be a great help not only for the technicians of the guano company but for biologists. The resulting work might, in turn, benefit the guano company.

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NOTES ON THE TRANSLATION

1. El Niño as used by Vogt is a southward-flowing coastal current. More recently, the term has come to mean a suite of environmentally anomalous conditions in the Pacific (Barber *et al.* 1983). The term "El Niño/Southern Oscillation" or "ENSO" is now commonly used to describe a suite of world-wide anomalous events associated with El Niño.

2. Warm water may advect inshore from warmer oceanic areas or upwelled water may come from a warm rather than a cold source at greater depths (Barber *et al.* 1983, Smith 1983).

3. Quinn *et al.* (1978) found that the frequency of El Niño depended on their severity: “strong” events occurred at 12.3 year intervals, strong and moderate events at 5.4 year intervals, and strong, moderate and weak events at 3.7 year intervals.

4. Conditions appear to have been normal along the Peruvian coast during Darwin's visit since he writes:

"In the night anchored in the outer part of the harbor of Callao. Our passage (from Chile) was a short one owing to the steady trade wind. . . The temperature is by no means warm; in approaching these low latitudes I did not experience the delicious mildness, which is known for a few days in the Spring of England, or in first entering the tropics in the Atlantic. . . during nearly every day there is a thick drizzle or Scotch mist which is sufficient to make the streets muddy and one's clothes very damp. People are generally pleased to call this “Peruvian dew" (Keynes 1979).

These are typical conditions during upwelling along the Peruvian coast.

5. Other analyses of guano bird populations include Hutchinson (1950), Jordan & Fuentes (1966), Schaefer (1970), Duffy (1983a, b), and Tovar *et al.* (1987) for Peru; and Crawford & Shelton (1978), Duffy & La Cock (1985), and Duffy & Siegfried (1986) for southwestern Africa.

6. Duffy (1983b) found a density of 3.0 Guanay Cormorant nests/m^2 in 1977 - 1978 when the population was smaller than during Vogt's work.

7. Vogt's estimate of guano production appears to be misprinted. The original gives total guano production on ten squares of area 100 m^2 as 19,293.1 kg but Hutchinson (1950) points out that it should probably be the mean of the ten squares of 100 m^2.

8. Heavy rainfall is a common feature of El Niño, both in Peru and elsewhere throughout the world, although other changes such as droughts or increased frequencies of storms also occur (Murphy 1925a, Berlage 1966, Caviedes 1975, Rasmusson & Wallace 1983, Vines & Tomlinson 1985).

9. Winds suitable for upwelling may persist or even increase during El Niño (Enfield 1981).

10. Hutchinson (1950) concluded that Peruvian guano deposits date from 2,000 - 3,000 yr B.P. and that, previous to this, most deposits took place south of Bahia de la Independencia, extending into Chile. Hutchinson suggested that the present-day zone of guano deposition was previously exposed to much heavier rainfall, corresponding to the tropical climate found today in northern Peru and Ecuador. De Vries & Schrader (1981) and De Vries & Pearcy (1982) provide independent support for this, based on diatoms and fish-scales found in coastal sediments off Peru. They suggest that, during the

Second Neoglacial Period (2700 - 1800 yr B.P.), Peruvian coastal waters north of 12^0 S (approximately the latitude of Lima) were affected by warm-water intrusions that would have produced conditions similar to those suggested by Hutchinson. Guano deposited before the Neoglacial Period would have been washed away by rains and the guano birds would presumably have moved south during this period.

11. Kubler (1948) discusses human artifacts from guano deposits. The deepest artifacts, attributed to the Mochica culture, have been found at 18 m depth.

12. Hutchinson (1950) reviews estimates of guano deposits on the individual Peruvian islands.

13. Murphy (1925b) provides a vivid picture of the human devastation caused by the industry. Heyerdahl (1958) discusses the effects on the inhabitants of Easter Island. After being taken into slavery to work on the guano islands, the survivors were returned to the island, infected with smallpox which almost annihilated the remaining population.

14. Ward & Zahavi (1972) subsequently developed a theory that aggregations of birds serve as "information-centres" for the location of food (see also Waltz 1982). The role of flocking in Guanay Cormorants may be adaptive when feeding on schools of fish (this study, Duffy 1983b) but its role in locating food needs to be investigated.

15. Although Vogt argues that regurgitation may benefit the whole colony, it is hard to see how the individual providing the food benefits, especially if it has its own young to feed. A simpler explanation may be that the adults are harassed until they

regurgitate, so the behavior is a form of kleptoparasitism or food piracy, rather than altruism.

16. Berry *et al.* (1979) working on Cape Cormorants (*Phalacrocorax capensis*) along the desert Namibian coast at 22^0 S concluded that photoperiod and seasonal changes in wind-patterns were most likely to control seasonal patterns of sexual activity.

17. cf. Smith (1966) for analogous experimental work on *Larus* gulls.

18. Vogt anticipated findings (e.g. Patterson 1965, Coulson 1968, Tenaza 1971, Gochfeld 1980) that nests at the peripheries of colonies have lower nesting success than do central nests. Siegel-Causey & Hunt (1981) examined group vs. solitary or edge nests in Double-crested (*Phalacrocorax auritus*) and Pelagic Cormorant (*P. pelagicus*) colonies.

19. Again, Vogt suggests an idea developed independently by Lack (1968) that breeding season is linked to maximum availability of food. More recently, Ricklefs (1983) has suggested that many aspects of the breeding biology of seabirds are limited, not by food itself, but by the ability of adults to bring sufficient food to the nest. Nest guarding and brooding represent major constraints, as Vogt suggests, since they limit adult foraging to one adult at a time. While absolute food demand may be greater after the young can be left alone, Vogt argues that food delivery by adults may be under most pressure in the first month after hatching when one adult must remain at the nest.

20. African Penguin (*Spheniscus demersus*) stomachs are almost completely evacuated (< 20% mass) eight hours after ingestion (Wilson *et al.* 1985). Evacuation by flying seabirds may be faster (Laugksch & Duffy 1986).

21. Average mean daily food intake as a percentage of body weight has been estimated for Guanay Cormorants as 23% (Jordan 1959, 1966), while Laukgsch and Duffy (1985) provide data that yield values of 14 - 15 %. The ratio of conversion of fish to guano has been estimated as 5.7: 1 (Forbes 1914); 32: 1 (Gamarra 1941, but this value is almost certainly wrong according to Hutchinson 1950); 9.8 - 15.3: 1 (Hutchinson 1950); 6.7 - 7.8: 1 (Avila 1954); 7: 1 (Barrero 1959); and 8: 1 (Jordan & Fuentes 1966) for Peruvian birds; and 7.26: 1 (Jarvis 1970) for guano birds off southwestern Africa. Jordan & Fuentes (1966) note that fish is converted to fishmeal at a ratio of 6: 1. Jarvis (1970) calculated that fish converted into guano had twice the economic value of fish used by fish-processing plants in South Africa.

22. The importance of guano run-off from nesting islands is unclear. Vogt, (this paper), Hutchinson (1950), and Sears (1954) suggest that guano may be an important source of nutrients off Peru. MacCall (1984) suggests that guano run-off may replace upwelling as a source of nutrients during El Niño events, sustaining local marine productivity. Golovkin & Garkavaya (1975) show that seabird colonies in the Barents Sea produced heightened levels of nutrients up to 2.5 km from the colony site. Murphy (1923), Golovkin (1967), and Zelickman & Golovkin (1972) report stability of plankton communities near guano islands, apparently caused by guano input. However, Bedard *et al.* (1980) consider that seabird guano had a negligible effect on nutrient levels in the St.

Lawrence Estuary, Canada. The Canadian study involved non-breeding birds; the others involved breeding colonies and this may explain the different results.

23. Anchoveta off northern and central Peru feed primarily on phytoplankton while those off southern Peru and Chile eat zooplankton (de Mendiola 1980).

24. Foraging trips in 1977 - 1978, following an El Niño, usually lasted less than two hours (Duffy 1983c).

25. Although nothing appears to be known of Sooty Shearwater diets in Peru, the birds are predominantly piscivorous in the upwelling ecosystems off the west coast of the United States (Wiens & Scott 1975, Chu 1984), off South Africa (S. Jackson pers. comm.), and in subantarctic waters of the western Pacific (Ogi 1984). In the non-upwelling but seasonally-productive northwest Atlantic, euphausiids predominate in their diets (Brown *et al.* 1981). Given their abundance in mixed feeding aggregations in Peru (Duffy 1983d), Sooty Shearwaters probably depend on the same fish as do the guano birds.

26. In subsequent El Niños, four factors appear to have reduced anchoveta spawning success: predation by other fish species (Santander & Flores 1983); the wrong sorts of food being available to allow survival of small young (de Mendiola & Ochoa 1980); spawning adults being more densely distributed than in normal years, leading to a greater degree of cannibalism of eggs and young (Csirke 1980); and adults not coming into breeding condition (Tsukayama & Alvarez 1980). Walsh *et al.* (1980) support Vogt's conclusion that, during El Niño years, anchoveta move south (cf. Santander & Flores 1983) and spawn in unsuitable conditions for the survival of larval anchoveta.

27. Subsequent tagging of anchoveta (Jordan & Málaga 1972) showed that fish marked at 13º 05'S moved up to 480 km north and 770 km south to the Chilean border during 1970, a non El Niño year.

28. Q. M. Geiman (in litt.) spent five days working with Vogt to determine the diseases present in guano birds during El Niño. Unfortunately, lack of funds prevented further work.

29. Ticks have been found to cause extensive desertions of nesting sites on numerous Peruvian islands (Lavalle 1923, Duffy 1983c).

30. Huacho and Punta Salinas arboviruses are known from *Ornithodoros arnblus* ticks in Peru (Nuttall 1984). They may be associated with human illness following bites (Clifford *et al.* 1980), but there is no evidence they affect guano birds.

31. Murphy (1954) and Paulik (1971) also warn against overfishing; nevertheless, a combination of overfishing and an anchoveta recruitment failure during the 1972 El Niño led to the collapse of the fishery (Idyll 1973). Guano birds were affected by the fishing industry even earlier, never recovering from the 1965 El Niño (Jordan and Fuentes 1966, Duffy 1983a, Duffy *et al.* 1985).

32. Johnson (1965) reports both a regular, annual migration during the non-breeding season and irregular, massive emigrations to Chile during El Niño years. He also reports that Guanay Cormorants breed in central Chile (see also Schlatter 1985).

33. Johnson (1965) notes that Peruvian Boobies occur in "fairly large nesting colonies ... at certain points along the Chilean coast" but he was unable to locate breeding colonies of Peruvian Brown Pelicans. Guerra (in Schlatter 1984) reports a Chilean

population of Peruvian Pelicans of 400 pr. Resident numbers are considerably augmented by migrants from Peru, ranging south to about 40^0 S (Johnson 1965).

34. Jordan & Cabrera (1960) report on 464 recoveries resulting from banding activities in 1939 - 1941 and 1949 - 1953, finding a southerly movement after the breeding season.

35. Murphy (1925b), Hutchinson (1950), Nelson (1978), and Duffy (1983d) discuss competition for nesting space among the guano bird species. The species differences in thermal tolerances mentioned by Vogt are mediated by differences in dominance, tolerance to human disturbance, and slopes at nest sites.

36. Nelson (1978) reports Peruvian Booby nest densities of $1.5/m^2$ at high population densities; Duffy (1983) found densities of $1.9 n/m^2$ in 1977 - 1978.

37. Galarza (1968) reports the fledging period to be 98 days and Nelson (1978) believes Vogt's estimation of 60+ days to be too short, but noted that even 98 days is much briefer than for other booby species. In 1977 - 1978, at Isla Mazorca, the first Peruvian Booby eggs were laid on 25 November and the first young booby was seen flying on 28 February, suggesting a fledging period of 95 days, assuming that the first eggs laid produced flying young (Duffy pers. observ.).

38. Comparison of the number of young in cliff or flat areas on Isla Mazorca showed no consistent differences (Duffy 1983b). While young from cliff nests may fall into the sea, young from nests in flat areas are vulnerable to attacks by neighboring adults.

39. See also Fuentes (1965) for a report on guano bird numbers near Guayaquil, Ecuador, during El Niño.

40. Jordan (1958) reports on subsequent band recoveries which confirm both north and south dispersal and evidence of a post-breeding movement to the far south.

41. Galarza (1968) found that 77% of the diet (number of prey items) of three young pelicans on Isla Chincha Norte was anchoveta.

42. On Isla Mazorca in 1978, pelican nest densities were 2.7 and 3.0/m^2 at two sites (Duffy 1983b).

43. Peruvian Brown Pelicans are regular pirates of both Peruvian Boobies and Guanay Cormorants; "cooperative" piracy by pelicans, as described by Vogt, was frequently observed at Isla Mazorca (Duffy 1980).

44. No further work was done because of lack of funds (Q.M. Geiman in litt.).

45. Perene is a small Andean town, 200 km inland, near Cerro de Pasco, Peru, on the Amazonian side of the cordillera.

46. See Duffy *et al.* (1985) and Tovar *et al.* (1987) for estimates of recent guano bird populations in Peru.

47. Jarvis (1970) argued that annual guano extraction removes nesting material for Cape Gannets (*Morus capensis*) in South Africa, reducing nesting success. On the other hand, Duffy (1983c) has shown in Peru that tick populations build up with increasing number of years since the last guano extraction and this would presumably reduce nesting success.

48. On Isla Mazorca, tick desertions began on the windy, coolest part of the island (Duffy 1983c), suggesting that temperature may have minor effects on ticks compared to other factors.

49. Clifford *et al.* (1980) describe life stages and hosts for *Ornithodoros amblus,* and Khalil & Hoogstraal (1981) summarize life-history data.

50. Vogt (1939) records that stomachs of *Tropidurus peruvianus* on islands contained 50% ticks by frequency of occurrence. Duffy (1983c) found ticks even more prevalent in lizard diets on Lobos de Tierra. Dixon & Wright (1975) report the mainland diet of *peruvianus* as "sand fleas, cockroaches, beetles, ants and flies." Pefaur & Lopez-Tejeda (1983) found that *T. peruvianus* on the mainland is "omnivorous and captures arthropod prey in proportion to its availability. The most important items in the diet were adult and larval beetles, ants, and flies."

51. Huey (1974) has shown that *Tropidurus peruvianus,* even in northern Peru, is under severe lower thermal constraints during winter. The colder, more southerly guano islands would be an even more difficult thermal environment.

52. Galarza (1968), Duffy (1982), and Duffy *et al.* (1985) list other bird species from guano islands.

53. Killing of condors by guano island guards has been stopped.

54. Not all of the references cited by Vogt in his text could be located. The information printed is that provided by his text or the original references, when these could be identified, rather than those in the Spanish translations of his papers reprinted in the *Boletín de la Campañia Administradora del Guano.*

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FIGURES

Figure 11. Monthly reports of nesting by Guanay Cormorants, Peruvian Boobies, and Peruvian Brown Pelicans in relation to reports of food abundance and absence of birds.

Figure 12. The relation between the perimeter and the area of a circle, illustrating that area grows much more rapidly than the perimeter.

Figure 13. The percentage of nests where one bird had returned from foraging by the time observations ended on different days.

Figure 14. The food web of the Peruvian upwelling.

TABLES

Table 1. Monthly percentages of reports of Guanay Cormorants nesting and reports by guards indicating that food was 'abundant.'

Table 2. Food ingested per day as a percentage of body mass.

Table 3. Reports by guards on food abundance in relation to absence or colony abandonment by Guanay Cormorants. *The column is unlabeled in the original but is inferred to represent "rare."

IMAGES

Image A. Photograph of a flagellate, many times augmented.

Image B. Wooden shelves placed on the western side of Isla Chincha Norte where, as you can see, boobies are nesting.