THE FLAMINGOS ON BONAIRE
(NETHERLANDS ANTILLES)

HABITAT, DIET AND REPRODUCTION OF
PHOENICOPTERUS RUBER RUBER

BY

JAN ROOTH

UITGAVEN „NATUURWETENSCHAPPELIJKE STUDIEKRING VOOR SURINAME EN DE NEDERLANDSE ANTILLEN"

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With 48 text illustrations and 20 plates

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FOREWORD

Aan 't uiteind van het eiland, uit de tijd,
de staande zerken van de slavenhuisjes,
graftekens van een wrevelig verleden
die op de lijkwa der zoutpannen staren.
Maar aan de rand van dat loodgrauwe rijzen
een rij doodstille, smalle vlammen op,
rechtstandig, kaarsen in een doodskapel,
en naar men kijkt ontvlammen er steeds meer.

Flamingo's, kleine fakkels, in het rijk
der doden onuitdoofbre vreugdevuren.
Zielen die in het zielloze gebied
der afgestorvenen glans en gloed behielden?
En aan de oevers van die Acheron
één eenzaam wakend bij de overtocht.
Maar als zij zich verheffen, slaat een vlam
zwierend uit het grauw zoutmoeras omhoog
alsof die zwerm naar een nieuw leven vloog.

ANTHONIE DONKER, Een half jaar op Bonaire,
Antilliaanse Motieven, januari 1959.

It is with great pleasure that the committee of the 'Natuurwetenschappe-lijke Studiekring voor Suriname en de Nederlandse Antillen' (Foundation for Scientific Research in Surinam and the Netherlands Antilles) contributes a few words of introduction to this monograph on the Bonaire flamingo by JAN ROOTH.

Ever since the earliest days of the Foundation the flamingos of Bonaire have received the closest attention of the committee because of their great value to the island and its inhabitants, and equally to the world outside. The continued undisturbed existence of these birds and their breeding and feeding grounds was therefore a matter of prime concern.

On 26th September 1957 the Government of the Bonaire Island Territory approached the Netherlands Foundation for the Advancement of Research in Surinam and the Netherlands Antilles (Wosuna), Amsterdam, with the request that an extensive scientific investigation be carried out into the life of the flamingos so that, if possible, the Government could take measures to increase or at least maintain the numbers of these birds.

Following this request, a visit was paid to Bonaire at the beginning of

1958 by Mr. J. H. WESTERMANN, a member of the committees of the Wosuna and the Foundation for Scientific Research, who composed a memorandum entitled "Observations on the Flamingos of Bonaire, in April 1958, and proposals for further research" (30th May 1958).

After further development of the plans, and with the support of Wosuna in a statement of guarantee of 26th March 1959, it was decided at the meeting of the Foundation committee of 26th June 1959 to commission the biologist Mr. J. ROOTH to carry out a field investigation of some twelve months' duration on Bonaire. In a resolution of 12th June 1959 the Netherlands Antilles Government granted the Foundation a subsidy for the investigation during 1959, and on 29th October 1960 made a further sum available for that year. We should like to express our thanks here for this kind assistance.

Mr. ROOTH and his wife HENNY ROOTH-REIJS arrived on 28th August 1959 on Bonaire and left the island on 3rd August 1960. They carried out the field and laboratory work with great skill and perseverance and established pleasant relations with the government and people of Bonaire. The committee is grateful to them both for having accomplished their task with such spirit.

Notwithstanding the extensive and much valued co-operation of Mr. ROOTH's principal, the State Institute for Nature Conservation Research (RIVON), the processing of the data took longer, for various reasons, than was foreseen. Now that the work has been completed we are gratified, however, that this masterly and thorough monograph can be offered to the people of the Antilles, and particularly of Bonaire, who are the most closely concerned with the welfare of the flamingos.

We hope that this book will contribute towards the protection of these birds, which is one of the concerns of the Government of Bonaire. This is true to an even greater extent now that the flamingos are facing a real threat as a result of interest in the development of the salt industry in South Bonaire. The value which is attached to their preservation is evident inter alia from the fact that The World Wildlife Fund has included the protection of the biotope concerned as Full Project No. 102 (Flamingo National Park, South Bonaire, Netherlands Antilles) in its so-called "Green Book", an inventory of the world's threatened nature areas which are worthy of preservation.

The number of flamingos in the Caribbean has declined considerably in the last few decades. Their disappearance on Bonaire and elsewhere would be an ethical, aesthetic and scientific loss. The biologist LESLIE BROWN, who carries out his work in East Africa, has described very aptly the wonder of these remarkable birds in *"The Mystery of the Flamingos"* (London 1959). His words, which we quote below, apply equally well to the flamingos of Bonaire:

"... Flamingos are, at the least, remarkable, at best sublimely beautiful, and at all times strange, rather remote beings inhabiting a world only they can inhabit with enjoyment. They live on the ... growth in the foul water of the alkaline lakes and they are the only large animal that does so in numbers.... Yet they always manage to be clean and beautiful in their pink and crimson dress.

They lay their eggs and rear their young in appalling heat and glare, in surroundings fatal to any ordinary animal and inimical to even the most determined and well-equipped human investigator. They move about on their ordinary affairs for reasons at present beyond our knowledge, but possibly connected with variation in their food supply. Suddenly they appear in their ... thousands, delight us for a while, and then are gone again ..."

The Committee of the Foundation
for Scientific Research in Surinam
and the Netherlands Antilles

Utrecht, June 1965

LIST OF ILLUSTRATIONS IN THE TEXT

LIST OF PLATES

Bonaire has harboured flamingos for many centuries and these birds are still called by their old Indian name "Chogógo". They breed here more or less regularly and with variable success; the poor breeding results in a number of years — e.g. in 1958 and 1959 — gave rise to the present study.

The "Foundation for Scientific Research in Surinam and the Netherlands Antilles", the local Government of the Island of Bonaire and the Government of the Netherlands Antilles all feared a reduction in the flamingo population, especially since these birds form a tourist attraction on the "Flamingo Island" Bonaire.

In the light of the reduction of the total population of the West Indian Flamingo in the Caribbean (ALLEN 1956), the possible disappearance of the Bonaire flamingos caused alarm also. Food-shortage in the first place, and then factors such as drought and the silting-up of the salt-lakes were thought of as being of negative influence on the habitat selection.

Although the problematics of this study are of practical significance and the research took on a marked practical character, the "Foundation" and its Flamingo Commission set up for this purpose, insisted on a study being made of the feeding ecology and other flamingo life-history problems, and then as complete as was possible.

Flamingos breed in fact throughout the world in very isolated places, whereby much is unknown of their biology, despite the work of ALI (1945) and McCANN (1939, 1947) in the Rann of Cutch (India), ALLEN (1956) and CHAPMAN (1905, 1908) in the Caribbean, BROWN (1958, 1959) and RIDLEY et al. (1954, 1955) in the Rift Valley in E. Africa, GALLET (1949, 1950), HOFFMANN (1954—1960, 1962) and LOMONT (1953, 1954) in the Camargue (S. France), JOHNSON et al. (1958) and PEÑA (1961) in Bolivia and Chile, and MIDDLEMISS (1953, 1958, 1961) in South Africa.

In addition to the collection of data on the occurrence and migration, feeding behaviour, nature and quantity of food, habitat selection and so forth, observations were also made in connection with the breeding-cycle, e.g. pair formation, copulation, nest building, brooding, the young, etc.

The fact that I was able to observe a particularly good flamingo year, and hereby carry out much field work, has determined the nature of the present publication, consisting as it does largely of original observations.

Although the most important and essential literature has been considered here, the reader interested in a more extensive literature survey is referred to ALLEN (1956), whose monograph considers flamingo literature from the dawn of history to 1956. Since ALLEN has done this

thoroughly, I consider myself relieved of the duty of repeating this attempt, this being simply double work and particularly since the problematics of this investigation — species and place — are much more restricted.

II. THE COURSE OF THE INVESTIGATION

It was possible to complete nearly a one-year cycle of observations on the flamingos, their food and environment since we remained, without break, on Bonaire from the 28th of August 1959 to the 3rd of August 1960. The relatively stable environmental conditions allow us to form a reliable and representative picture on the basis of this period of study.

After the first reconnaissance, the following areas (found to be the most important for the flamingos) were visited regularly: the "Pekelmeer" (= brine lake) and the southern part of Bonaire, Goto (Salinja Grandi) and the salina at Slagbaai in northern Bonaire. These three areas were visited weekly as far as possible, although this was altered at times in connection with the activities of the birds whereby more attention was generally given to the Pekelmeer than to Goto or to Slagbaai.

In these three salinas (saltlakes), three scales were set up, so that the water-level could be recorded; samples were also regularly taken at these points for the determination of the chloride content. At the same time plankton samples were taken at different places to establish the number of Brine Shrimps (*Artemia salina*) and other large plankton species. At various points, a given number of stones was inspected for the presence of Salt Fly (*Ephydra gracilis*) chrysalids. The numbers and activities of the flamingos here were also continually observed and recorded and in this way changes in the environment, the density fluctuations in the food animals and in the birds themselves could be regularly established.

From time to time, these three areas were visited in one day, so that a total count of the birds on the entire island could be carried out. This gave a representative picture, since at other places only small numbers of flamingos incidentally occurred; these were also visited now and then and the number of food-animals present was then more closely examined. These surveys were, however, superficial.

The meteorological data from various stations were collected and put at our disposal by the Government and the Meteorological Service. Maximum and minimum thermometers were hung up in the three salinas.

At spring and neap tides, the ebb and flood movements of the sea were studied for a period of 12 hours by means of a scale on the old Kralendijk pier; this was important in connection with the water relations of the salt lakes themselves.

Field-days (usually at least 3 per week) were followed as a rule by a laboratory-day, when the water and plankton samples were studied and the field observations worked out.

Whenever reference is made to "several" individuals (several tens, several hundreds, etc.), the range meant is from 1 to 5; "many" (etc.) signifies 5 to 10 and "very many" (etc.) from 10 to 15.

A number of observations were carried out more accurately in the course of the study period. For example, the chrysalid counts of the Salt Fly (*Ephydra gracilis*) were at first carried out simply by establishing the number of stones occupied and by rough numerical estimates.

Although, as it will be seen, various observational series — quantitative in particular — were not carried out throughout the whole year, or carried out with a similar accuracy throughout the whole year, it can be said that a representative picture has nevertheless been obtained of the numbers and behaviour of the birds and the variations in the biotic and abiotic factors in the environment.

On Bonaire, data on the occurrence and breeding of flamingos in earlier years was searched for as much as possible, and data for the flamingos in Venezuela and the Guianas were elicited by correspondence.

The techniques involved in the various observational series will be given in greater detail in the corresponding sections.

For weights, measurements, etc., of the collected specimens see the Appendix (p. 146).

III.   DISTRIBUTION AND NUMERICAL REDUCTION IN THE WEST INDIAN FLAMINGO

American literature (PETERS 1931) differentiates 6 species of flamingos, while HARTERT (1915) and other European ornithologists consider that there are only four species, with the *Phoenicopterus* forms treated as a single species and two subspecies or geographic races as follows (ALLEN 1956):

1. *Phoenicopterus ruber ruber* (Linnaeus) (Am. *Ph. ruber*)
1a. *Phoenicopterus ruber roseus* (Pallas) (Am. *Ph. antiquorum*)
1b. *Phoenicopterus ruber chilensis* Molina (Am. *Ph. chilensis*)
2. *Phoeniconaias minor* (Geoffroy)
3. *Phoenicoparrus andinus* (Philippi)
4. *Phoenicoparrus jamesi* (Sclater).

ALLEN employs the classification of PETERS, but here we shall keep to the European classification.

From these 4 species and 2 subspecies only the West Indian flamingo (*Ph. r. ruber*) is more or less restricted to areas at sea-level. The other species and subspecies occur at places from below sea-level to 16,500 ft. above, i.e. in Andes lakes (JOHNSON *et al.* 1958).

DISTRIBUTION

Voous (1960) writes of the distribution of *Phoenicopterus ruber:* Very patchy palae-arctic, oriental, aethiopian, nearctic and South American distribution in mediterranean, steppe and desert climatic zones. All breeding areas are on or within the 24°C isotherm for the warmest month. The high degree of discontinuity in the breeding areal is correlated on the one hand with the very particular biotope demanded by this species, but on the other as a direct result of disturbance and destruction of the breeding sites by man. The distribution has, for this reason, a relic-like aspect everywhere. In historical times exterminated by man in many places, e.g. Sicily, Egypt, mouths of the Volga and Ural, Florida, many Bahama islands and others in the West Indies area, north coast of South Africa.

According to ALLEN (1956, p. 34) the areal of the West Indian flamingo is charac-terised by slight temperature fluctuations and falls namely inside the mean extremes of 25 and 27.8°C. He says of the original distribution (p. 27–28): "The original distribution of the West Indian flaminго, following the retreat of the Wisconsin glaciation and the end of the last postglacial climax phase, beginning perhaps when the seas first approached present levels (2,000–1,500 B.C. ?), is more readily estimated than in the case of *antiquorum*. Although it would seem reasonably certain that Arawak and Carib Indians and their contemporaries raided flamingo colonies throughout much of the West Indies, both for food and for the colorful feathers, the impact of these natives on the distribution of the species was probably negligible. Unlike the situation that prevailed at the head of the Persian Gulf and along the Mediterranean, the more enterprising and more effectively destructive white race had no important con-
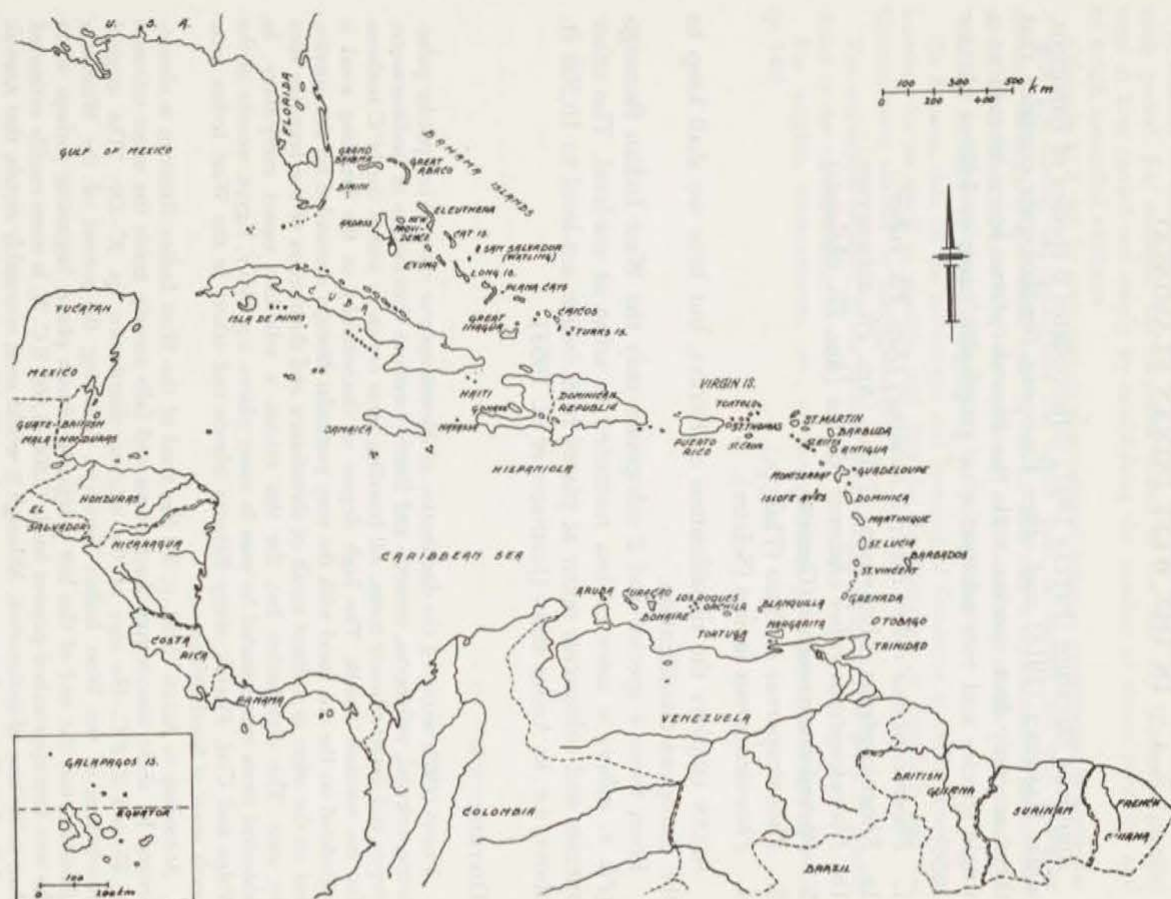
MAP 1. Sketch-map of the Caribbean.
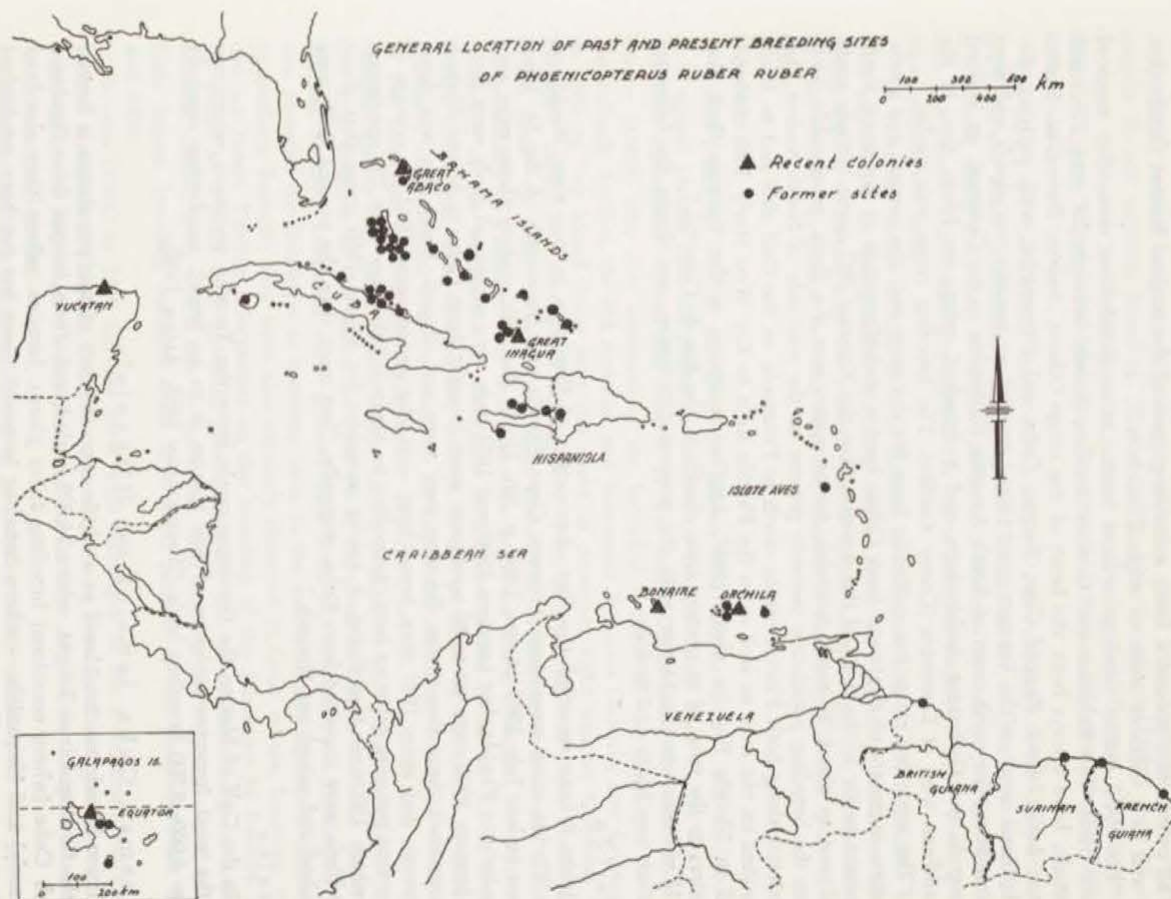
MAP 2. General location of past and present breeding sites (after ALLEN 1956).

tact with *P. ruber* until the early days of the 17th century. Although a good many individual colonies must have been disturbed and scattered by 17th century voyagers without written record, these flamingo populations doubtless shifted to other sites, so that for some time, so long as reserve sites were still available, the total population may have remained virtually intact. Thus, the breeding colonies on record for this species, in all probability, present a fairly accurate picture of the original Recent distribution, as well as a valuable index to original numbers."

"The West Indian flamingo is more insular in its distribution than other races of these birds. The Bahamas and Greater Antilles, mainly between 18° and 27° north latitude, have always been the heart of the range (*Abaco, Andros, Rum Cay, Exuma Cays, Long Island, Ragged Cays, Inagua, Cuba* and *Hispaniola*), with outlying distributional areas on the Yucatan coast (*Rio Lagartos*), at Jamaica, on islands and river deltas along the north coast of South America (*Colombia* to the *Guianas*), an isolated group in the Galápagos Archipelago, and a detached colony on Islote Ave, in the Caribbean west of Dominica (*Lesser Antilles*). The breeding range was similar."

"The wintering range has evidently been for the most part the central and southeastern segments of this area, from Cuba, Inagua and Hispaniola to northeast South America as far as the delta of the Amazon near the Equator (22° north latitude south and east to about 2° south latitude). An exception was the flock, presumably birds from the breeding population formerly present on the west side of North Andros, that wintered along both Florida coasts, north to Pensacola on the Gulf side and to South Carolina on the east, as well as in the Florida Keys to Key West (early 19th century), and in Florida Bay (to about 1903). Another exception is the Yucatan flock that winters to the west of its nesting area, chiefly in the Ría de Celestún."

If we compare the former with the present distribution, we obtain the following picture (see Maps 1, 2 and 3):

Florida

JOHN SPARKE recorded the first observation of flamingos in the New World, on the Florida coast somewhere between Cape Florida and the mouth of the St. Johns River in late July 1565 (ALLEN 1956, p. 39). Up to the 20th century these were seen regularly in Florida, but between 1902 and 1931 only very occasional birds were seen. In January 1931 some 20 to 30 specimens were brought from Cuba to Miami Hialeah Racecourse; these flew away, because they were not clipped. Later this was done, however, and since 1937 they breed here — in the period since 1942 an average of 65 young per year grow up here. According to ALLEN (1956) there were 750 specimens, of which 150 were free flying. A tourist pamphlet for Miami 1959 states that about 350 birds were imported from Cuba originally, "but more than the present flock were hatched and raised out Hialeah."

Mexico

In the Gulf of Mexico the flamingos rarely leave the Yucatán peninsula where one of the most important colonies of this species is to be found, numbering regularly some 4,000–4,500 breeding birds (WESTERMANN 1953, ALLEN 1956).

Bahamas, Cuba, Jamaica and Hispaniola

These islands are considered as a whole since the core of this population is formed by the flamingos from Inagua, where 14,000 birds breed. From Inagua these flamingos reach Cuba (where occasional breeding takes place), Jamaica (where they also bred formerly) and Hispaniola — where breeding in recent years has not been established with any certainty (BOND 1947, WESTERMANN 1953, ALLEN 1956).

Puerto Rico and Lesser Antilles

Flamingos are only seldom observed on Puerto Rico (BOND 1947, ALLEN 1956). Both here and on the Virgin Islands, however, breeding took place in former times.

There are only a few records for the Lesser Antilles (ALLEN 1956), but, at the begin of the 18th century there was a colony on Islote Aves, west of Dominica (WAGENAAR HUMMELINCK 1952).

Galápagos

A small, isolated and non-migrating population bred here formerly, but recent records do not mention breeding (ALLEN 1956). EIBL-EIBESFELDT (1960) saw 13 individuals, and since the flamingos are praised locally for their flavour, the situation does not appear hopeful. LÉVÊQUE (pers. comm.) found some 150 specimens in 1960–1961, however.

The area of Bonaire, the Venezuelan islands and the adjacent mainland coast (Colombia, Venezuela, the Guianas as far as Brasil) is considered as a whole, since, according to ALLEN (1956), it is covered by one population that he calls the (South) Caribbean population. He states that no migration takes place with other population units.

The breeding centre of this area is formed by Bonaire, and ALLEN estimated the 1955 population as being 2,400 breeding birds. From the breeding area the birds would appear to spread over the coastal area of South America and the islands. ALLEN (p. 49) writes: "It cannot be said that the species is flourishing in this part of its range."

Bonaire

VOOUS (1957, p. 77–78) surveyed the known observations up to 1952 as follows: It is almost certain that the flamingo rookery in Bonaire dates back to the time that the first Europeans visited the islands in the south Caribbean Sea. According to SWAEN (1943), who ably summarized the historical records of the flamingos in the Netherlands Antilles, the old traveller and buccaneer WILLIAM DAMPIER saw flamingos in 1681 in "an island lying near the main of America, right against Querisao (= Curaçao), called by Privateers Flamingo Key, from the multitude of these Fowls that breed there" (p. 165). SWAEN states that WAGENAAR HUMMELINCK does not exclude the possibility of Flamingo Key being another name for Klein Curaçao. The first real statement of the occurrence of flamingos in Bonaire seems to be by G. B. BOSCH (1836). From that time onward the records of the presence of flamingos in Bonaire gradually accumulated, but continued to be vague and therefore remained unnoticed in the literature outside the Netherlands. HARTERT, on 12. VI. 1892, was the first ornithologist to visit the breeding colony in the Pekelmeer (salt pans), but found only two eggs floating in the water. In 1909 P. A. EUWENS, a Roman Catholic priest at Rincón, Bonaire, compiled some general data from the literature on flamingos, but also reported the flamingos as breeding birds in the extensive salt lagoons (Pekelmeer) in southern Bonaire; they were also regularly observed in Goto, where, however, they did not breed. Further information on the breeding of the flamingos in Bonaire can be found in a book with splendid photographs by the government surgeon ALFONS GABRIEL (1938), from which can be extracted, that both in the Pekelmeer and in the Goto lagoon breeding colonies must have been present in the years between 1920 and 1930.

RUTTEN (1931) in 1930 did not meet with flamingos in the Pekelmeer, but found several hundreds of them in Goto. He states, however, that the flamingos were known to breed in the Pekelmeer (Oranje Pan) and not in Goto. He did not observe flamingos in Curaçao and Aruba.

Probably the birds continued breeding in Bonaire rather undisturbed and protected by the government from 1931 onwards, until 1944, when — without any necessity — a Netherlands speedboat and United States aircraft disturbed the breeding places fundamentally by their incessant noise and shooting (WESTERMANN 1946, 1947). Consequently the flamingos left Bonaire; some returned in 1945 and 1946 for a short period, but disappeared soon afterwards. In 1947 up to 500 flamingos appeared in

the salt lagoons of Goto and Slagbaai (GERHARTS *in litt.*; PHELPS & PHELPS), but VAN OORDT did not see more than 2 of the birds in the Pekelmeer and 13 in Goto when he visited the island in March 1948. At irregular intervals those few flamingos disappeared for some time, but gradually the numbers of returning individuals increased, until in 1950 breeding again could be established in the Pekelmeer, where the photographer H. WEENER took photographs and moving pictures of the rookery in August. In the summer of 1951 the number of breeding pairs in this locality was estimated at about 1,000.

In the meantime flamingos had also been reported from the other islands, but there their occurrence remained restricted to the appearance of irregular stragglers. In historical times at least the flamingo does not seem to have bred in Curaçao (N. VAN MEETEREN *in litt.*). Two stray individuals were recorded by M. DE JONG ("VOGELVRIEND") from Santa Cruz and Playa Abau on the south coast of Curaçao in 1941. HARTERT (1893) observed a solitary specimen in Aruba in 1892.

Voous met with flamingos only in Bonaire, where he saw them in three localities, *viz.* Pekelmeer, Salinja Grandi of Goto, and Slagbaai.

Recently, occasional flamingos have been observed in Curaçao and Aruba.

For a discussion of the status of the flamingos on Bonaire in recent years, the reader is referred to Chapter VII and VIII.

Colombia

MEYER DE SCHAUENSEE (1948, p. 368) states that the flamingo occurs in the tropical zone of the lower Magdalena Valley (La Peña, Laguna de Guájaro — also said to breed on the shore of the Ciénaga Grande. It also is reported from Laguna de Zapatora near El Blanco, and the salt-marshes in the vicinity of Bocas de Ceniza).

Venezuelan islands and mainland coast

PHELPS & PHELPS (1958) reported the occurrence of flamingos on the following islands (or island groups): Margarita, La Orchila, Los Roques and Las Aves off the
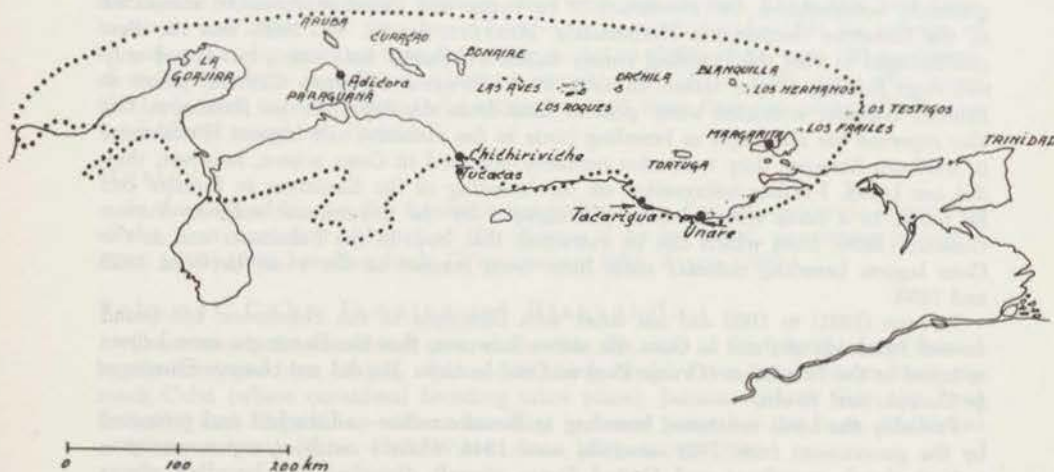
MAP 3. Sketch-map indicating the area of low rainfall along the North coast of South America. The dots indicate sites in Venezuela where flamingos regularly occur.

Venezuelan coast. Along the coast they are reported from the states of Falcón (Chichiriviche, Adícora) and Miranda (Laguna di Tacarigua). (Map 3)

As far as breeding is concerned, PHELPS & PHELPS (1959) say that a colony of about 50 abandoned nests was found on La Orchila in 1952 — fishermen having caught the birds for food. The government has since forbidden the trapping of flamingos; although the birds have been observed a number of times since this, breeding has not been seen.

G. YÉPEZ (Caracas) stated in a letter dated 23. II. 1960 that in Chichiriviche in June 1955 a group of some 1,000 to 1,500 flamingos was seen; this was repeated in August 1956, August 1957 and April 1958. In the Laguna of Tacarigua (State of Miranda) a colony of some 200 birds was known up to 1949, but since this date he had no more information. In 1959 he was informed about a group in the Laguna of Unare, and he considered it likely that these originated from Tacarigua, where they were hunted.

YÉPEZ further reports a group of 500 birds on Cayo Pirata in 1950. This is one of the islets in the Roques archipelago where flamingos were also regularly seen in later years. On the island of Margarita a group of about 500 birds was observed in 1951 and later years and which remained (until 1960) at the same strength. They were seen flying away twice in an easterly direction; destination unknown.

W. H. PHELPS Jr. (Caracas) stated in a letter dated 2. III. 1960, that the flamingos "feed on the east coast of Paraguaná Peninsula, near Adícora, in the mangrove swamps near Tucacas, in the Laguna de Tacarigua (east of Higuerote); in Margarita Island, and the islands Aves de Sotavento and Aves de Barlovento, as well as Los Roques. They have been found breeding in La Orchila Island. We have seen them flying eastward along the coast of the Distrito Federal, a few miles offshore from La Guaira."

VAN DER WERF, ZANEVELD & VOOUS (1958) reported 1 flamingo on Aves de Sotavento (Las Aves), May 1956. YÉPEZ (1963, p. 195–196) again mentions as temporary breeding grounds the islands of Los Roques and Orchila, and the mainland localities near Adícora, Chichiriviche and Tacarigua.

The Guianas and Brasil

CHUBB (1961) reported for British Guiana (Demerara) that flamingos were seen irregularly along the coast and that one of the known breeding sites is Waini Creek (in the neighbourhood of the Orinoco delta).

VON BERLEPSCH (1908) reported "no records from Cayenne (Fr. Guiana)." PENARD & PENARD (1908) mentioned much migration along the coast and that "the most important of the few nesting-colonies of "sea-geese" in Surinam was, according to hunters, behind the Hermina mudflats near Coronie."

HAVERSCHMIDT (1955, p. 32) says from Surinam: "Not numerous along the coast, recorded in December in the Lagoons near Nickerie." He wrote (*in litt.* 15. XII. 1959): Dr. D. C. GEIJSKES told me that he saw a large flock of standing flamingos from a fishing boat on the 10 or 11th of June 1959, not only along the coast, but also in a lagoon near the coast between the mouths of the Coppename and the Surinam river, close to the former. He was unable to approach them, however. This is an extremely wild section of the coast and there is perhaps chance that the birds were breeding there. Any information gained from the inhabitants here should be examined with care, since the Scarlet Ibis is called "flamingo", and the Flamingo "sea-goose". For this reason I consider the statement in PENARD's book questionable.

The wild and almost unapproachable nature of the coast of the Guianas may also be a reason why there are so few recent observations from this area. ALLEN (1956) is not very optimistic about the flamingos along these coastal regions.

Various authors, e.g. ALLEN (1956), PHELPS & PHELPS (1958) and VOOUS (1957) mention the occurrence of flamingos in Brasil, with the Amazon delta as the southern boundary of their area.

REDUCTION IN NUMBERS

ALLEN (1956, p. 75) says in a summary on this point: The former abundance of *ruber* is analysed on a basis of the distribution and probable size of the original population units, and the average number of mounds in various types of colonies. It is concluded that this species formerly numbered no less than 95,000 individuals, distributed in 12 major and 17 minor population units. *Phoenicopterus ruber* was never as abundant as certain other flamingo species, notably *antiquorum, chilensis,* and *Phoeniconaias minor,* and the reason for this may have been the limited insular environment of *ruber* and the drastic losses experienced periodically during hurricane cycles. Present numbers, based on recent estimates, chiefly from nest mound counts and the calculated productivity averages in the various colonies. It is shown that 2 major and 3 minor population units survive, and that the 21,500 flamingos of this species that comprise the current population, indicate a possible reduction of between 70% and 80% from former numbers. The present population trend in *ruber* appears to be slightly below a line of equilibrium, but it is proposed that continued protection may result in a stablised population, as an improvement can already be noted in the two major units (Inagua and Yucatán).

ALLEN (p. 126–127) found 22 nest-sites in the literature for the period 1601–1879, for the species *Ph. r. ruber*; from 1880–1905, 10 colonies (all on Andros); from 1905–1955, 36 colonies. A total therefore of 68 nesting sites, of which, according to ALLEN (p. 187) 10 active, 50 extinct, 6 potential and 2 unknown. He then continues (p. 188): "Of the active *ruber* sites, five are in Yucatan, three on Inagua, and one each on Abaco and Bonaire. Potential *ruber* sites — that is, locations where there have been more or less recent nesting attempts and where the birds may conceivably try again — are Lake Windsor (at large), Inagua; the Jackass Cay and Cotton Cay sector on Inagua; two locations on Cayo Romano, Cuba; the north coast west of Nuevitas, Cuba; and the island of La Orchila off Venezuela. The *ruber* sites of unknown status are Ile de la Gonâve, Haiti, and the Cienaga Grande, Colombia. Both may be either definitely extinct or only vaguely on the potential side.

Although ALLEN estimates a marked reduction from 95,000 to 21,500 individuals, he presumes that at the moment this number (thanks in part to protection) remains stable, with perhaps a small reductive tendency.

There is, however, something to be said against his calculation. ALLEN (p. 70) comes to a total of 41,122 nests on the basis of earlier and especially more recent data, and hence an average population of 82,244 breeding birds. The criticism of this is that birds from nests used more than once in a single breeding season, are not included in the count. This was the case on Bonaire (see Chapter VI d).

There are also birds, which do not yet breed. ALLEN presumes that this category will be 15% of the population and therefore arrives at a total of 95,000. This percentage of 15% seems to me to be very much on the low side, particularly since ALLEN (p. 72) considers that flamingos already breed in their second year. HOFFMANN (1957, p. 181) has evidence from ringing data, however, that they are adult after 5 to 6 years. It seems to me, therefore, that both numbers given by ALLEN are too low, since then only 15% of the total population would include the first 5 or 6 year classes. Although flamingos can reach a great age — in zoological collections up to 40 years (see Chapter VIII) — I think that in any case some 50% of the total population will consist of the year classes in question. In this way the numbers given by ALLEN of from 95,000 to 21,500 will be increased by several 10s of thousands and many thousands respectively, which in fact makes little difference in the percentage reduction of 70–80%.

No data after 1955 are at my disposal, with the exception of those from Bonaire, where the breeding population in 1959–1960 was approximately twice that given by ALLEN for 1955 and roughly equivalent to that for 1953.

At present we can conclude, therefore, that — at least in the period 1953–1960 — there is no reason to speak of a reduction in the numbers of flamingos on Bonaire. The reader is referred, however, to Chapters VII, VIII, and X.

IV.   HABITAT AND HABITAT SELECTION

a. TOPOGRAPHY AND GEOLOGY

The topographical position of Bonaire is Long. 68°25′—68°12′W, Lat. 12°2′—12°19′N. It is situated 40 km to the east of Curaçao and 87 km from the continent of South America. Its greatest length is 35 km, its greatest width 11 km, with a surface (land) area of about 265 sq. km; the highest point is 243 m (Brandaris). Klein Bonaire, situated about ¾ of a kilometer west of Bonaire, is roughly 7 sq. km in size, with a highest point not exceeding 6 m.

Bonaire itself consists of two topographically and geologically clearly differentiated parts. To the south it is lowlying and flat, and its surface consists (as does Klein Bonaire) entirely of recent coral limestone, and shell sands. To the north the island is much higher and markedly accentuated, and here the oldest formations are found. In the north-west part of the island, handshaped bays occur; they are separated from the sea by a wall of coral shingle and may be of considerable depth or entirely dry. These bays are also referred to as salinas.

According to WAGENAAR HUMMELINCK (1953, p. 69, see also 1940, p. 24) the salinas ("saliña — salinja, zoutmeer, zoutvlakte — saltlake, salty mud-flat") are "Parts of bays, salt flats or marine pools, separated from the sea by a porous wall of coral and/or rock debris and/or sand, often turned into salt pans". He writes (1933, p. 309): "Die Salinen sind fast alle durch einen durchlässigen Trümmerwall vom Meer geschieden; sie können jedoch geologisch auf gänzlich verschiedene Weise entstanden sein (als Typen nenne ich: Goto, Salinja Martinus, Pekelmeer und Salinja Plenchi). Bei höherem Salzgehalt findet sich in ihnen die bekannte, mehr oder weniger kosmopolitische Salzlakenfauna mit *Artemia* und *Ephydra* als Haupttypen; bei niederen Konzentrationen kann ihre Flora und Fauna dagegen einen sehr eigenartigen Charakter tragen. Übergänge zwischen hohem und niedrigem Salzgehalt finden sich oft an der Seite, who das Meer liegt; hier sickert häufig Seewasser ein; seltener ist Vermischung mit dem süszen Grundwasser" (cf. 1933, figs. 6—8, map of Bonaire; 1953, figs. 10, 15, pl. V*b*).

WESTERMANN & ZONNEVELD (1956, p. 16; cf. phot. 3—4, 6, 10, 53, 59—61) have given the following description: "Barren alluvial areas, usually the embouchures of dry watercourses in the sea or in land-locked bays. During the rainy season they are occasionally flooded. The soil is sandy and often of a high salinity. The sandy and salty flats of South Bonaire bear the same name. The term salinja (Spanish: saliña) is also used for salt lakes and land-locked bays which have a salinity higher than that of sea water."

Goto, Slagbaai and Pekelmeer are thus salinas. The deepest is Goto, with a maximum of 16 m; in Slagbaai the deepest places are several meters, and the Pekelmeer has a maximum depth of about 1.5 m.

Comparing our depth measurements with those performed by WAGENAAR HUMMELINCK in 1930, and studying the topographical maps of 1915, it is obvious that the silting up of the salinas proceeds very slowly. Apart from limestone, sand, etc., near the walls of coral debris, the bottoms of the salt lakes of Goto and Slagbaai consist of fine black mud and recent limestone deposits, while in the Pekelmeer the greater part of the bottom consists of soft, often light-coloured mud with salt and limestone crusts.

b. CLIMATE

Bonaire lies within the area of low rainfall which extends along the north coast of South America, between Trinidad and the mouth of the Magdalena river. The climate of this semi-arid region is largely characterised by an annual rainfall varying between 340 and 680 mm, and a mean annual temperature of 27°C; the 'steppe' climate of Köppen (see WAGENAAR HUMMELINCK 1940, p. 5, fig. 1; WESTERMANN & ZONNEVELD 1956, p. 53, fig. 2). Although the rainfall varies slightly from one place to another as a result of altitude and situation with regard to the prevailing easterly winds, it may be said that the whole island has a semi-arid climate.

In connection with the characteristics of the flamingo biotope, it is important to examine the various determining factors for the climate, such as precipitation, temperature, wind and evaporation. To do this we make thankful use of the data published in the Statistics of the Meteorological Observations (Curaçao, vols. 3—8, 1955—1960), and the data given by WESTERMANN & ZONNEVELD (1956, p. 53—54).

Precipitation

Data for the period 1940 to 1960 give a picture of the annual fluctuation; quoted here are the averages of the year-precipitation, measured at various stations on Bonaire, to the nearest whole number, in mm:

1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950
255	258	557	482	952	430	404	279	338	530	948

1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
589	466	317	586	928	739	398	286	201	218

The average monthly and annual rainfall in mm in the period 1931—1960 is:

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Year
54.2	29.2	16.6	11.3	21.8	20.0	20.1	33.9	32.0	77.7	129.3	87.4	533.5

The number of days with 1.0 mm or more precipitation for the years 1959 and 1960 was for the station Willemstoren 37 and 37, and for Rincón 38 and 39 respectively. The maximum on one day in the period August 1959 to July 1960 for the Willemstoren was 33.5 mm on the 6th of July. From these figures it is clear that many years occur, when the rainfall is far below the average.

MOLENGRAAFF (1929) calculated the following dry periods from the rainfall data for 200 years for Curaçao: 3 periods of 68 months, 3 of 56 months, 3 of 44 months, 3 of 32 months and 10 of 20 months. The difference between the periods is always 12 months — 8 dry and 4 poor rain months (i.e. Oct.—Jan.).

In 1959—1960, we experienced a dry period, which lasted from 1957 to the late summer of 1961 — a period of 56 months. From the observations of the various

ANNUAL RAINFALL

1954:	1955:	1956:	1957:	1958:	1959:	1960
621,9 mm	902,6 mm	825,7 mm	408,2 mm	256,1 mm	170,9 mm	1/I.-1/VIII 106,2 mm

MONTHLY RAINFALL (in mm)   PEKELMEER (WILLEMSTOREN)
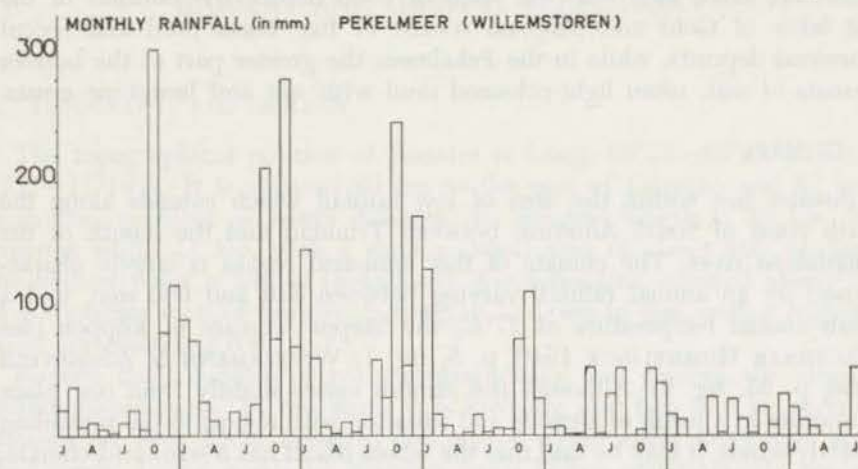
GRAPH 1.   Annual and monthly rainfall in Pekelmeer (Willemstoren).

ANNUAL RAINFALL

1954:	1955:	1956:	1957:	1958:	1959:	1960
508,9 mm	1030,5 mm	841,4 mm	457,8 mm	430,1 mm	304,2 mm	1/I.-1/VIII 106,5mm

MONTHLY RAINFALL (in mm)   RINCON
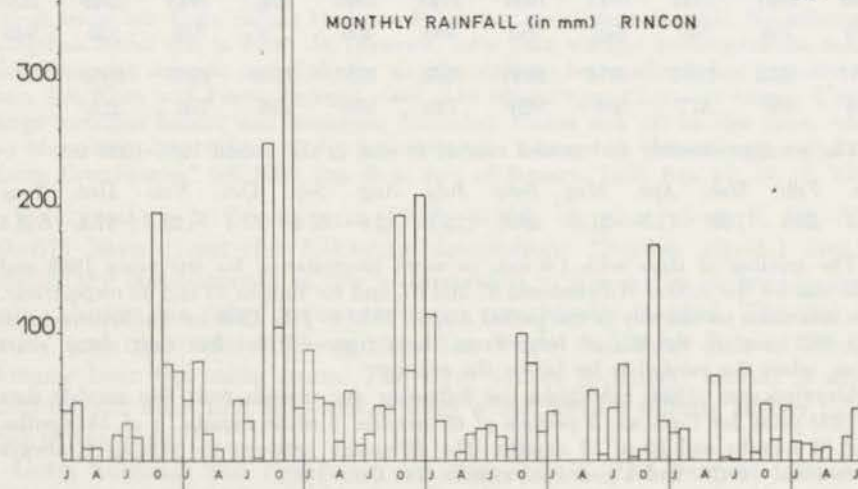
GRAPH 2.   Annual and monthly rainfall in Rincón.

weather stations, it is apparent that Rincón has the most rainfall, Washington the least, and Willemstoren usually somewhat more than Kralendijk.

For the Pekelmeer we have used the data from the Willemstoren station (which is situated at the southern extremity of Bonaire, close to the salt lake), and these are given in Graph 1, per month. For the salinas Goto and Slagbaai the precipitation is somewhat higher and we can compare these with the data for Rincón station (see Graph 2), which — as Goto and Slagbaai — is situated between the hills.

High rainfall figures in a year are sometimes caused by the passage of a hurricane at a short distance from the island — e.g. Hazel on 7. X. 1954 and Janet on 23. IX. 1955. This occurs only sporadically, however, since Bonaire lies outside the normal hurricane zone.

Temperature

The Dr. A. Plesman Airport on Curaçao has, over a period of 14 years (1947—1960), calculated the average values for the temperature, based on hourly observations. These are given here, in degrees centigrade.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Year
26.2	26.1	26.5	27.1	27.7	28.0	28.0	28.4	28.8	28.3	27.8	26.9	27.5

In 1959 and 1960, the dry-bulb temperatures at the same airport were (averaged) 27.4 and 27.7° C respectively. The average daily maxima were 30.1 and 30.4° C; the absolute maxima 33.7 and 33.6° C; the average daily minima 25.5 and 25.8° C and the absolute minima 21.3 and 22.0° C.

The temperature records carried out by Mr. FAULBORN at Kralendijk since January 1960, are somewhat higher: the maximum was there (15. VI. 1960) 35.0° C. One reason for this may, however, be the situation of the instruments in the garden of the Governor's house, where there is less wind. In general the temperatures recorded at the Dr. A. Plesman Airport, on the flat north coast of Curaçao, will closely resemble those applying to the flamingo biotopes.

Wind

The monthly average of wind speed in knots in the period 1947—1952 at the Dr. A. Plesman Airport on the *Hato* plain, that at *Kralendijk* in 1959 and 1960, and the averages of wind direction at the latter station in 1960, are as follows:

	Wind speed			Wind direction
	Hato 1947–1952	Kralendijk 1959	Kralendijk 1960	Kralendijk 1960
January	12.6	14.4	13.5	114
February	14.0	16.3	12.2	120
March	15.2	16.9	15.0	113
April	14.6	16.7	15.1	105
May	14.9	13.9	14.8	93
June	16.3	17.6	16.2	91
July	14.8	16.4	13.7	93
August	13.0	15.2	13.7	94
September	12.6	13.3	12.8	106
October	11.2	14.4	13.9	110
November	11.1	11.7	12.3	100
December	12.4	14.0	11.5	84
Year	13.6	15.1	13.7	102

16

17

mean sea level

−10 cm

−20 cm

−30 cm

−40 cm
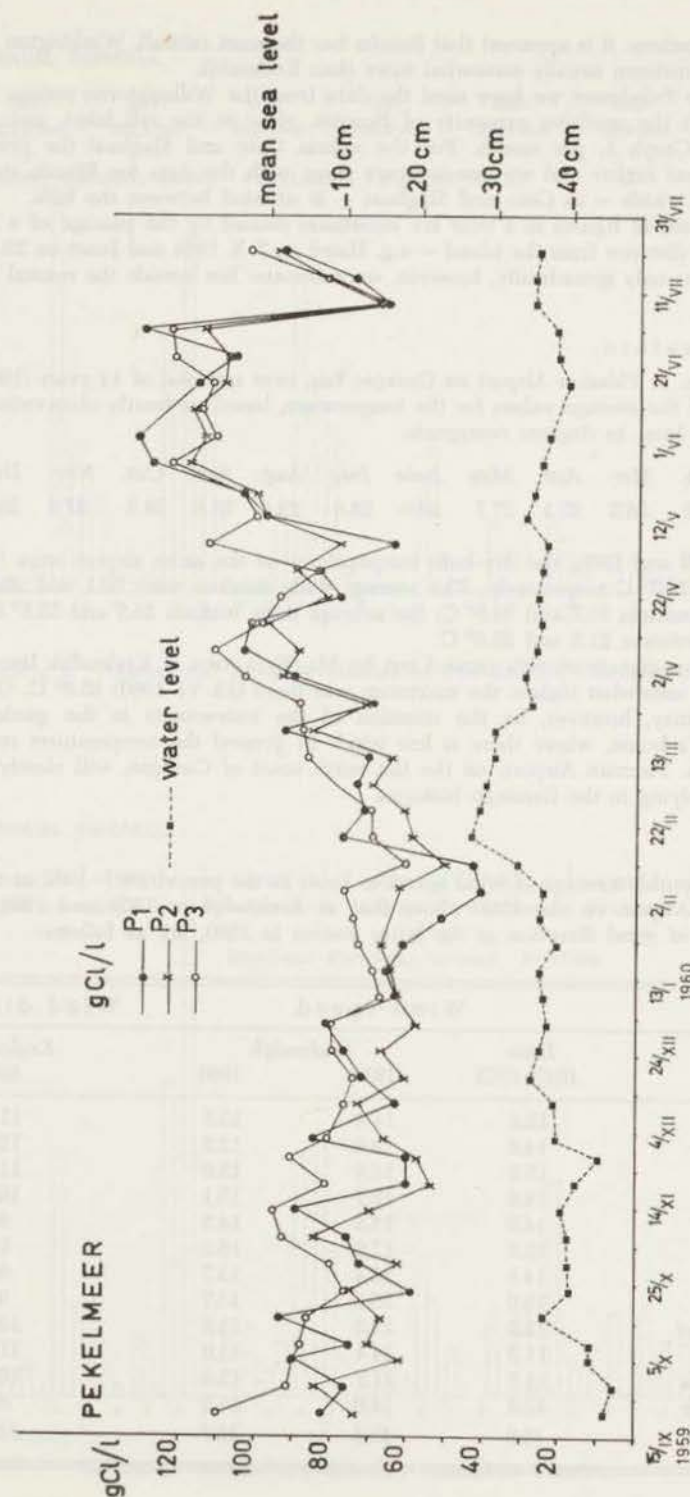
GRAPH 3. Water level and chloride content in Pekelmeer.

water level

gCl/l

P1
P2
P3

31/VII
11/VII
21/VI
V/VI
12/V
22/IV
2/IV
13/III
22/II
2/II
19/I
1960
24/XII
4/XII
14/XI
25/X
5/X
15/IX
1959

PEKELMEER

gCl/l

120
100
80
60
40
20

18

In general there is an eastern trade wind, in 1960 even an average of east by south. In 1959, at the Plesman Airport, the average was 95° for the year and in 1958, 90°. It is, in fact, rare that the wind is still; usually there is a wind with a speed of 7−21 knots, i.e. 3.4−10.7 m per second.

Evaporation

The high temperature and strong winds cause, despite a relatively high humidity, a rapid evaporation. The relative humidity in the period 1947−1960, once more at the Plesman Airport, had an annual average of 74.5%. In the years 1959 and 1960, the absolute minimum here was 46% and the absolute maximum 100%.

MOLENGRAAFF (1929) computed the evaporation from a free water surface on Curaçao and found it to vary between 4.5 mm (December) and 7.5 mm (August) per day. Investigators at the Caribbean Marine Biological Institute recently found values between 4 and 15 mm, average 7 mm, per day.

On the basis of the climatological data it is obvious that the marked evaporation (and only incidentally the precipitation) plays an important role in the hydrology of the salinas.

c. HYDROLOGY OF THE SALINAS (see Plates I−V, VII−IX)

Because of the high evaporation rate and the low precipitation, the salt lakes, which have a relatively stable water level, must receive water from another source, i.e. the sea, in the following ways:

1. Through the wall of coral debris which separates the salina and the sea by a number of tens to 200 m. This is the case, for example, in the Boca of Goto, Boca Slagbaai, Boca Bartool, and at a number of points along the western shore of the Pekelmeer, as also at "Ven" and "Duinmeer".

2. By way of underground connections with the sea, sea-water bubbles up through more or less circular openings, referred to as "eyes" ("ogen"), which have a diameter of anything between a few centimeters to several decimeters, and may appear at a distance of 100−1400 meters from the sea, e.g. western and eastern banks of the Pekelmeer, respectively.

3. By way of seepages. In this case the opening is not circular, but is often a break or fault or other permeable point in the limestone. The distance from the sea is very variable: from many tens of meters to almost 2 km! For example, the western and eastern banks of the Pekelmeer, respectively.

It is known that the water entering the salinas in these ways is sea water, since the chloride content has been ascertained at various points of entry. This was found always to be 20 gr Cl/liter, just as the control samples of sea water. In addition, the nature of the water is reflected in its fauna and flora − see Chapter IV e.

This flow of sea water is possible since the salinas are situated under sea-level. This could be demonstrated, with the help of Mr. P. H. DE BUISONJÉ, for the three most important salinas, with the aid of depth-scales and the triangulation points of the Department of Survey. From these measurements it was found that:

on 16. XII. 1959, the Pekelmeer was 36 cm below the average sea-level;
on 23. XII. 1959, Goto was 13.7 cm below the average sea-level;

19
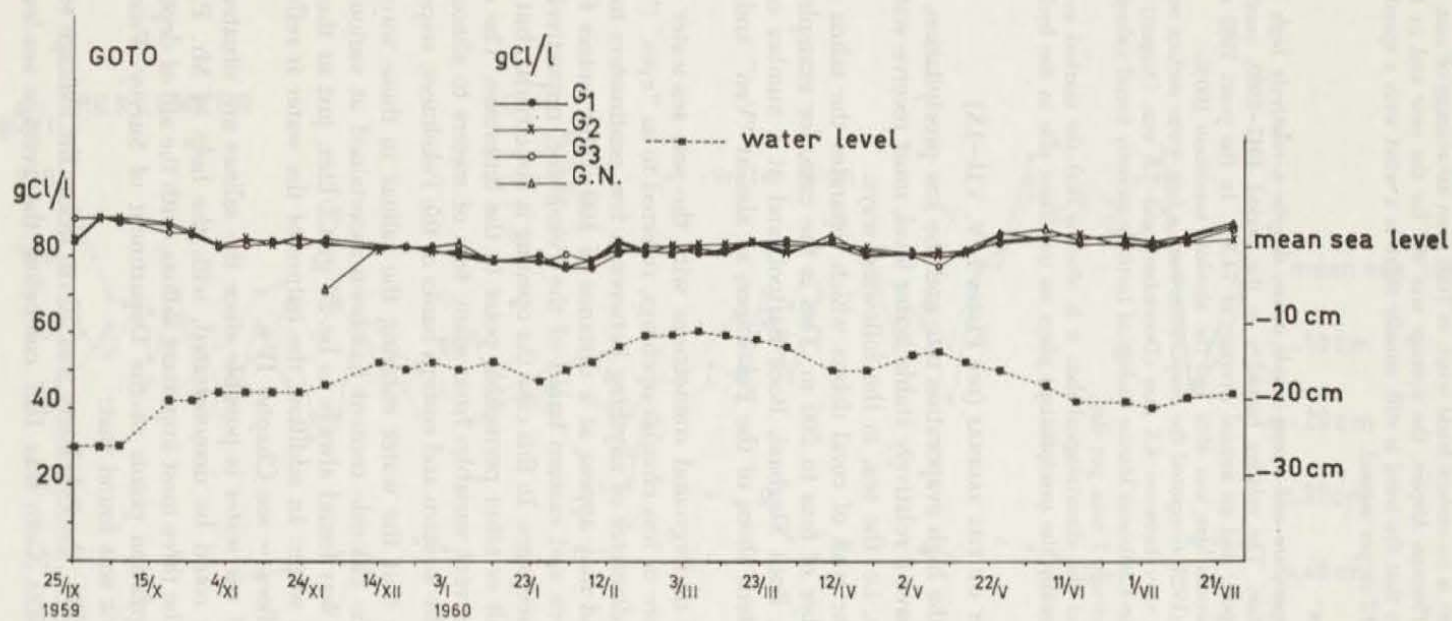
GRAPH 4. Water level and chloride content in Goto.
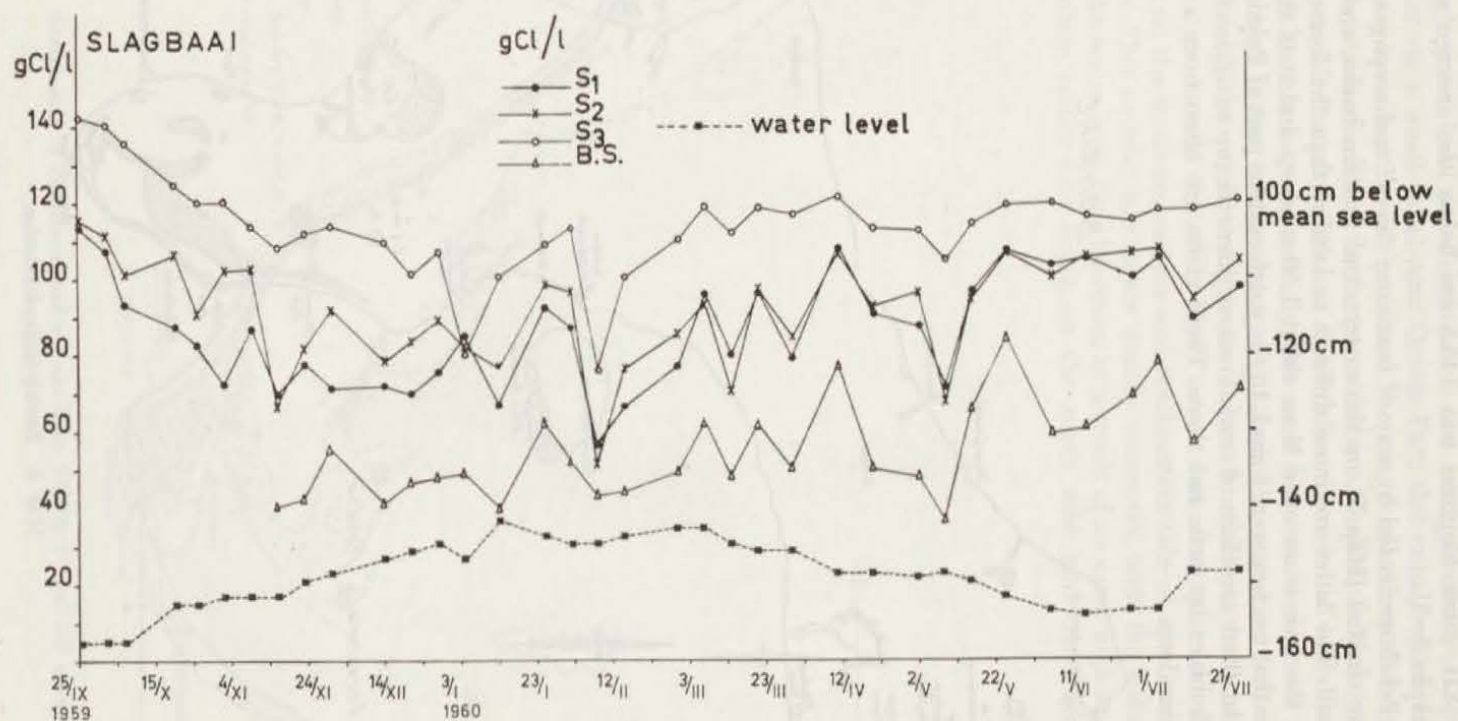
GRAPH 5. Water level and chloride content in Slagbaai.

on 23. XII. 1959, Slagbaai was 145.5 cm below the average sea-level (see Graphs 3—5).

The Pekelmeer is fed by way of numerous "eyes" and seepages, which we have charted (Map 5), on the eastern and western banks, and in the lake itself. The latter are more difficult to localise than the former, even though the lake is no more than about 1.50 m deep and it is therefore possible that too few were found. In the south-eastern part of Pekelmeer in particular there are clefts of several meters diameter (up to 5), from which water bubbles up here and there. These clefts are often from a few to many dm deep.

At high water level the Pekelmeer is fed with previously evaporated sea water via a small canal near Oranje Pan; this canal, which forms a connection between the salt pans and the sea, is closed on the seaward side by a wooden wall and on the pan side by a small dam. This was used formerly to fill the pans with sea water, after the salt had been dug out; since this has not be used recently, the canal has remained closed but at extreme high water (storm and spring tides), the sea water comes over the wall with the result that the small dam is unable to hold back the water, runs over and the water flows into a sort of circular lake ("Ring-meer"), on the southern, eastern and northeastern side of the Oranje Pan complex. This circular lake is not usually connected with the Pekelmeer. When the water level rises however, as a result of an extra high sea-level, an overflow comes into being on the north side into the Pekelmeer.

MAP 4.   Sketch-map of Bonaire.
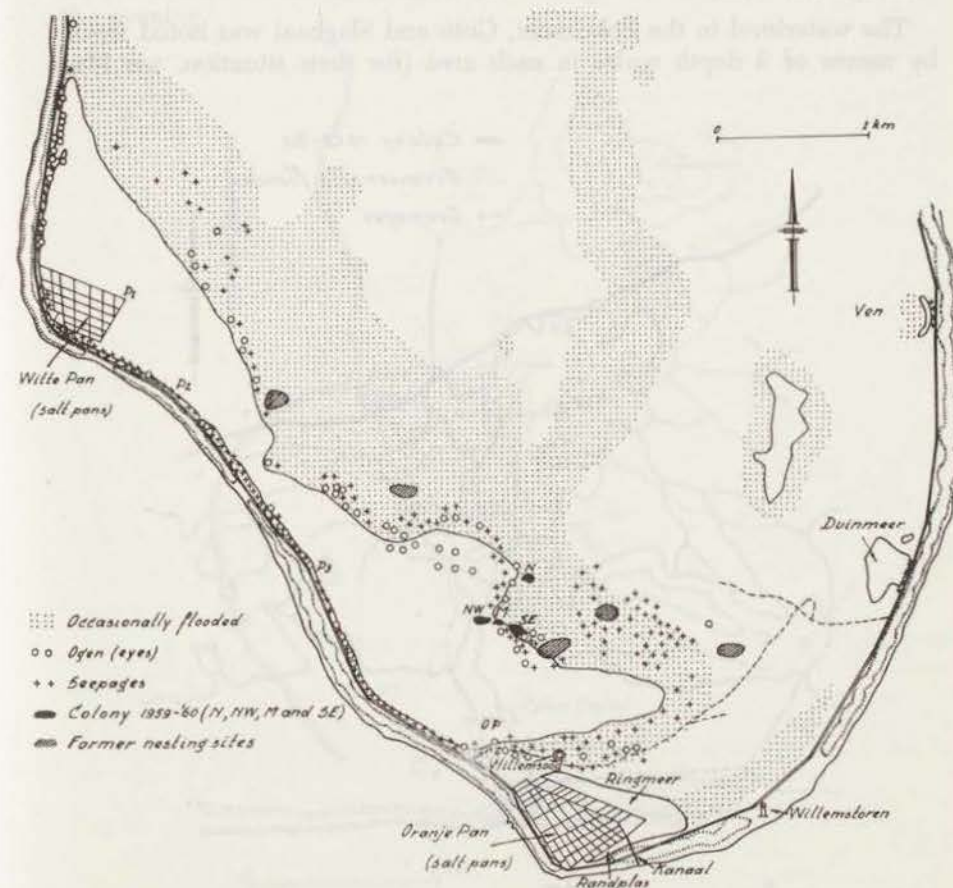
MAP 5.   Sketch-map of Pekelmeer and surroundings. P1, P2, P3 and OP are permanent sampling points.

Water flowing into Pekelmeer from the "Ringmeer" does so under special circumstances only, and has already a high Cl content: 70 g Cl/liter, so that there is no "freshening" of the lake water.

Goto (Map 6) is fed with sea water mainly via the wall of coral debris. Slagbaai (Map 7) is fed with sea water via a small "canal" near the Boca, where the wall of coral debris is smallest and where water continually seeps or flows in. There are also points to the south and north of the canal where water seeps or flows through the coral debris. To the south of the canal there is such a marked flow of water that a small "stream" has formed here, which meanders to the salina.

At Boca Bartool (Map 4), "Duinmeer", "Ven", "Ringmeer" and "Randplassen" near the Oranje Pan and the Witte Pan (Maps 4–5) the water enters in a similar fashion to that in Goto, i.e. through the coral debris wall; the salinas on Klein Bonaire (Map 4) are fed in the same way, although here and there, "eyes" have been seen.

The waterlevel in the Pekelmeer, Goto and Slagbaai was noted weekly by means of 3 depth scales in each area (for their situation, see Maps 5–7), P1, P2, P3; G1, G2, G3; S1, S2, S3, respectively. Differences in water level of 20 to 30 cm were found to occur throughout the year (Graphs 3–5). During this period the precipitation was very low (Graphs 1–2) and was not concentrated in any particular rainy period, but more or less regularly spread over the period from September 1959 to August 1960. Before September 1959 there was for a long period no rain of any significance. This being so we can ignore the influence of precipitation on the fluctuations in waterlevel during the period of study, and — seeing the erratic course of the fluctuations — it is also impossible to consider evaporation only as the source of this phenomenon. The most important factor is that of changes in the sea-level; both tidal movements and seasonal fluctuations in the sea-level will have to be considered here. To do this, a depth scale was attached to the pier in Kralendijk bay where the level of the sea was recorded, as far as possible on the days of spring and neap tides, and hourly from 6 o'clock in the morning until 6 o'clock in the evening.

MAP 6. Sketch-map of Goto. G1, G2, G3 and GN are permanent sampling points.
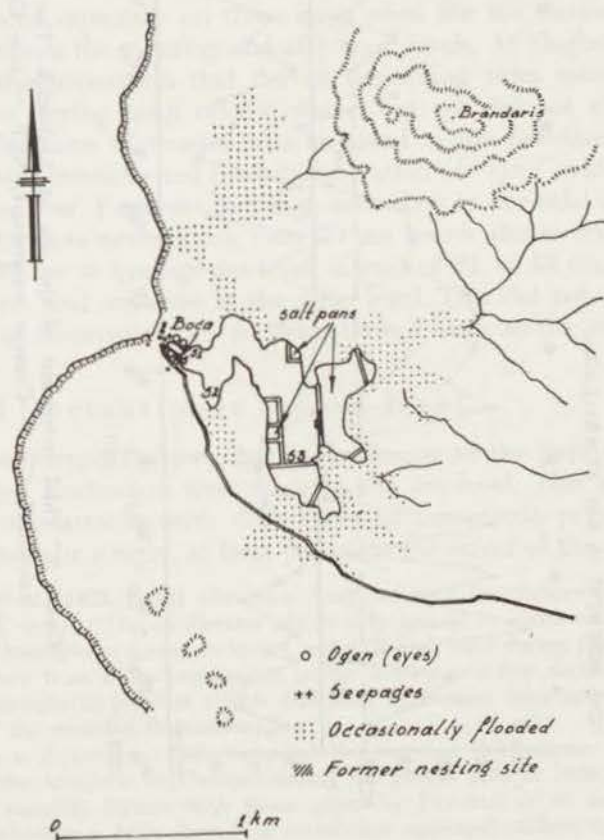
MAP 7. Sketch-map of Slagbaai. S1, S2, S3 and BS (southwest of S1) are permanent sampling points.
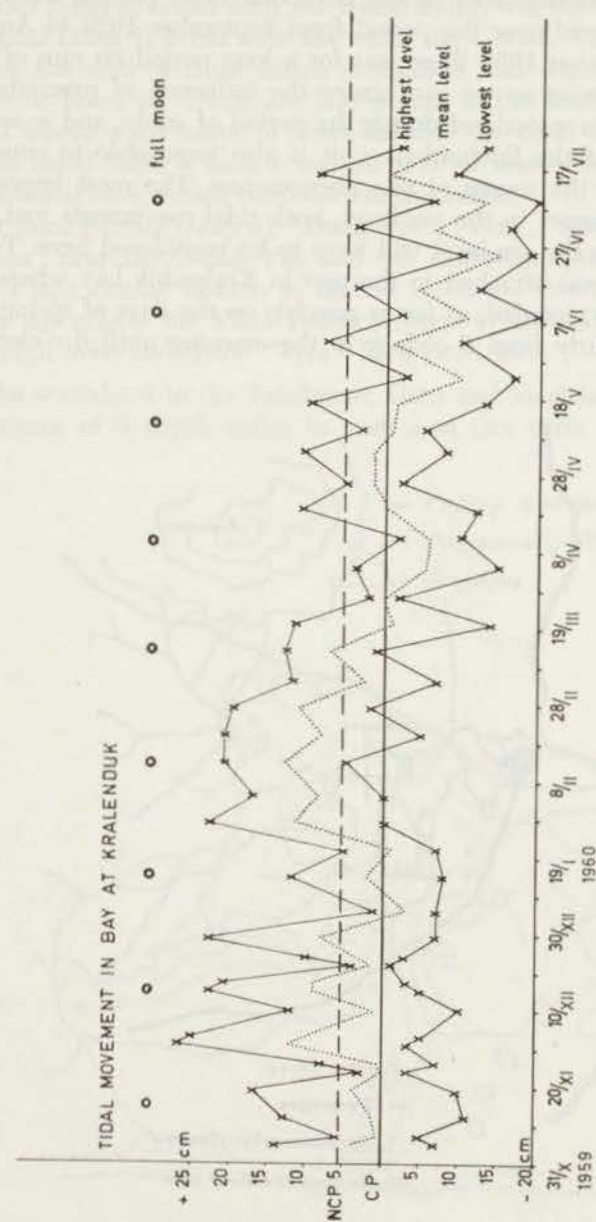
GRAPH 6. Tidal movement of the sea at Kralendijk. The mean level has been calculated. CP = Curaçao water-mark, NCP = new Curaçao water-mark.

Tidal movements

The difference between high and low water was found to be at most 30 cm (during the daytime at least). The ebb and flood movements occur very gradually, so that at times during a period of 12 hours a difference of a few centimeters only could be recorded (Graph 6). This can happen by both neap and spring tides when there is frequently only one high and one low water in the 24 hours (see also WAGENAAR HUMMELINCK 1953, fig. 1, for the Annabaai on Curaçao). DE HAAN & ZANEVELD (1959) state: "On the basis of the available tide gauge records over the period 1950–1956 the character of the tides in Annabaai Harbour, Curaçao, was determined. A periodic change of a diurnal and semidiurnal period, comprising 13.7 days, was observed. The average daily ranges between the tides in the period mentioned proved to be 29.7 cm." Our lower figures are perhaps the result of daytime readings only.

Many daily observations showed that there was hardly any, or no influence from the tidal movements on the water level in the salinas. This was noted especially on those days when the sea showed large differences between the morning and afternoon levels. At Slagbaai we sometimes had the impression that during the spring tides more sea water entered than during neap of low water, but we did not measure this, however. The same impression was obtained in the Pekelmeer; here the impression was strengthened by the observation of "eyes" which, at times, had no water flow. From the fact that, according to our tidal observations, the sea water was never more than 20 cm below the average sea-level, and P1 = 69 cm = average sea-level, a level of P1 = 49 cm implies that the Pekelmeer and sea were at the same level. This did not occur during our period of observation, i.e. no brine flowed away to the sea.

Seasonal fluctuation in the sea-level

A study of Graph 6 shows that in the course of the period observed a fairly marked fluctuation took place in the sea-level. This could not be correlated satisfactorily with differences in barometric pressure so that the cause must be sought, at least partly, in the effect of the wind.

PATULLO et al. (1955, p. 88) who have described such fluctuations for a large part of the world, write: "The oscillations are largely annual in character, with low sea level in each hemisphere during its spring and with high level during the fall. Recorded amplitudes vary from a few centimeters in the tropics to a few decimeters at higher latitudes. Atmospheric pressure effects and long astronomic tides account for only a small part of the recorded fluctuations."

DE HAAN & ZANEVELD (1959) recorded the seasonal fluctuations in the average sea-level in the Annabaai on Curaçao during the period 1950 to 1956, and compared the average monthly figures with those given by PATULLO et al. for the coast of Venezuela, whereby a high degree of correlation appeared. When we compare the monthly averages for atmospheric pressure (at the Plesman Airport, Curaçao) in the period 1948–1960, a fairly good correlation appears – high atmospheric pressure with a low sea-level and vice-versa. The data of DE HAAN & ZANEVELD on the seasonal

fluctuations show a trough in January, February and March, a rise to May, small fluctuations follow until in August; a marked rise follows in September lasting until November with small fluctuations, followed by a fall in December, continued in January once more. Between individual years, however, very marked differences may occur, so that the singularity of our observations is by no means exceptional.

PATULLO *et al.* also write: "The seasonal departures differ considerably from one year to the next, due largely to anomalies in weather (atmosphere and ocean). The fact that neighbouring stations show similar anomalies in a given year eliminates observational error as an important factor."

When we compare Graph 6 with 3, 4 and 5, we see a large measure of agreement between the seasonal fluctuations of the sea and the water levels of Pekelmeer, Goto and Slagbaai. This is then the explanation for the fact that in (even extensive) periods of drought, the water in these salinas is nevertheless replenished, i.e. with sea water. Without doubt heavy precipitation will also influence the water level, for example after the rainfall of 33.5 mm on the 6th of July 1960!

The influence of precipitation is clearer, however, when we study the chloride content in the salinas.

d. CHLORIDE CONTENT IN THE SALINAS

Weekly water samples were taken in the Pekelmeer, Goto and Slagbaai, to determine the chloride content. In the first case this was done at the sample points P1, P2 and P3, where the water-level was also measured. Here and there, both in and around the Pekelmeer, other samples were taken, for example in the "Duinmeer", "Ven", "Ringmeer", "Randplas", "Willemsoog" and in various salt pans in the Oranje Pan and the Witte Pan, also along the banks of the Pekelmeer (Map 5).

In Goto the samples were taken at G1, G2 and G3 (the measuring points) and GN (= North Goto — Map 6). Here and there other samples were taken, e.g. near the Boca.

In Slagbaai, regular samples were taken at S1, S2 and S3 and at BS (= Boca Slagbaai), where the "stream" flows into the salina (see Chapter IVc, and Map 7).

In addition incidental samples were taken in the salinas of Boca Bartool and Playa (or Paloe) Lechi, and in the salinas on Klein Bonaire.

The water samples for the Cl' determinations were always collected from the upper 10 cm, although sometimes the difference between bottom and surface water was examined; the salter, heavier water is generally found at the bottom, with the lighter, less salt water at the surface.

The chloride content was determined according to the method Mohr-Knudson, with Van Dam's modification. POSTMA (1954, p. 411—412) has described the method in detail. We have used the data on Cl/liter, although a qualification as to temperature must be made. The titrations were carried out always after the samples had stood for a night and half a day, with as a result, a fairly equal temperature for any one series. Due to changes in the weather, the titration temperatures throughout the year varied between 28.4 and 32.6° C. Both extremes occurred only once and in general we can say that the majority of the titrations took place at temperatures between 30 and 31° C.

The temperatures in the salinas were measured with the help of hanging maximum and minimum thermometers, which were read once per week. They were suspended in the upper 10 cm, from which the water samples were taken.

In the Pekelmeer (P1), the maximum temperature fluctuated between 34.7 and 27.8° C, and the minimum between 26.7 and 21.9° C. Both the highest and the lowest maximum and minimum temperatures were noted on the same day, indicating that the difference between maximum and minimum temperature is fairly constant. In Goto (G1), the maximum temperature fluctuated between 35.2 and 28.0° C, while the minimum fluctuated between 26.0 and 21.5° C. For Slagbaai (S3), the values were 34.8 and 28.0° C and 28.6 and 22.4° C respectively.

Pekelmeer and surroundings (Graph 3)

The chloride content fluctuated markedly in the course of the year, but the graphs of the three sample points run in general parallel. There is a clear relation between the water level and the chloride content: the higher the level, the lower the chloride content and vice-versa. Changes in the water level are, as we have seen in Chapter IV c, especially dependent on the seasonal fluctuations in the sea-level. In addition we see in the chloride content, more than in the water level, the influence of spring and storm tides, which are superimposed as smaller fluctuations on the general trend. The points P1, P2 and P3 were so chosen that they gave a more or less representative picture of the various parts of the Pekelmeer. A slight fall or rise in the water level caused a large change in surface area by reason of the very shallow slopes of the banks of the Pekelmeer; a fall left then areas covered with a salt crust or very briny mud with a layer of salt crystals.

The "Duinmeer" varied between 65 and 92 g Cl/l.

The "Ven" had a Cl-content of between 22.7 and 25.5; an excellent connection is (apparently) present, so that the water contains hardly any more Cl' than the sea water.

The "Ringmeer" varied between 55.5 and 114.7 g Cl/l, the "Randplas" was on the average much lower, due to a greater infiltration of sea water (31.2—48.5 g Cl/l).

The "Willemsoog" varied between 20.3 and 59.0 g Cl/l (Graph 7). The increase in salinity took place in the period when sea water which entered via the small canal from Oranje Pan (during high storm and spring tides during the high seasonal level) and via the "Ringmeer" and the "Willems-oog" had an overflow into the Pekelmeer. This water was in the mean-time highly evaporated (see Chapter IVc).

Various pans in the Oranje Pan, as far as our samples go, varied in their Cl-content between 38.5 to 154 g Cl/l, depending on the flow of sea water and the degree of evaporation and crystallisation.

There were, naturally enough, "fresher" places where much sea water flows in, and other places where the opposite is true. We found, for example, (22. VII. 1960) a value of 100.0 g Cl/l near the north-western flamingo colony and near the south-eastern colony — on a few tens of meters further — 41.5 g Cl/l; various "eyes" and seepages were present at this point.

At the Witte Pan there is a "pipe" carrying much sea water and where the water, at two points had only 19.8 and 22.0 g Cl/l. In various pans belonging to the Witte

Pan the value varied in much the same way as in the case of the Oranje Pan between 30.7 and 154.3 g Cl/l.

I. KRISTENSEN and MARIAN EMEIS (pers. comm.) found similar values at the same points in February 1961. That the majority of their values were somewhat higher is explainable by the lower water-level at that time.

Goto (Graph 4)

In Goto also, a relationship between the water-level and the chloride content of the water can be seen. The fluctuations in the Cl-content are, however, very small and the absolute data vary only very slightly between the 4 sample points. This is probably a result of the damping effect of this large body of water, since Goto is by far the deepest of the salt lakes. Depths of 8—16 m are by no means rare (WAGENAAR HUMMELINCK 1933, p. 296, and 1953, fig. 15).

Close to the wall of coral debris in the Boca of Goto a value of 74.5 g Cl/l was found on 9. V. 1960, while at a distance of about 10 meters from the shore, where sea-water bubbled up, only 26.4 g Cl/l was analysed.

Slagbaai (Graph 5)

There is a definite correlation between the water-level of Salina Slagbaai and the Cl' contents at S1, S2 and S3. The Cl' line for Boca Slagbaai (Map 7) shows at times a deviating picture; the Cl-content here reacts very markedly, as might be expected, to the variable amount of sea water
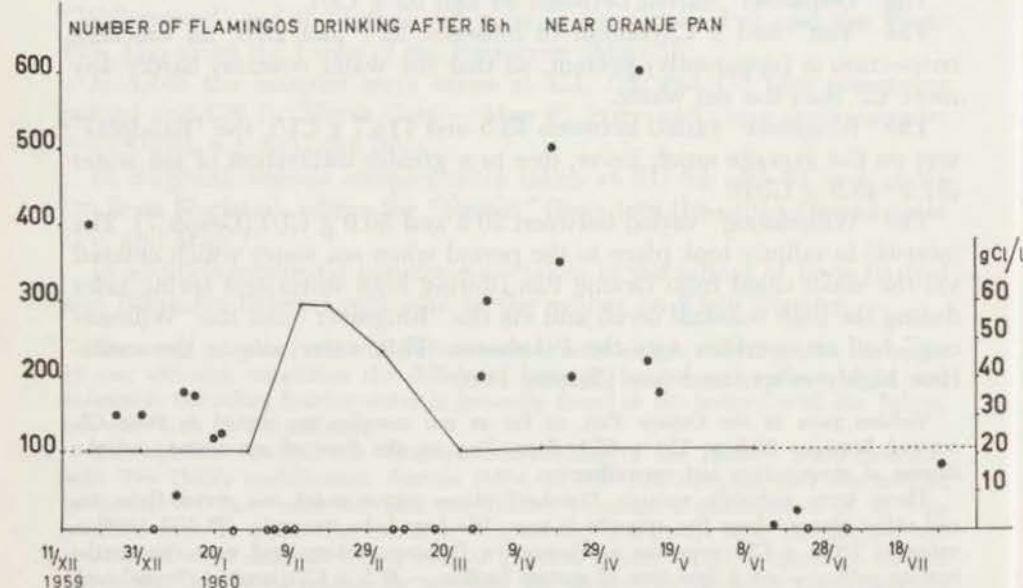
GRAPH 7. Number of flamingos drinking after 4 o'clock in the afternoon in Willemsoog, near Oranje Pan. — o indicates no drinking flamingos observed.

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flowing in. Despite the low-lying situation of the salina with respect to the average sea-level, we have the impression that the influence of the spring and storm tides and the seasonal fluctuations is here very marked. In all probability the permeability of the upper layers of the coral wall is of great significance here. The large amounts of sand found in the lower layers of the separating wall support this.

The majority of the sea water is fed to the salt lake via the small canal (see Chapter IV c) and the eyes on the southern and northern shores of the Boca. The Cl' contents at these points were found to be 21.4, 21.3 and 20.0 g Cl/l respectively. On the southern shore we know of the stream whose mouth in the salina is situated some 10 meters from the sample point BS, which offers an explanation for the lower Cl-content and also for the deviations in the fluctuations, which react markedly to the influx of sea water. S3 (see Map 7) is situated the furthest from the sea and this is probably the reason why this sample point has the highest Cl' values.

Salinas on Klein Bonaire: These have values, from east to west, of 45.9, 47.6 and 64.0 g Cl/l respectively. They are shallow and have a soft muddy bottom, with the exception of the far western, which has a hard sandy bottom. In the far eastern salina we found "eyes" on the north shore which fed in water with a Cl-content of 4.4 g/l. This is probably stored rainwater from deep limestone layers and potholes.

Salina Paloe (Playa) Lechi: The water samples contained 14.2 and 17.7 g Cl/l. The salina has an open connection with the sea, and is also fed from a large basin which catches rainwater. This small amount of fresh water then mixes with the salt and gives as a result, water with a slightly lower Cl' value than sea water itself.

Salina Bartool: Two samples had values of 60.1 and 61.1 g Cl/l. The water in the far side of the salina is, in all probability, more salt, so that the situation here is further comparable with Goto — seawater enters via the coral debris wall.

e. FLORA AND FAUNA OF THE SALINAS

Because of the, for the most part, hyperhaline water, the diversity of organisms in the salinas is restricted (see also HEDGPETH 1959), but certain species may occur in very large numbers.

Flora

STOFFERS (1956, p. 38—39) says of the neighbourhood of the salinas near the Pekelmeer: "It is either absolutely bare or covered by a Conocarpus community which greatly varies in density from point to point. Whole fields are covered by a thin sinter deposit, often broken up by the temporary root-action of *Conocarpus*. Between the shrubs — pressed down by the wind — some scattered tussocks of *Cyperus planifolius* var. *brunneus, Cyperus fuligineus, Fimbristylis ferruginea, Sporobolus pyramidatus* and *Lithophila muscoides* occur." "Along the west coast there is a wall of coral debris, overgrown by a low shrub vegetation . . . . Remnants of a halophytic vegetation comprise patches of *Sesuvium portulacastrum, Salicornia ambigua* and *Batis maritima* beside the salt-pans and Pekelmeer."

The other salinas are mostly surrounded by thorny woodland and cultivated and semi-cultivated areas with Aloes (Slagbaai and Goto), Cactus-thorn shrub (Salina

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Bartool), Cactus shrub (Salina Paloe Lechi) and Croton-Lantana-Cordia thicket (Klein Bonaire), according to the vegetation map of Bonaire made by STOFFERS (1956).

The lower plants collected were all Cyanophyceae, the exceptions being *Enteromorpha* and *Batophora* (Chlorophyceae) which were collected in less salt areas of Goto and the "Ven" respectively. The "eyes" and seepages could be recognised by the occurrence of green algae. In addition, a well-developed flora of bacteria and diatoms is to be found in various places. Compare the papers of FRÉMY (1941, p. 102—118) and KOSTER (1943, 1963).

The following blue algae were named by KOSTER (1963, p. 45—46) from author's collections:

Pekelmeer and surroundings: *Coccochloris elabens* (numerous everywhere), *Anacystis dimidiata* (at two less salt places), *Entophysalis conferta* (at one less salt locality in large numbers), *Gomphosphaeria aponina* (found once at P2), *Johannesbaptistia pellucida* (frequent at P2 and P3), *Schizothrix lardacea* (very frequent at P2), *Lyngbya aestuarii* (frequent at several localities), *L. semiplena* (in large numbers), *Spirulina subsalsa* (in low numbers), *S. labyrinthiformis* (found once in Oranje Pan), *Microcoelus chthonoplastes* (large numbers for two localities). In nearly all samples many to very many Bacteria occurred, only in the sample from "Willemsoog" diatoms were present in small numbers. In the mud samples taken close to the tracks of flamingos (see Chapter V), many *Coccochloris elabens* were found, a large number *Entophysalis deusta,* and also *Phormidium subsalsum,* with, in addition, many bacteria. In the "Ven" large numbers of *Bathophora oerstedi* var. *occidentalis* occurred on the sandy bottom, and on this the snail *Cerithidea costata* was often found.

G o t o: *Coccochloris elabens* (at various places at various numbers), *Entophysalis deusta* (cushion-shaped colonies on stones, fairly frequent), *Phormidium subsalsum* (in several samples), *Spirulina subsalsa* (numerous in various localities), *Spirulina labyrinthiformis* (the same). In general many Diatoms and locally also many Bacteria. Near the seepages *Enteromorpha clathrata* was found.

S l a g b a a i: At various points, both on the Boca and on the far side of the salina, *Coccochloris elabens* and *Phormidium subsalsum* were found in large numbers.

Flagellates were found nearly everywhere; several species were able to cause a red colouration of the water at high Cl' concentrations — in general: the higher the Cl' concentration, the redder the water.

Fauna

Ephydra gracilis, Salt Fly (Plate X)

The most important animal as far as the flamingos are concerned is the Salt Fly, which can occur in enormous numbers in the salinas. The imagos can occur in such high concentrations along the edges of the salinas that these become dark in colour. They live here, in all probability, on detritus. The larvae live for the most part on and in the bottom, but can also move around by means of lashing movements. Their gut contents proved to be largely algae. The larvae reach a maximum length of 15 mm, while chrysalids are on the average 12 mm long. The large larvae seek out stones and salt-crusts, on (and especially under) which they attach themselves and metamorphose; the chrysalis' skin hardens and the chrysalis becomes a stiff, chitinous tube. The fly frees itself from this by way of an operculum at the top of the tube. These empty chrysalids remain for some time attached to the substratum, until dislodged by rough water, often

forming a broad flotsam line along the shores of the salinas. The larvae show no preference for a given salt concentration, but occur everywhere, in the highest salt concentrations as well as near the "eyes" and seepages. In less salt water they are prevented from occurring, or from occurring in any numbers, by the presence of small carp, which are also confined to this type of water (see below).

Artemia salina, Brine Shrimp

RAMMNER (1936) described two varieties for Bonaire: *Artemia salina arietina* and *A.s. milhauseni.* As far as we were able to see, both varieties occur in the same area. According to MARIAN EMEIS, who studied *Artemia* on Curaçao and Bonaire in 1961, intermediary forms occur and mixed copulations have been observed. In the majority of the salinas these animals occur in large numbers, although in the less salt parts they occur in smaller numbers (e.g. where sea water enters), since at these concentrations predators occur, such as small carp, and also — according to MARIAN EMEIS (KRISTENSEN 1963, p. 20) — *Cyclops.* In areas with concentrations that are very high — saturated or supersaturated salt solutions — these shrimps can still occur, although they do become "pickled" here and there. HEDGPETH (1959) states that they can occur in brines up to $300^0/oo$.

According to MARIAN EMEIS the eggs hatch in all lower concentrations up to about $85^0/oo$; when the concentration is higher, the female shrimps become viviparous. The eggs are able to withstand long periods of drought, when they occur between the stones of small dams around the salt pans and on the shores. The environment of *Artemia* is often poorly supplied with nourishment. The shrimps swallow water continually, using as food algae and Dinoflagellates. The adult shrimps are variable in length and this depends on the salt content of the water and the amount of foodstuff present. In less salt water they are pale in colour, this darkening in higher concentrations to a frequent dark red-brown as a result of haemoglobin synthesis (cf. GILCHRIST 1954, 1956).

The shrimps swim on their back with regular but sluggish movements; fast reactions are unknown to them. The adults were 5—10 mm long and could reach an age of at least 2 months.

The gut contents were mostly green and or brown, in which algae and detritus could be recognised. KUENEN (1939, p. 8) states that they can also live from bacteria, and GILCHRIST (1954) also mentions Diatomae as food. These animals have a "purifying" effect on the water, since everything present in the water passes through their gut and anything not usable as food is then fixed in their excrements. In this way dirty water can become completely clear through the action of Artemias, as BAAS BECKING (1934) showed experimentally.

Despite their good osmoregulation (WARREN, KUENEN & BAAS BECKING 1938) and their occurrence in sea water and various concentrations of brine, there would appear to be a certain preference, at least in some

developmental stadia, for a certain degree of salt (Cl'). We shall return to this in Chapter V f and V g, where we shall consider in more detail the fact that Artemias and Rotatoria hardly ever occurred together. In the Pekelmeer, for example, Artemias were never found throughout the whole period of study, although earlier (WAGENAAR HUMMELINCK 1933, RAMMNER 1936) and later (EMEIS and KRISTENSEN) they were found to occur there (see Chapter V f—g).

Gastropods

In less salt areas in the salinas *Batillaria minima* and *Cerithidea costata* occurred (cf. COOMANS 1958). *Nodilittorina tuberculata* was found only in the "Ven".

In some places the shores of the Pekelmeer were covered with a layer some centimeters thick and sometimes several tens of meters broad with the empty shells of *Batillaria* and *Cerithidea*. This suggests that they occur in large numbers when the Pekelmeer is less salt (e.g. after much precipitation or during high sea-level). HEDGPETH (1959) reports, however, that *Batillaria minima* occurs in salt concentrations of between 36.5–170°/oo in the Bahamas, Florida and the Antilles and *Cerithidea costata* from 44.9 to 154.5°/oo. ALLEN (1956) states that both species are most numerous at a salt concentration of 119.8°/oo.

Fish

The carp *Cyprinodon dearborni* and *Mollienesia sphenops vandepolli* (cf. SANDERS 1936, p. 449–451; DE BEAUFORT 1940, p. 111) are restricted to those parts of the salinas with low salt concentrations, though WAGENAAR HUMMELINCK found *Cyprinodon* still living in small pools at Witte Pan having a chlorine contents of 88 g/l, 11.V.1955. HEDGPETH (1959) reports that both genera (other species) occur between 20 and 142°/oo. We saw them between 20 and 75 g Cl/l. EMEIS and KRISTENSEN reported them from Curaçao up to about 135°/oo, a fair agreement.

Other animals

At places where sea water entered the salinas Crustacea could be observed, e.g. Amphipoda (see also STEPHENSEN 1933, 1948), and also, here and there, Ostracoda (see also KLIE 1939). Protozoa were also always present here. Rotatoria occurred locally and temporarily in large numbers. Annelids (see AUGENER 1936) were rarely found; only twice a single Polychaete was observed in the Pekelmeer and the "Ven" at places with about 20 g Cl/l. In similar places Corixids were sometimes noticed, whereas in the brine of Goto lake Coleoptera were found locally. All these animals occurred in such small numbers, however, that they could not be of importance for the flamingos.

f. HABITAT SELECTION

All flamingo biotopes throughout the world have many characteristics in common. ALLEN (1956, p. 85) gives a table in which the salient features of the biotopes for all species are included; with inclusions from modern publications, this can be summarised more or less as follows.

Nearly all biotopes have shallow water with a high salt concentration, in general accompanied by a red colouration, generally ascribed to Flagellates (e.g. *Dunaliella*). In many places the water level is very variable, since the biotopes are situated in dry areas, or in areas where at least periodically droughts can occur.

The literature frequently mentions the influx of fresh water via vulcanic

springs (Andes and Rift Valley), or seawater may flow in. These places are of importance for bathing and drinking. Usually the biotope is situated in a desert landscape and the (summer) temperature is high.

As food in these biotopes ALLEN reports especially algae, Protozoa, Mollusca, Crustacea, insects and water-plants. These food-sources do not, to any important extent, occur simultaneously — in general only a few of the aforementioned organisms occur as species in the biotopes. In this way, it would appear that the flamingos are locally monophagous and various species appear often to be specialised for one or more types of food e.g. by way of the structure of the bill (see Chapter V a).

Breeding in desolate places under inclement circumstances may well afford a certain degree of protection against predators, at any rate against mammals. Practically all species (with the possible exception of *Ph. minor*) are extremely shy; it is difficult to determine if this is a cause or an effect of their living in isolated places.

It is known for several species that they are easily disturbed, and may disappear for a period of time. There are, however, examples known where continual removal of the eggs (e.g. ZAHL 1951, Andros-Bahamas; JOHNSON *et al.* 1958 and PEÑA 1961, Atacama-Chile and Laguno Colorada-Bolivia) did not prevent the birds from laying more. In addition, they often return in the following breeding season and there is, it would seem, a great attachment to these sparsely distributed biotopes. ALLEN's data on the original distribution points to the same conclusion.

The cause of the habitat selection is difficult to determine. Are the flamingos such marked food specialists? Do they search by preference for extreme circumstances, because there, usually speaking, a biocoenosis poor in species may occur, but rich in numbers for a few species? Or does (dietary) competition play a role in the selection of the habitat, since they cannot maintain themselves next to many other species? Is their choice made on the basis of general physiognomical features in the landscape (PALMGREN 1949), or is the choice made with respect to the amount of food available?

Most of the above questions will remain unanswered, but some light can be thrown on several by considering the food study reported in the following chapter.

V.   DIET

a. STOMACH CONTENTS

ALLEN (1956, p. 96) gives a list of flamingo stomachs which have been examined, belonging to all species, and from various biotopes. The number of examinations of stomach contents in the West Indian flamingo, *Phoenicopterus ruber*, turns out to be very restricted:

1859, several?	from Inagua, Bahamas	(BRYANT 1866)
1890, one?	from Andros, Bahamas	(NORTHROP 1891)
1904, several	from Andros, Bahamas	(CHAPMAN 1905)
1952, one	from Inagua, Bahamas	(ALLEN, field notes)
1952, two	from Río Lagartos, Yucatán	(ROCHE, in litt.)

These stomachs had the following contents (ALLEN, p. 98):
Andros: Molluscs; mud (organic?).
Inagua: Molluscs; seeds of *Ruppia* and *Salicornia;* one report of fish.
Yucatán: Molluscs; gravel.

The only data in the literature on the stomach contents of flamingos from Bonaire is to be found in Voous (1957), who shot one adult male and two adult females in Goto on the 25th and 26th of March 1952. The contents were remains of numerous larvae of *Ephydra* and a few very small fish scales.

To obtain concrete data on diet and quantity of food we had five specimens shot, which together with one dying specimen and one found shortly after death, gave us a total of 7 stomachs for investigation. Later, this was increased by two stomachs collected by Prof. Voous in 1961 from Bonaire.

Pekelmeer

JUVENILE, 11. XI. 1959, 17.30 hours, near Oranje Pan. – Stomach contents 3 g: about 300 small stones of about 1–5 mm; 14 *Ephydra* larvae were still recognisable; 12 *Ephydra* chrysalids were more or less complete, but there were also numerous pieces derived from a number of tens of chrysalids. Intestinal contents: an orange coloured porridge, here and there also small brown flakes, the remains of *Ephydra* chrysalids. (Between 50 and 100 cm from the cloaca there were dark and thin-walled areas, which turned out to contain tens of hymenolepid cestodes.) The gut caecae contained again the remains of *Ephydra* chrysalids.

MALE ADULT, 31 XII. 1959, 6.20 hours, between Witte Pan and Oranje Pan. – Stomach contents 14.5 g: 538 *Ephydra* larvae and the cuticular remains of about 10 chrysalids; 150 stones of 3–8 × 3–5 mm, and about 50 smaller ones, from ½–2 mm. The stones were smooth and rounded, probably the effect of the milling action of the stomach wall. – Intestinal contents: a grey, brown and green mass. Caecae: grey sand and mud, with small brown flakes, probably from *Ephydra*.

MALE ADULT, 21. I. 1960, found dead near Oranje Pan; cause of death unknown. – Stomach contents 16 g: a green porridge with very numerous small brown pieces, probably from *Ephydra* chrysalids; about 300 small stones, of which the largest 11 × 6 × 6 mm, and the smallest 1 mm, but with all possible intermediate sizes. Intestinal contents: alternate black, brown and green masses; from the caecae to the cloaca, black; the former were empty.

JUVENILE, 11. VI. 1960. This bird, born about February 1960 was seen on 10. VI. 1960 in the Salina Martinus and on the 11th on Playa p'Ariba. The bird had broken

a humerus and was captured at the Flamingo Beach Club, where he was released from his sufferings. – Stomach contents 1 g: about 300 stones, smaller than 1 mm, and a few larger ones, a few mm in diameter, together with about 8 small black, pear-shaped seeds about 2 × 1 × 1 mm.

Goto

Voous collected in Goto on the 13th of July 1961 two females, whose oesophageal and stomach contents consisted of:
a. About 1700 *Ephydra* larvae, remains of a number of *Ephydra* chrysalids and about 300 small stones, the largest 4 mm, the smallest 0.5 mm.
b. About 1300 *Ephydra* larvae, about 50 chrysalids and also remains of the same; about 350 small stones, 7–0.5 mm in size.

FEMALE ADULT, 24. III. 1960, shot in the morning on the north side of the Goto lake. The stomach was unfortunately damaged. Stomach contents 16 g: many hundreds of small stones, most of them very small (1 mm), but also a number of larger ones (3 mm); remains of a number of *Ephydra* chrysalids and of about 25 larvae; 2 legs, belonging to *Ephydra* flies; 2 Artemias and thousands of *Artemia* eggs (derived from the digested females, or by chance from the water ?). Intestinal contents: close to the stomach, light brown, here and there beige coloured and also somewhat yellowish; the terminal part, between the caecae and the cloaca contained a green-brownish porridge. Caecae: brown-black contents.

(SUB?) ADULT FEMALE, 23. VI. 1960, shot in the afternoon on the north-east side of Goto. Stomach contents 9 g: 785 *Ephydra* larvae, of all sizes, some partly or almost completely digested; a number of chrysalid remains; 900 small stones, the largest 4 × 3 × 2 mm (a few), the smallest ½ mm; the majority of the stones (several hundreds) about 1 mm. The intestines were damaged and therefore not further examined.

Slagbaai

(SUB?) ADULT MALE, 27. VI. 1960, about 12 o'clock, shot in Boca Slagbaai. – Stomach contents 6 g: 900 small stones, max. 7 × 5 × 3 mm, min. ½ mm; brown, digested remains of *Ephydra* chrysalids (some fragments still clearly recognisable) and grey, digested remains of *Ephydra* larvae and a few more or less complete specimens.

For further details of these birds, see the Appendix of weights and measurements (p. 146).

From the investigation of the stomach contents, it appeared that especially the *Ephydra* larvae and chrysalids form an important item of the diet. Only now and then were Artemias or *Artemia* eggs encountered, while the stomachs investigated by VOOUS (1957) contained a few fish-scales. This composition of the food of the Bonairian flamingos differs markedly from ALLEN'S report for the birds of Bahama and Yucatán, where molluscs were the staple item of the diet. We have already seen in Chapter IV, that molluscs do not occur in any numbers in the salinas on Bonaire.

The composition of the food, with as the most important component the *Ephydra* larvae and chrysalids need not surprise us when we consider the way in which the birds search for food, see Chapter V c.

If we compare the diet, on the basis of the stomach contents with the other (sub)species, we obtain the following picture:
Phoenicopterus ruber roseus: molluscs, water insects, crustaceae, seeds, organic mud, annelids and insects.

Phoenicopterus ruber chilensis: molluscs, crustaceans, algae, organic mud.
Phoeniconaias minor: algae, seeds, water insects.
Phoenicoparrus jamesi: especially diatoms (PATRICK 1961, PEÑA 1961 and
JOHNSON *et al.* 1958).
Phoenicoparrus andinus: probably also lives mainly from diatoms (PEÑA
1961, JOHNSON *et al.* 1958).

RIDLEY (1954) and RIDLEY *et al.* (1955) have pointed out that in Kenya *Ph. ruber roseus* and *Ph. minor* do not compete with each other, although they occur next to each other, since they utilise other food. The three small species *Ph. minor, Ph. jamesi* and *Ph. andinus* appear to live from algae in particular, while both South American forms – belonging to *Phoenicoparrus* – live from diatoms. This difference in the diet of the 3 (sub)species in the genus *Phoenicopterus* on the one hand and the 2 *Phoenicoparrus* species and *Phoeniconiais minor* on the other, is according to JENKIN (1957) explainable in the difference in the structure of the bill and filter apparatus between both groups. In addition, the presence of stones and sand of different sizes by different species is connected with the differences in the filter apparatus.

b. BILL AND FILTER APPARATUS (Plate XI*a*)

JENKIN (1957) has given an extensive description of the anatomy and function of the filter. In the following the most important details concerning *Ph. ruber ruber* are considered, while two illustrations have also been reproduced (Fig. 1 and 2). In the genus *Phoenicopterus* the bills are more or less identical, so that the drawing of *Ph. antiquorum* is valid for the West Indian forms also. The bill is bent halfway along its length and the upper-bill is flat, but provided with a ridge or keel; the under-bill is much heavier and higher in its construction (Fig. 1 and 2). This differs from the situation by the majority of birds and since the bill is usually employed upside down, the upper-bill then takes on the function of an under-bill and vice versa and is very movable. On the inside the edges of the bill are provided with dense rows of lamellae which work as a filter.

The tip of the bill cannot be opened more than 4 cm, due to the curved form of the bill itself, and by normal feeding this happens only during the seizing of larger prey, which itself does not happen very frequently. The hardly extensible oesophagus is, in fact, unsuitable for dealing with larger objects so that in general the bill is only slightly open during the feeding process with as a result a more or less regular space between the halves of the bill.

The filtering system works in two ways:

1. The bill is in turn opened and shut. – When larger organisms are to be eaten, the bill is opened slightly, so that the opening itself works as an "excluder". If the bill is then closed, the water is forced out through the filtering lamellae with the aid of the well-developed tongue. According to JENKIN, if the bill is opened for 4–6 mm, then objects larger than 4–10 mm cannot enter, although long, slim objects not wider than this can
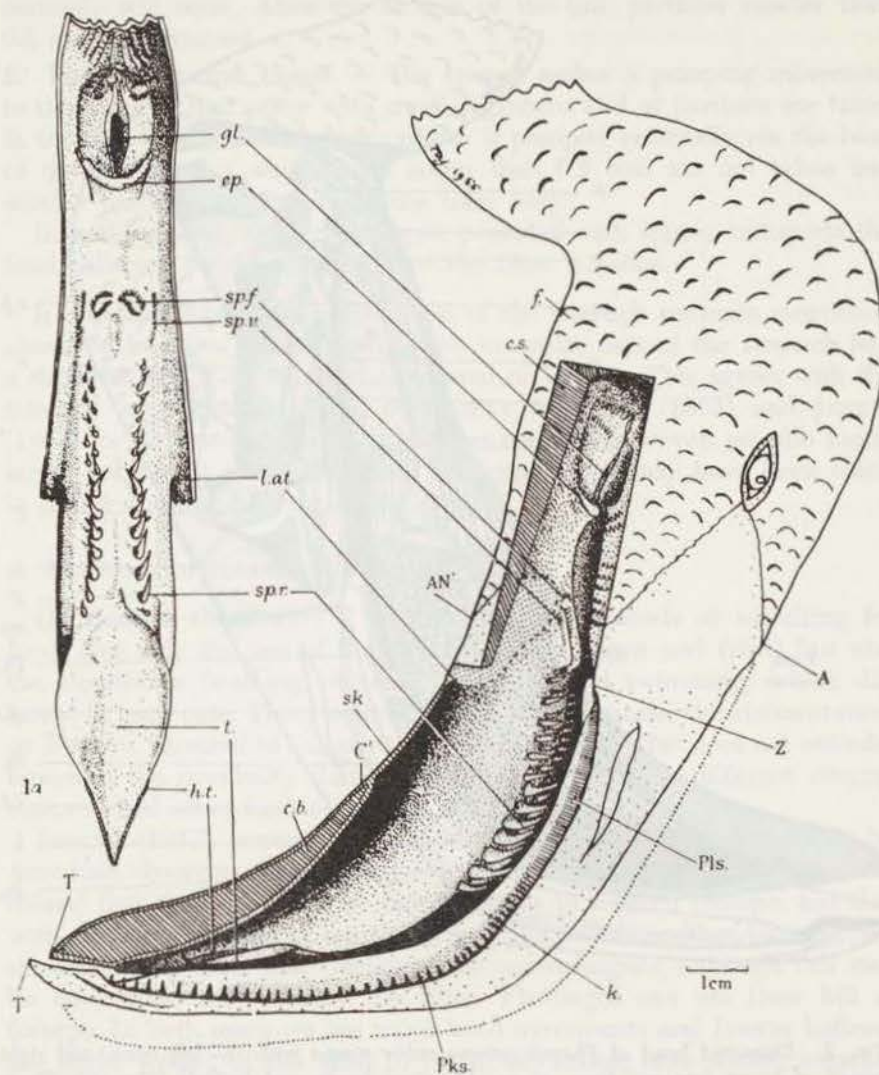
FIG. 1. Head of *Phoenicopterus ruber roseus* shown with its shallow-keeled bill closed for filtering. The extent to which it is opened in feeding (as in figure 2) is indicated by the dotted line. The right ramus of the lower jaw has been cut away to expose the mouth cavity, the tongue and the keel (k.) on the upper jaw. 1a. Upper surface of the tongue, flattened out; c.b. cut surface of bony fusion between the rami of the lower jaw; c.s. cut surface of skin and muscle round lower jaw; ep. epiglottis; f. feathers extending to A dorsally and AN' ventrally; gl. glottis; h.t. horny plate underlying the tip of the tongue; k. keel, hiding inflexed border of lower jaw behind; l.at. limit of attachment of tongue to the floor of the mouth cavity; Pks, marginal hooks forming main part filter; Pls, marginal leaflets, forming proximal part of filter; sk. skin of "naked throat" unsupported by bone from AN' to near C'; sp.f. double fan of spines on tongue; sp.r. large recurved spines on tongue; sp.v. vertical spines at the side of the tongue; t. flattened area of tongue, with raised edges; Z. posterior limit of lamellated area (after JENKIN, 1957).
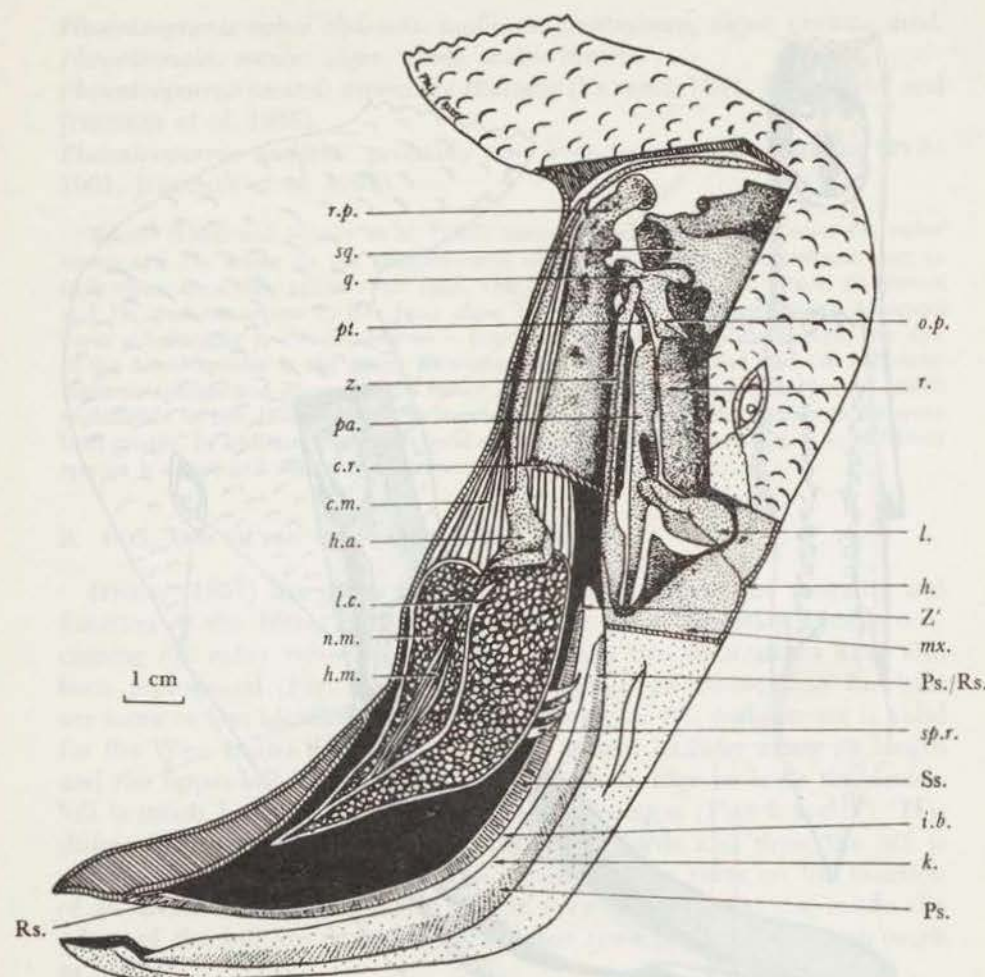
FIG. 2. Dissected head of *Phoenicopterus ruber roseus* with the bill open, and right ramus of lower jaw cut away at c.r. Marginal hooks and leaflets (Pks and Pls in figure 1), and all but the three most distal recurved tongue spines, sp.r., have been omitted for clarity. The finely stippled skeleton shows the means of raising the upper jaw about the fibrous hinge, h., by contraction of muscles attached to long processes, o.p., on the quadrate, q., which rocks on the squamosal, sq., and transmits its thrust to the maxilla, mx., both through pterygoids, pt., and palatines, pa., and through the zygoma, z. The tongue, with its hyoid apparatus, h.a., is withdrawn by contraction of the muscles, c.m.; its non-muscular part, n.m., supported by the lingual cartilage, l.c., is bent by contraction of the hypoglossus muscle, h.m., to increase the mouth cavity and suck in food. Inner lamellae on the inflexed border, i.b., of the lower jaw with retro-articular process, r.p., from smooth ridges, Rs, or serrated ridges, Ss. Inner lamellae on the lamellated area of the keel, k., are partially, Ps/Rs, or wholly, Ps, subdivided into smooth platelets. The lachrymal bone, l., has the large olfactory foramen between it and the rostrum, r. (after JENKIN, 1957).

certainly still enter. After the closure of the bill, particles smaller than 0.5 mm are removed.

2. The bill remains closed. — The tongue makes a pumping movement in this case, so that water with small organisms and or particles are taken in through the filter. The excess water is pumped externally via the base of the bill. In this way objects larger than 0.5 mm are not taken and smaller particles enter through the filter only.

In both methods the large tongue, provided with spines, transports the food collected on the inner side of the filter lamellae.

It appeared from our investigation of the stomach contents mentioned above on Bonaire, that the grit in the muscular part of the stomach had a maximal size of 11 mm and a minimal of $\frac{1}{2}$ mm. This agrees with the minimal measurements given by RIDLEY & PERCY (1953) and JENKIN (1957) for *Ph. antiquorum* (= *Ph. ruber roseus*). However, we also found larger pebbles of maximal $11 \times 6 \times 6$ mm, which may have been taken in during the non-filtering eating process.

c. METHODS OF SEARCHING FOR FOOD

On Bonaire there were 7 clearly different methods of searching for food. Not only the use of the bill (as seizing organ and filter) but also the locomotion (walking, standing, stamping and swimming) where different in each case. These methods were, at least under the circumstances on Bonaire, directed to one particular form of food. This does not exclude, however, the possibility that the same methods under different circumstances yield other food organisms.

JENKIN (1957) wrote, in connection with the earlier statement by American observers that flamingos were monophagous (the mollusc *Cerithium*) that they may well be monophagous in a given biotope, but that with the same method of searching, polyphagous in another biotope. She showed in any case, that flamingos are microphagous, although this may be only when they employ the filter. Flamingos can use their bill as forceps. In both cases we see rapid head movements and JENKIN believes the slight weight of the skull to be an advantage here which, together with the long neck facilitates the reversed use of the bill.

The following methods of searching for food were observed on Bonaire:

1. "Skimming" — walking and swimming — for *Artemia* in the surface water.
2. "Grubbing" — in the bottom, probably especially for *Ephydra* chrysalids.
3. Walking: seizing (forceps movements) — for *Ephydra* chrysalids, gastropod molluscs — and filtering — for *Ephydra* chrysalids, *Artemia* etc.
4. Stamping — "marking time" — for *Ephydra* larvae.

5. Stamping, describing a circle around the bill as centre — for gastropods.
6. "Running" — heron-like — for small fish or fry.
7. Walking, leaving tracks of the bill — for organic ooze.

1. "Skimming" (Figure 3)

During this method of searching only the extreme curved part of the bill is in the water and the head is moved by the neck through 90° to and fro, while only the last part of the curved point of the bill skims through the upper layer of the water. This method can be seen by both walking and swimming birds. The behaviour as a whole reminds one of swans, especially since the long legs are then invisible and part of the long neck disappears under water — the section by the root. This method has been seen in Goto only and then 4 times: 30 March in about 150 swimming birds; 11 April in a number of tens of swimming birds; on 20 April in many tens of walking and swimming birds and on 2 May in a few tens.
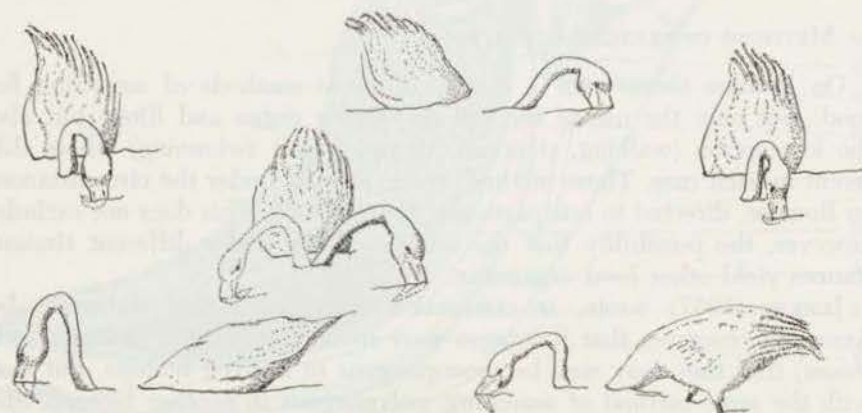
FIG. 3. "Skimming", walking and swimming.

This method would seem to be directed against Artemias, at least as far as these observations are concerned. In fact the way in which we took samples of Artemias was, in principle, the same: filling a bucket of water and then straining this through a plankton net, so that the Artemias are left behind. Other large plankton organisms hardly occur here and it is, for example, striking that in this period a record was made of the fact that the water here was exceptionally clear, so that there was no question of the development of plankton (phytoplankton) for which, in fact, the flamingo filter is not fine enough.

It is remarkable that this form food-seeking behaviour was restricted to the month of April or thereabouts, particularly in that before or after this period there were no noticeable changes in the biotic or abiotic milieu to be seen. There was no question of a diminution in the numbers of

Ephydra chrysalids and only a slight increase in the Artemias (from an average of about 35 to 90 Artemias per 10 l water). During periods with exceptional numbers of *Artemia* in Goto or Slagbaai, this behaviour was not observed. It can be imagined, however, that during a possible absence of other food but with the occurrence of several hundreds of Artemias per liter water, this method would certainly have some effect.

As far as I know, this method of searching has not been described in the literature for the genus *Phoenicopterus*, although it has also been observed by Voous in 1961 in Slagbaai. It seems possible that *Phoeniconaias minor* in Africa has the same behavior (MIDDLEMIS 1958, BROWN 1959).

2. "Grubbing" (Figure 4)

This method of food-seeking is also reminiscent of that seen by swans and ducks. The head, neck and the rostral part of the body are totally immersed, more or less straight down. The rear part of the body then sticks up out of the water, so that the legs have to carry out all possible movements to preserve the balance of this position. Usually the feet
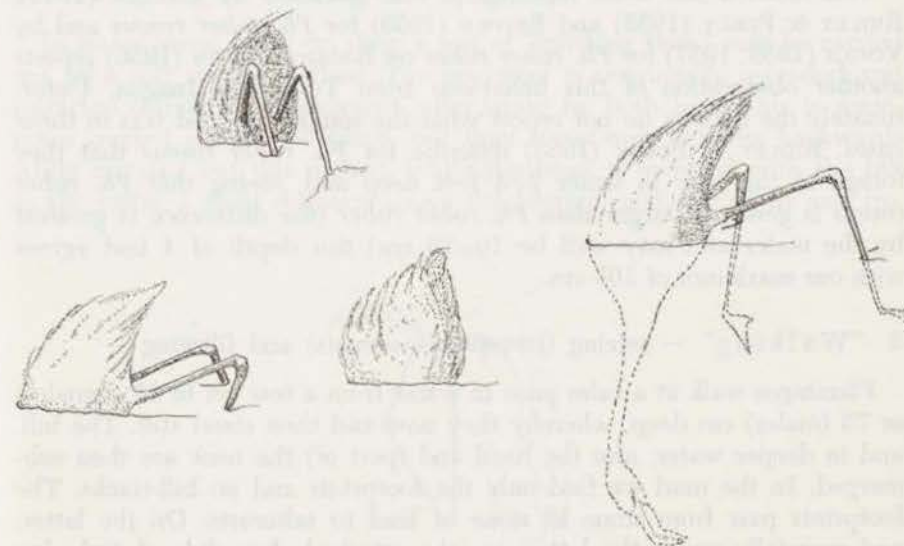
FIG. 4. "Grubbing".

alternate in producing stepping movements backwards with open webs and forwards, towards the body, with closed webs. This unsteady position necessitates that the movements of the feet can take place in the surface water only. It can be seen that the tibiotarsus is directed at an angle upwards and that only one half or three quarters of the tarso-metatarsus is in the water.

When the flamingos search the bottom in this way, they can reach a

depth of at most 90 cm (females) or 105 cm (males), that is, some 30 cm deeper than when they walk. This behaviour does not occur, however, at places where the water is more than about 1 meter deep and this method of searching is almost certainly aimed at the bottom and therefore at *Ephydra* chrysalids, which are to be found on and under stones, rocks and salt-crusts.

Grubbing often occurs in troops of from several to very many tens of birds (10—150), and is seen regularly in the Goto area throughout the year; regularly, but less often in the lagoon in Slagbaai and only incidentally in the Pekelmeer and the "Duinmeer". The reason for this is fairly obvious, since the lake of Goto is the deepest of these four areas, followed by Slagbaai; Pekelmeer reaches a depth of 1—1½ meters only here and there.

All four areas, where this behaviour was seen more or less frequently, are characterised by the occurrence of large numbers of Ephydras, whose chrysalids are attached on stones and salt-crusts. The capture of *Ephydra* larvae in this way would appear to be impossible, since the bird's feet are active too far above the bottom to disturb it and thus uncover the larvae.

This method has been reported in the literature by GALLET (1949), RIDLEY & PERCY (1953) and BROWN (1958) for *Ph. ruber roseus* and by VOOUS (1955, 1957) for *Ph. ruber ruber* on Bonaire. ALLEN (1956) reports another observation of this behaviour from Tunis and Inagua. Unfortunately the authors do not report what the sought for food was in these cases. RIDLEY & PERCY (1953) describe for *Ph. ruber roseus* that they forage in this way in water 2—4 feet deep and, seeing that *Ph. ruber roseus* is generally larger than *Ph. ruber ruber* (the difference is greatest by the males and may well be 10—20 cm) this depth of 4 feet agrees with our maximum of 105 cm.

3. "Walking" — seizing (forceps movements) and filtering

Flamingos walk at a calm pace in water from a few cm to 60 (females) or 75 (males) cm deep, whereby they now and then stand still. The bill, and in deeper water, also the head and (part of) the neck are then submerged. In the mud we find only the footprints and no bill-tracks. The footprints pass from stone to stone of lead to saltcrusts. On the latter, and especially under the latter, are the attached chrysalids of *Ephydra*.

We can be certain therefore that in this way the *Ephydra* chrysalids are "grazed off" so that probably the filtering action hardly, or does not work, at all. The bill serves here as a seizing organ, as a pair of forceps, and the tongue with its papillae holds the captured chrysalids and from time to time, transports them back to the throat. This method is the most usual in searching for food, and the flamingos do it in large numbers at all places where *Ephydra* chrysalids occur. In the Salina of Playa Lechi and the "Ven" only was it not seen, but here indeed there are no Ephydras. In the same walking fashion molluscs are here and there sought

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for; they are also found by sight and the bill acts once more as a pair of forceps and the filtering action is not employed. This was seen in particular in the "Ven" where *Cerithidea costata* and *Nodilittorina tuberculata* occur. Molluscs occur at hardly any other places; when they do, they are mostly *Cerithidea costata* and *Batillaria minima*. It is obvious that in this way other prey could be captured in other areas.

Walking-filtering also occurs (see also *1*) as a means of foraging, whereby the birds catch *Artemia* or other small organisms and also *Ephydra* chrysalids released by the grubbing method as described above.

In shallow water it can be seen that the flamingos lift up stones with the reversed bill or search under clumps of weed. In this case water leaves by the base of the bill, so that they are therefore pumping and filtering. ALLEN (p. 90) describes this method of food-seeking also: "Apparently small mollusks are sifted from the mud, when present. ... I have also seen individual birds striding along a beach and picking up small gastropods (*Cerithidea costata*) which they quite obviously located by sight. In this instance the tips of the mandibles are used as a forceps".

4. Stamping — "marking time" (Figure 5)

In water about 5—60 cm deep a sort of "marking time" may be carried out on a soft muddy bottom. The heel-joint is continually extended and retracted during this movement, alternating by both legs. This is sometimes carried out at one place, but they sometimes progress backwards while carrying out this motion, while the head is reversed with the bill in the water a short distance above the bottom, and moved to and fro.

FIG. 5. Stamping — "marking time".

If we imitate this movement with hands or feet at the places where flamingos were seen to be busy, then we find that innumerable *Ephydra* larvae drift up from the bottom, which at first passively and later actively disperse through the water. With their large webbing, the flamingos obtain the same effect and it is obvious that, in this case, they are searching for *Ephydra* larvae.

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The number of larvae living in or on the mud bottom is often very high: sampling yielded often some 10–30 *Ephydra* larvae per dm², so that this method of searching for food is probably lucrative. The larvae are probably caught with the filter mechanism — they may reach 15 mm long, but they are too small and active to be caught on sight or by touch in the muddy water. It is likely that tens of liters of water are pumped through the filter, so that the larvae remain there.

This method of searching occurs, just as did the foregoing (3) at a high frequency and is performed *en masse* as well; it is to be seen at all places where *Ephydra* occurs.

Young flamingos, rummaging around by the nest, have also been observed carrying out the same actions on a muddy bottom without water, or with only very little. With their as yet unbent bill they stare at the ground or peck in it. It would appear that this method of searching for food is innate, for it occurs by young birds who have probably not yet learnt by imitation from older birds, since this behaviour does not take place near the colony itself. There are also other indications that this behaviour is hereditary (CHAPMAN 1905).

This method, which was described as early as the 18th and 19th century by BUFFON and CLARKE respectively, makes sense only when it is directed against organisms in or on the bottom, which as a result of the actions of the birds then appear and are filtered off.

5. S t a m p i n g — circling around the bill (Figure 6, Plate VII*b*)

In this method the reversed bill forms the locus around which the birds stamp. One such circle (clockwise or anticlockwise) takes 45 to 60 seconds and during one turn the head is raised 8 times above the water — sometimes swallowing, but not always. This tempo is more or less constant.
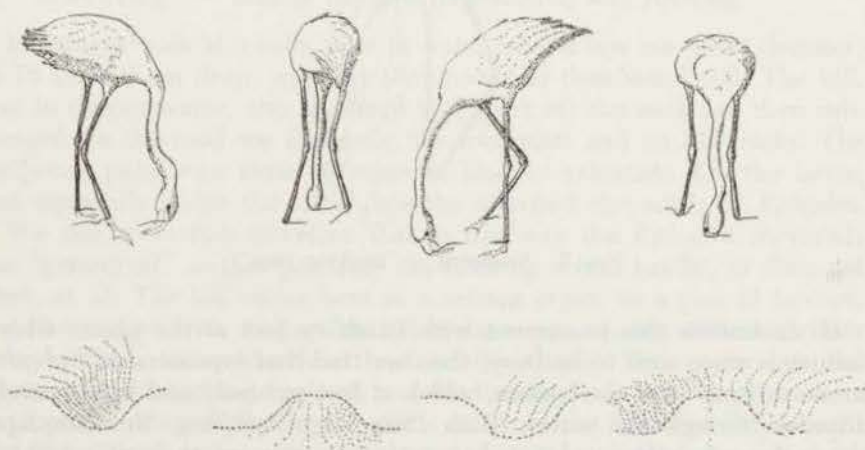
Fig. 6. Stamping — describing a circle around the bill as centre.

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We have observed this more or less incidentally in the Pekelmeer and more often in the "Ven", usually in shallow places where, at most, the water is 30 cm deep. It has not been seen in Slagbaai or in Goto.

When this method has been carried out, what remains is a small round mound, a few to 15 cm high and which has a diameter of 20–150 cm, the majority being 50–100 cm. A groove runs around this from a few to several cm deep. This mound consists of mineral particles — chiefly coral sand — and the groove contains mainly organic material or detritus.

When we imitate this behaviour, we can, as before, explain its action and at the same time see what sort of food is being sought. If we strike the hands or feet on the bottom and at the same time describe a circle such that the movements are centripetal (the flamingos do this with their webbed feet), then mineral and organic material is thrown up. The heavier mineral material sinks first and, since the movement is centripetal, it sinks in the middle of the circle, giving rise to the small mound. The lighter organic material (detritus) is carried with the current over this mound and sinks into the groove created by the removal of the bottom.

During our imitation it appeared that a large number of molluscs — *Cerithidea* and *Batillaria* — are left behind on the central mound, since they are lighter than the coral sand, but heavier than the organic detritus. In this "goldpanning" method the material in the bottom is sifted according to its specific gravity, with, as a result, a concentration of molluscs on the mound of coral sand.

It is not clear if the prey is taken up by filtering or by being seized by the mandibles. The latter is probably the case, since otherwise there would be no collection of organic detritus, algae, etc., in the groove. These do not appear to interest the flamingos, who do not touch them.

This circling around the bill was also seen in young birds, e.g. in Goto, where the absence of molluscs meant that adult birds never did this, so it would seem once more that this behaviour is innate.

The methods described under 4 and 5 are mentioned in the literature on flamingos although the descriptions are sometimes confused: CHAPMAN (1905, 1908), GALLET (1949, 1950), MIDDLEMISS (1953, 1961), ALLEN (1956) and BROWN (1958). ALLEN's problem as to whether the bill or feet are centrally placed in this method would appear to be resolved by our observations. There are two methods of searching: in the one case (4) the stamping feet are central and the bill moves around, collecting the floating food; in the other method (5) the bill is central and the feet then describe a circle. There is, however, the following difference with GALLET's (1949, 1950) opinion about the "cônes alimentaires". He writes that in this way organic material is filtered out of the mud, so that the mineral particles remain behind and form the mound or "cône alimentaire" (see also under 7). We have shown that in this way, gastropod molluscs are separated from the heavier mineral particles and the lighter detritus, which collected in the groove around the mound. The latter detritus was not eaten.

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ALLEN saw this method of food searching (5) on Inagua and traces on Cuba. MIDDLEMISS (1953, 1961) reported similar behaviour from the Rondevlei Bird Sanctuary in S. Africa for *Ph. ruber roseus*, but had evidence that feeding took place in the groove around the mound.

6. "Running" — Heron-like (Figure 7)

The otherwise so inactive flamingo runs in very shallow water (1—15 cm deep) or along banks, sticking with a swift unexpected movement its bill in the water, without inverting it, but using it as a pair of forceps.
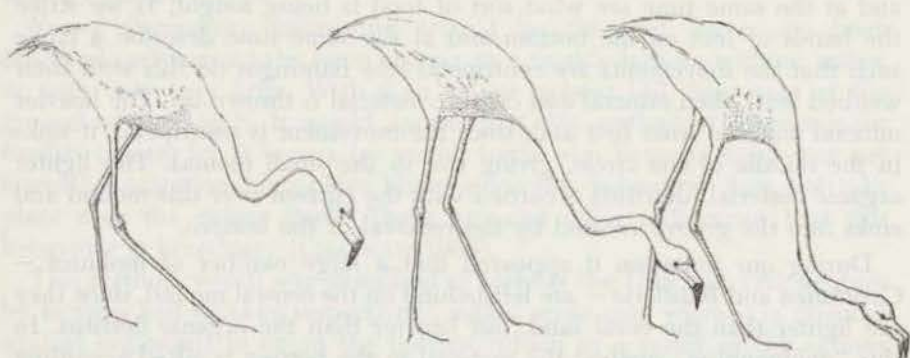
Fig. 7. "Running" — heron-like.

This behaviour is very reminiscent of the fishing of the Little Blue Heron (*Florida caerulea*), the Tricoloured Heron (*Hydranassa tricolor*) and the Snowy Egret (*Egretta thula*), who catch cyprinoids (*Cyprinodon dearborni* and *Mollinesia sphenops*) in this way. These herons do this in shallow water along banks where sea-water enters giving a Cl-content of not more than 75 g/l.

We have observed this behaviour once by one flamingo in the Boca of Slagbaai, where, along the banks, many cyprinoids and their fry occur. The flamingos go to the less salt places to drink and bathe and come, in all probability, in this way to attempt some fishing. It is not clear if they are very successful, but taking into account the very sporadic occurrence of this behaviour, and then by a single specimen, it would not appear to be lucrative. We have never seen this in the Pekelmeer where local concentrations of this small fish also occur.

VOOUS (1957) reports an observation by WAGENAAR HUMMELINCK in 1955 of the same behaviour in the Pekelmeer.

7. Walking, leaving tracks of the bill (Figure 8, Plate XIb)

The flamingos walk, in this method, with inverted bill forwards in an erratic fashion so that the bill passes over the surface or just in the mud bottom. This takes place for the most part where a few centimeters to about 30 cm of water is found. The head is sometimes moved from side to side, so that the bill leaves a very erratic track behind, up to 2 to 3 m long and 1 or 2 cm deep.

The only way to find out what is happening here, is to imitate the movement oneself. This was done with a small container or trowel in the same places where these tracks were found and here the upper layer of "mud" was collected. This is often a reddish mass, containing sediment and salt, but here and there it has a red or brown and green composition which suggests that many algae and microorganisms are to be found there. Blue algae where often found in these samples (*Coccochloris elabens, Entophysalis deusta* and *Phormidium subsalsum*). Many bacteria and protozoans also occurred in this mud; in addition to the sediment, detritus and salt crystals.

Fig. 8. Walking, leaving tracks of the bill.

Without further analysing the species content, we can still determine the food value of this "mud" by examining its organic content. The samples were first weighed, then leached of salt and then dried, weighed once more, heated and once more weighed.

The organic content was: near recent tracks in Pekelmeer on 8.VI, at two places close to each other, 21.1 and 21.8% dry weight; on 15.VII, at two places near one another (twice), 10.8% wet weight and 20.1% dry weight.

On 7.VII. two mud samples were examined from the Salina Playa Lechi, which contained 4.9 and 4.5% wet weight, and 15.5 and 15.5% dry weight of organic matter respectively.

In all probability, this mud was eaten, just as in the Pekelmeer, during poor food conditions. No tracks could be seen, however, through the muddy water.

This method was not seen very often, but the tracks remain visible for a long time, since the soft mud holds the impressions of both the bill and the feet, both being 1 to 2 cm deep. The amount of mud that flamingos must eat in this fashion is considered in Chapter VI.

This method is referred to in the literature by ALLEN (1956), BROWN (1958) and MIDDLEMISS (1961). JENKIN (1957) writes that during the operation of this method, the filtering process must work backwards — "the

mud must presumably be sucked in while the gape is practically closed, and the marginal platelets (the normal filter) be used to exclude the sand grains."

Ph. ruber ruber shows this behaviour while walking forwards (ALLEN, and our observations on Bonaire), but MIDDLEMISS (1961) saw it in *Ph. ruber roseus* both forwards and backwards. JOHNSON *et al.* (1958) established that *Ph. chilensis, Ph. jamesi* and *Ph. andinus* walk backwards during this method. Mud and stomach analyses (JOHNSON *et al.* 1958 and PATRICK 1961) have shown in these species that the method is directed against diatoms.

d. QUALITATIVE ASPECTS OF THE FOOD

ALLEN (1956, p. 101–107) gives a list of "potential food items" for flamingos. By combining the stomach analyses, the methods of searching for food and the biotopic data for Bonaire, we can compare the list of food items for West Indian flamingos with those on our island.

1. "Organic ooze"

ALLEN (p. 101) writes: "The significance of a high organic content in the muds and waters frequented by flamingos has been generally overlooked until recently." He gives analyses of the mud in Yucatán, which contains 12 species of bacteria, 20 of algae, 4 of diatoms, 9 of protozoa and a number of species of molluscs, arthopods and nematodes. The organic content of mud on Inagua varied in March from 85.87 to 91.88% and in June from 8.07 to 18.15%. In Cuba he found an organic content of 40.43% in May.

The percentages dry weight found in the Pekelmeer agree with ALLEN's June figures: 21.1 and 21.8; twice 20.1, and twice 15.5% in the Salina of Playa Lechi.

ALLEN states (p. 104): "Unquestionably this "organic ooze" or "slime", as it has been variously termed, is a major food of these birds when available in sufficient quantity. In certain habitats and under given circumstances it may even be a critical food item."

On Bonaire this eating of mud was noted with certainty in the Pekelmeer only, but then never on a large scale. We had the impression that this behaviour was restricted to those periods when hardly any other food was available. Other indications for the eating of mud were the goose-like, hard excrements, which once again were found in or along the Pekelmeer only. These consisted chiefly of mineral matter, with some cuticular flakes and, seeing the size, it would appear that these excrements came from the gut caecae. It is possible that the undigestible mineral part of the mud is stored here and then got rid of in this fashion. The "normal" excrements are fluid and traces of these droppings are rarely to be found.

RIDLEY (1954) has pointed out that the "flamingo has the longest Meikel's tract (that is, the absorptive part of the alimentary canal) of any bird."

The alimentary canal may, in adult birds, reach a length of 3 to 3.7 m from stomach to cloaca! The digestive process, seeing the length of the gut and the nature of the droppings, must be very intensive and these facts enable us to understand the eating of mud as a source of food.

2. Annelid worms and Nematodes

"Marine forms of annelids ... may be extremely abundant in certain flamingo habitats and, in spite of a lack of conclusive evidence, may well constitute an important food" (ALLEN 1956, p. 104).

On Bonaire we have seen hardly any worms, so that it is unlikely that they should be considered as food items.

3. Molluscs

"Examinations of stomach contents seem to emphasize the importance of mollusks as a flamingo food, which is in line with the widespread belief that these animals are the principal item of diet. Some authors have even gone so far as to state that mollusks are the sole diet of flamingos, at least in the Bahamas, but this obviously is incorrect" (ALLEN, p. 104).

Large numbers of *Batillaria minima* (= *Cerithium minimum*) and *Cerithidea* occur on Bonaire in the "Ven" only, while some specimens may also be found in the "Duinmeer" and Pekelmeer. The small numbers of living animals can play no great role in the diet; the large number of empty shells, on the other hand, suggests that they might well do so, when they are numerous.

4. Crustaceans

"It is of interest to note that there are no reports of crustaceans as food of the West Indian flamingo, although analysis of organic muds from Inagua showed small numbers of copepods present, while examples of Ostracoda were found in mud collected from the nesting site at Río Maximo, Cuba. Apparently crustaceans in general may be taken as food, but it is possible they are of minor importance in this role" (ALLEN, p. 106).

On Bonaire we have certainly seen food-searching methods which could be directed against *Artemia*. It did not occur often, but in periods when other food items are scarce, it implies an important reserve which they may fall back on. In addition, in the examination of stomach contents, we encountered a number of remains of Artemias.

5. Aquatic insects

"As with crustaceans, there is no mention of aquatic insects or their larval forms in stomach contents or reports on food habits of the West Indian race (*Phoenicopterus ruber*). This may be an oversight or it may reflect a true state of affairs in which the Bahamas-Caribbean flamingo depends to a greater extent on mollusks and mud with a high organic content, while flamingos in other parts of the world, where mollusks are lacking or few in number, must search out smaller and more mobile creatures like water beetles and other water insects. On the other hand, we must realise that the same insect forms to be found in the Great Rann, Ab-istadeh and a lake in Kenya, also occur in many New World sites, where, to some extent at least, they are probably eaten by our flamingos" (ALLEN, p. 106).

It is very surprising that no data for West Indian flamingos are given by ALLEN for their eating of *Ephydra* larvae and chrysalids. We have observed that these form the staple diet and that various methods of searching for food appear to be directly directed against them.

6. Vertebrates

"After watching flamingos feed on many occasions and under varying conditions, we concluded that fish are taken as food rather sparingly and only when they are very small in size and unusually abundant. Young flamingos in captivity readily devoured quantities of small fish of this same form that were offered to them in shallow pans of water" (ALLEN, p. 106).

VOOUS (1957) reported a number of fish-scales in the stomach contents and we have seen (just as WAGENAAR HUMMELINCK) very incidentally a type of hunting (6) apparently directed against small cyprinoids. Fish would appear to play no significant role in the diet, however.

7. Vegetable matter

"We have seen that in addition to the list of plants reported from stomach contents, various forms of bacteria are contained in some quantity in mud from flamingo feeding places. Vegetable matter as a whole, especially the seeds of aquatic plants like *Ruppia* and blue-green algae, may be highly important food in some areas. It is significant that most of the plants taken have a high salinity tolerance" (ALLEN, p. 107).

In the most important flamingo biotopes on Bonaire, *Ruppia* does not occur, but bacteria and algae are certainly consumed by mud-eating. In a juvenile specimen a number of small seeds were found in the stomach. Since this specimen was observed in the Salina Martinus, we suspect that seeds have accidentally been taken in during filtering, derived from plants in the vicinity.

Summarising we can say that on Bonaire the situation is totally different to that in the Bahamas and in Yucatán. The *Ephydra* larvae and chrysalids form here, in our period of investigation at least, the staple item of diet. In addition, *Artemia,* molluscs and "organic ooze" played subsidiary roles and fish were eaten only incidentally.

e. DRINKING (Figure 9, Plate XIXb)

Flamingos must take up large amounts of salt by various means, during their search for food, and although this could be compensated by the
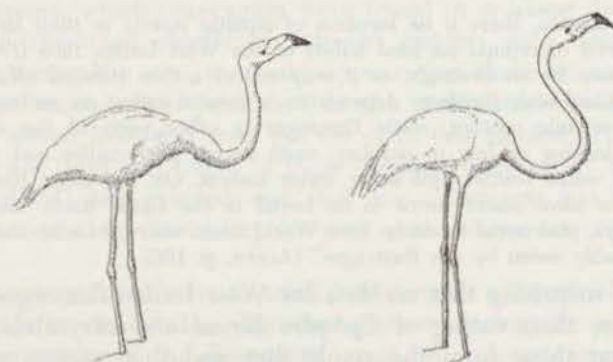
FIG. 9. Drinking, water runs down with the characteristic slanting of the neck.

drinking of fresh water, the latter hardly occurs on Bonaire during the long droughts. Flamingos regularly drink, however, at places where sea-water enters the brine lakes. At the end of the afternoon large groups of birds drink at these places. They are also bathing and preening here. This drinking resembles food-filtration but it can be seen in shallow places that now there is no exit current at the base of the bill. The water taken up is then transported by a characteristic slanting of the neck.

A definite choice is shown for places where the Cl-content hardly, if at all, exceeds 20 g/l (sea water). (BROWN, 1958, found a preference for water from springs or rivers). This preference for seawater was shown in the "Willemsoog" on the N.E. side of Oranje Pan. This is a small pool with an "eye" giving access to seawater, so that the entire pool usually contains water of about 20 g Cl/l. During extreme high water levels of the sea, the circular "Ringmeer" is much increased via the small canal and this has then an open connection with the "Willemsoog" (normally not the case, see Chapter IV c and d). Since water flowing through this canal to the "Willemsoog" travels a long way, it is markedly evaporated on arrival, to 72.7 g Cl/l on 12.II. and 55.5 g Cl/l on 4.III. 1960. This can be seen in Graph 7 where a marked increase in the Cl-content of the "Willemsoog" can be seen, during the period when the "Ringmeer" overflows.

Normally the Cl-content here differs hardly from seawater, i.e. 20 g Cl/l. The flamingos appear to have a preference for this, as can be seen in the same graph. The number of birds after 16.00 hours are given, since during the day they hardly drink, if at all. It can be seen that before the rise in the Cl-content, troops of flamingos came to drink regularly, only on two days was this not the case. Afterwards, however, they did not drink there (6 times after 16.00 hours! the rest of day as well, so this is not considered here). In the period of overflow, when the Cl-content returned to 20 g/l, birds drank there regularly once more, on 3 days only were they absent.

In the period around the middle of December, the birds drank and bathed chiefly at two other places where seawater seeped in, i.e. at Witte Pan and between P3 and Oranje Pan. During the period when the "Wil-lemsoog" was apparently too salt, the birds drank chiefly between P3 and the Oranje Pan, and the "Ven" was also popular. After the return to normal Cl-content in the "Willemsoog", the birds still drank at other places, but especially at the end of May and in June and July, their interest in the former slackened and other places were much preferred. The broken line in the graph indicates that, although no further Cl-analyses were carried out, the Cl-content probably remained the same, since the eye continued to admit seawater.

The other drinking-places also turned out to contain water of 20 g Cl/l; this was the case in Slagbaai (the Boca) — the Southern and Northern eyes, where the birds regularly drank. In the "Ven" the water contained everywhere about 20 g Cl/l. We have never seen birds drinking in Goto,

although flamingos were seen now and then near the Boca, where seawater also seeps in, but never in great numbers. "Eyes" were present near some parts of the colonies in the Pekelmeer and we sometimes saw flamingos drinking from their nests while brooding.

In particular in connection with the growth of the young birds, does it seem important that there be less salt water in or near the colony. ALLEN (p. 111) has reported something similar for Lake Windsor (Inagua). He has, at the same time, observed that flamingos collect at places where rainwater remains after heavy showers, to drink and to bathe.

Once (the 8th. of January) we saw that flamingos, during a short but heavy shower, stopped all other activities and stuck their heads in the feathers, just as they do to sleep. They could then collect the water which ran off their feathers and let this run down with the characteristic slanting of the neck.

Our observations follow here: 8. I., 12.45. A heavy shower from the south. During this heavy downpour only about 50 birds remained at the Oranje Pan that we could see, in shallow water near the edge. All of these (50!) show the following behaviour: they stand for 4—5 seconds with the head in or on the wings and/or back feathers, when their necks show all possible twists and turns. Probably they catch streams of water with their bills, since every 4—5 seconds they elevate their bills (Fig. 9) and swallow. It seems to me that they are drinking fresh water in this way. We have not seen them drinking at the "eyes" today! (12 mm of rain fell that day!).

Also on 28.III and 24.VI we have not seen flamingos drinking at the "eyes" after rain, and it is probable that this happens regularly after rainfall. On Bonaire, however, they do not often have the chance to drink rainwater, and therefore make do with seawater. This is important in connection with the excretion of salt. In addition to the kidneys there are other possibilities of getting rid of the excess of salt taken in. SCHMIDT-NIELSEN (1958, 1959) reports that various birds and reptiles living near the sea (e.g. gulls, pelicans, petrels, cormorants, turtles and leguans) have an organ in the head, near the eyes, which concentrates and excretes NaCl by way of the mouth or nostrils. He gives the following figures in this connection: Sea water — 3% NaCl, "nasal fluid" — 5% NaCl and urine — 3% NaCl.

Although, as far as I am aware, this has not been investigated anatomically in the flamingo, it seems likely that they also have an organ of this type. In fact, we frequently see flamingos shaking their head and bill, especially after drinking and/or foraging, so that droplets are shaken off the bill itself or from the nostrils. Sometimes these droplets can be seen quite clearly glistening in the sunshine, also when they are hanging on the tip of the bill. In this way, salt from the blood could be eliminated and relatively fresh water taken into the body.

If this supposition is correct, it is acceptable that they prefer to drink water with a low salt content, in this case seawater or, when available, rainwater. For bathing and preening, this preference is obvious since then it will be less difficult to remove salt incrustations from the feathers and body.

f. DENSITY CHANGES IN EPHYDRA AND ARTEMIA

Ephydra gracilis

As we have seen in the examination of the stomach contents and the way in which the birds search for food, only the larvae and chrysalids are of direct importance for the flamingo.

Since it was difficult to take bottom-samples due to the changing and sometimes "inaccessible" state of the bottom, the chrysalids were used as a measure of the density of the Ephydra. These pupae attach themselves to stones, usually on the underside, or at least in crannies or niches sheltered from above and also on or under salt crusts. These sites are not of the same magnitude everywhere and often cannot be examined, since the stones and/or salt crusts are "stuck" on the bottom.

It is therefore not possible to determine the number of Ephydra chrysalids per unit surface area. It is possible, however, to make a rough

TABLE I. PERCENTAGES OF OCCUPATION and NUMBERS of Ephydra gracilis chrysalids; comparison of 22 checks of double samples of 25 stones each (A and B).

A		B		
perc.	nrs.	perc.	nrs.	perc. difference
0%	0	4%	1	4
8%	7	8%	7	—
8%	8	8%	6	—
12%	13	12%	10	—
24%	17	24%	16	—
28%	38	32%	36	4
28%	34	32%	40	4
36%	57	32%	46	4
36%	52	36%	46	—
36%	39	44%	48	8
36%	32	48%	36	12
36%	53	52%	80	16
40%	53	40%	52	—
44%	69	44%	75	—
48%	49	48%	65	—
48%	151	60%	114	12
52%	90	56%	108	4
84%	1031	84%	1236	—
92%	1398	92%	1627	—
92%	2098	96%	1782	4
92%	1929	96%	1916	4
100%	1800	100%	1627	—

estimation of this by determining the number of possible sites per 500 sq. m, which suggests the number of chrysalids an area can support (see Chapter V g). In order to obtain a reliable impression of the density changes in the course of one year, and the role of the flamingos in this connection, samples of 25 stones were examined at random, more or less weekly, at various sample points in Goto, Slagbaai and the Pekelmeer.

In each sample the number of chrysalids were considered in addition to the percentage of stones having chrysalids on them (occupation percentage). The numbers of chrysalids were at first given somewhat vaguely,

TABLE II. OCCUPATION PERCENTAGES of samples from 25 stones and corresponding numbers of *Ephydra gracilis* chrysalids.

occ. perc.	numbers	average nr.	min. nr.	max. nr.	number of samples
4%	4, 2, 1	2.3	1	4	3
8%	6, 9, 8, 6, 7, 7, 7	7.1	6	9	7
12%	7, 8, 7, 13, 10	9	7	13	5
16%	23, 12, 12, 14	15.2	12	23	4
20%	17	17	—	—	1
24%	16, 17	16.5	16	17	2
28%	47, 38, 30, 34	37.2	30	47	4
32%	47, 45, 27, 36, 19, 40, 46	37.1	19	47	7
36%	71, 32, 52, 46, 53, 39, 57	50.3	32	71	7
40%	85, 56, 53, 52	61.5	52	85	4
44%	45, 48, 128, 96, 69, 75, 93, 51	75.6	45	128	8
48%	28, 38, 115, 36, 49, 65, 151	68.9	28	151	7
52%	90, 80, 70	80	70	90	3
56%	165, 127, 60, 108	115	60	165	4
60%	114	114	—	—	1
64%	214, 288, 155	219	155	288	3
68%	182, 127, 125, 1561, 169	432.8	125	1561	5
72%	207, 427, 157, 304	273.7	157	427	4
76%	206, 943, 1436, 331	729	206	1436	4
80%	499, 1425, 1032	985.3	499	1425	3
84%	1659, 1031, 1236, 1082	1252	1031	1659	4
88%	314	314	—	—	1
92%	2134, 1947, 1929, 1520, 2098, 1398, 1627	1807.6	1398	2134	7
96%	307, 1916, 1782	1335	307	1916	3
100%	1599, 1627, 1800	1675.3	1599	1800	3
		Total no. of samples			104

but later the number of full chrysalids on each of the 25 stones were counted, so that with a given percentage of occupied stones a certain number of *Ephydra* chrysalids were recorded. At certain places, where the number of loose stones was higher, regular countings of twice 25 stones were carried out. These double counts and the occupation figures give then a picture of the reliability of the method of sampling (Table I). The stones which were sampled had a minimum size of $7 \times 5 \times 3$ cm and a maximum of $30 \times 20 \times 15$ cm, and apart from this, were selected at random, and examined.

The average difference in the percentages of occupation is 3.45%, i.e. a little under the value of one stone (4%).

The 22 checks show in general such a high agreement that this can be termed a representative sampling. In addition, we can show something of the correlation between the occupation percentages and the numbers of *Ephydra* chrysalids on 25 stones from the data given above and the counts during the last $2\frac{1}{2}$ months of the study (Table II).

It would appear that there is a correlation between the percentage of occupation and the numbers of *Ephydra* chrysalids per 25 stones. Since Table II is concerned with 104 counts only, it is sometimes so that for a given percentage only one count appears, so that the trend is somewhat obscured.

If we translate these results graphically, then the correlation between the two factors appears clearly once more (Graph 8).

For the changes in density we shall use the occupation percentages, although in Graphs 9, 10 and 11 the numbers per 25 stones are given for the
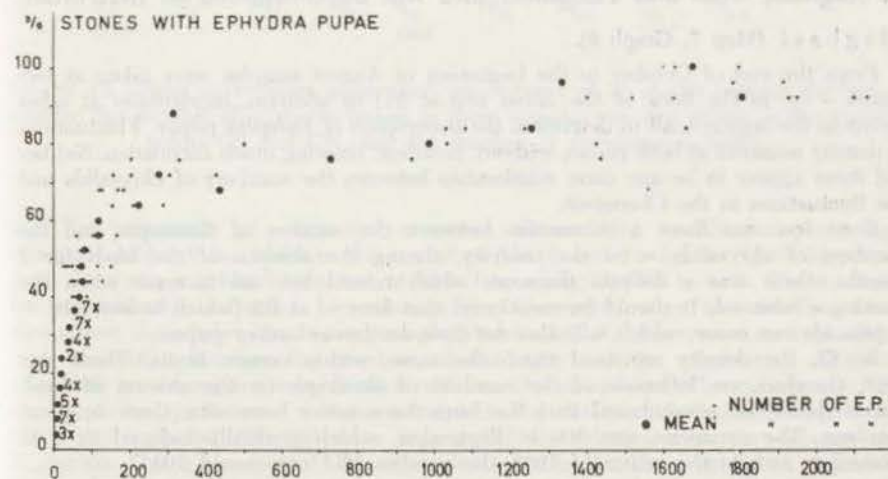
GRAPH 8. Correlation between the occupation percentage of *Ephydra gracilis* pupae on 25 stones and the number of *Ephydra* pupae in these samples. — ● indicates mean number of *Ephydra* pupae at the different occupation percentages: 4, 8, 12, etc. n x indicates the number of samples of 25 stones.
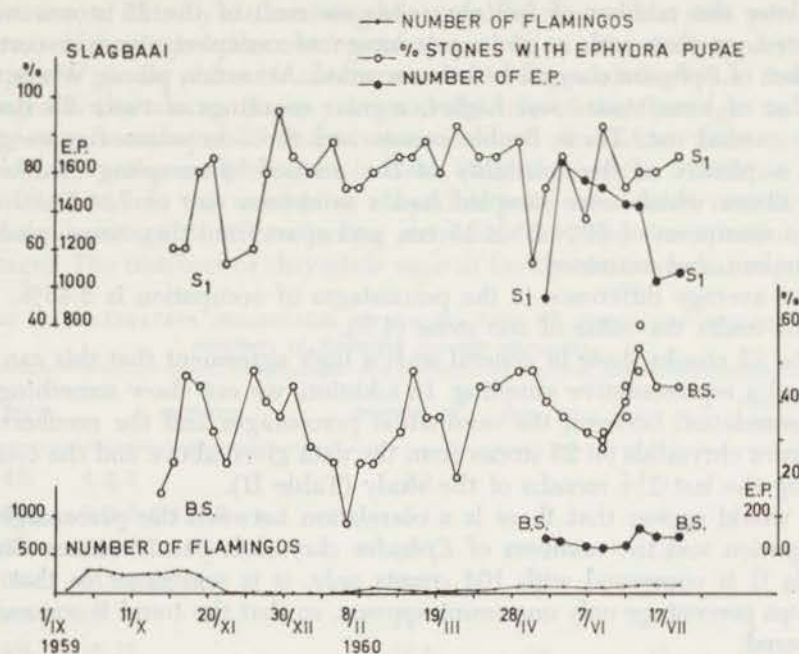
GRAPH 9. Relation between occupation percentages of 25 stones (during the last 2 months the number of *Ephydra* pupae in these samples are also given) at the sample points BS and S1, and the number of flamingos in Slagbaai.

last period, at the same time. These changes in density were established in Slagbaai, Goto and Pekelmeer and will be considered in that order.

Slagbaai (Map 7, Graph 9).

From the end of October to the beginning of August samples were taken at two places – i.e. in the Boca of the salina and at S1; in addition, incidentally at other points in the lagoon – all to determine the occurrence of *Ephydra* pupae. Fluctuations in density occurred at both places, without, however, showing much correlation. Neither did there appear to be any clear relationship between the numbers of chrysalids and the fluctuations in the Cl-content.

Even less was there a connection between the number of flamingos and the numbers of chrysalids — on the contrary, during the absence of the birds for 2 months, there was a definite decrease, which turned into an increase when the flamingos returned. It should be mentioned that here — at BS (which is less salt) — cyprinoids can occur, which will also eat *Ephydra* larvae and/or pupae.

At S1, the density remained much the same, within certain limits. There was here, therefore, no influence of the numbers of flamingos on the amount of food, but it should be remembered that the birds have never been seen there in great numbers. The maximum was 300 in September, which gradually reduced to 0 in December and, in the course of 1960, the numbers did not exceed 100.

Goto (Map 6, Graph 10)

Samples were taken here from the end of October to the beginning of August at regular intervals from two places — i.e. at G3 and GN (also now and then at other places). In GN the number of *Ephydra* chrysalids remained more or less the same
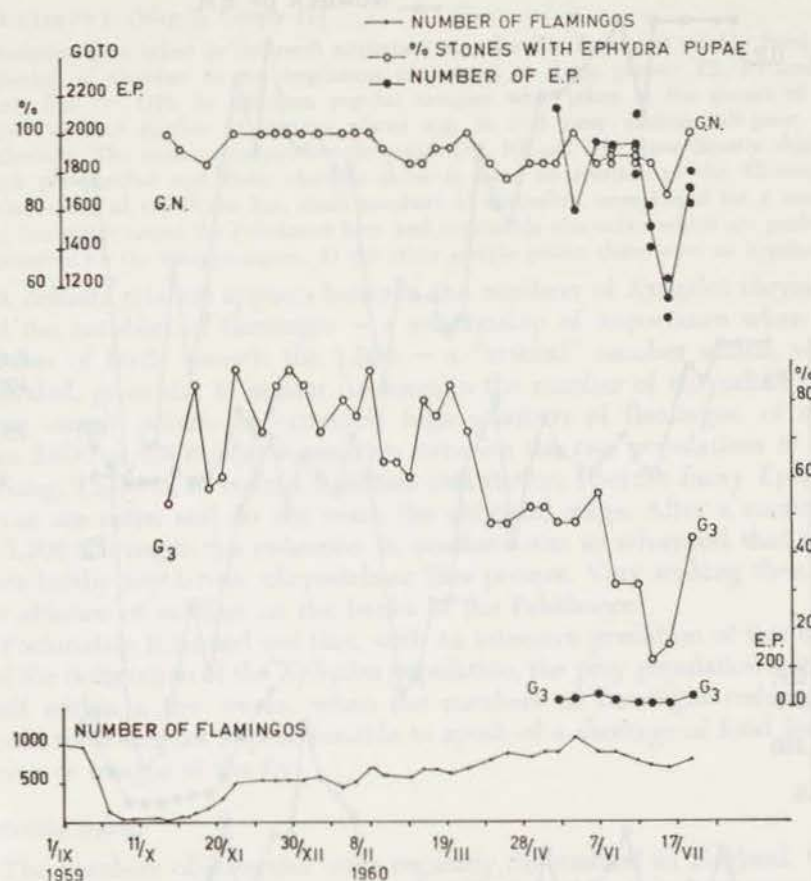
GRAPH 10. Relation between occupation percentages of 25 stones (during the last 2 months the number of *Ephydra* pupae in these samples are also given) at the sample points G3 and GN, and the number of flamingos in Goto.

and the percentage of occupation remained above 84%. At G3 the percentage remained under 88%, while in the course of March and further in April, May and June there was a gradual reduction to 12% later rising in July to 44%. There would be no noticeable influence here due to the Cl-content, since this hardly varied throughout the whole year. In the area sampled in the lake, there were no cyprinoids.

A correlation between the numbers of flamingos and the numbers of *Ephydra* chrysalids would appear to be demonstrable, on the other hand. The reduction at G3 appears to be synchronous with an increase in the numbers of flamingos, especially when this exceeded 600–700 there was a definite relation with the decrease in *E. gracilis*. This is also true of GN, although less markedly. The numbers of chrysalids show, clearer than the occupation percentages, that predation was making itself felt here. We may conclude that locally, where in addition there are few opportunities for the attachment of the chrysalids, i.e. at G3, the predation of a number of 600–700 flamingos (or more) is then operating and that at about 1,000 flamingos this is also valid for the areas richer in *E. gracilis* chrysalids, such as the northern side of Goto.
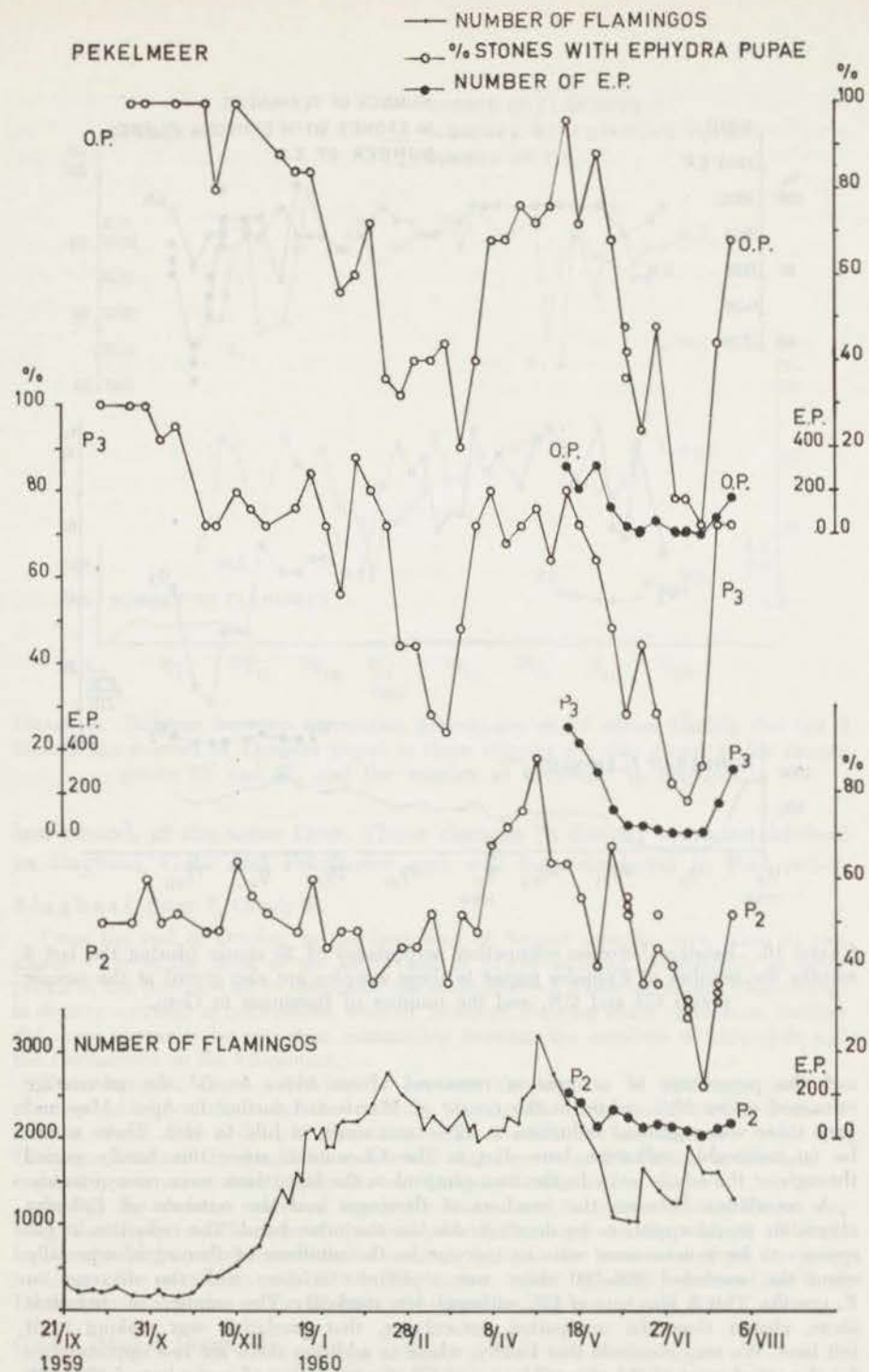
GRAPH 11. Relation between occupation percentages of 25 stones (during the last 2 months the number of *Ephydra* pupae in these samples are also given) at the sample points P2, P3 and OP, and the number of flamingos in Pekelmeer.

Pekelmeer (Map 5, Graph 11)

Samples were taken in the most important area for the flamingos weekly from the beginning of October to the beginning of August at three places: P2, P3 and at Oranje Pan (= OP). In addition, regular samples were taken at the corner of the Witte Pan and further at various places e.g. in and near various salt-pans, but incidentally. The most important sample points (P2, P3 and OP) show density changes which are parallel and these changes show in turn no relation to the Cl-content. In the corner of the Witte Pan small numbers of chrysalids were found for 4 months only. Sea water enters the Pekelmeer here and cyprinoids also occur which are probably responsible for the disappearance. At the other sample points there were no cyprinoids.

A definite relation appears between the numbers of *Ephydra* chrysalids and the numbers of flamingos — a relationship of importance when the number of birds exceeds the 1,500 — a "critical" number which, when exceeded, gives rise to a clear decrease in the number of chrysalids at all three sample points. At extremely high numbers of flamingos, of more than 2,000 or 3,000, this connection between the two populations is very striking. There is, of course, a certain retardation, because many *Ephydra* larvae are eaten and do not reach the chrysalid stage. After a maximum of 3,200 flamingos the reduction in numbers was so advanced that there were hardly any larvae, chrysalids or flies present. Very striking then was the absence of saltflies on the banks of the Pekelmeer.

Fortunately it turned out that, with an intensive predation of this order and the decimation of the *Ephydra* population, the prey population restored itself within a few weeks, when the numbers of flamingos reduced. It would therefore not appear feasible to speak of a shortage of food for the larvae or imagos of the fly.

Artemia salina

The numbers of Artemias were regularly determined in Slagbaai, Goto and Pekelmeer at a number of places. Although they were not present in the Pekelmeer throughout the year, we still took weekly samples there to check for the possible appearance of *Artemia*. We also took samples here and there at other places, when it was striking that they never occurred together with Rotatoria, but that we found either these or *Artemia* (see further Chapter V g).

The Artemias were sampled and counted as follows: At given points weekly (or every 10 days), samples were taken of 10 litres of water (twice a 5-litre bucket) and poured through a plankton net (greatest mesh 100 μ). The 10-l samples were concentrated in smaller pots. The numbers were determined by taking small amounts out with a pipette, so that the Artemias were counted in amounts of a few individuals to 25 specimens. At the same time, the details of size were recorded.

This method is representative only when the distribution of *Artemia* is presumed homogenous. Although the numbers between various sample points could differ widely, the distribution per sample point was still fairly regular. Only now and then did it appear that the distribution was not homogenous, and then at high densities. There were local examples of

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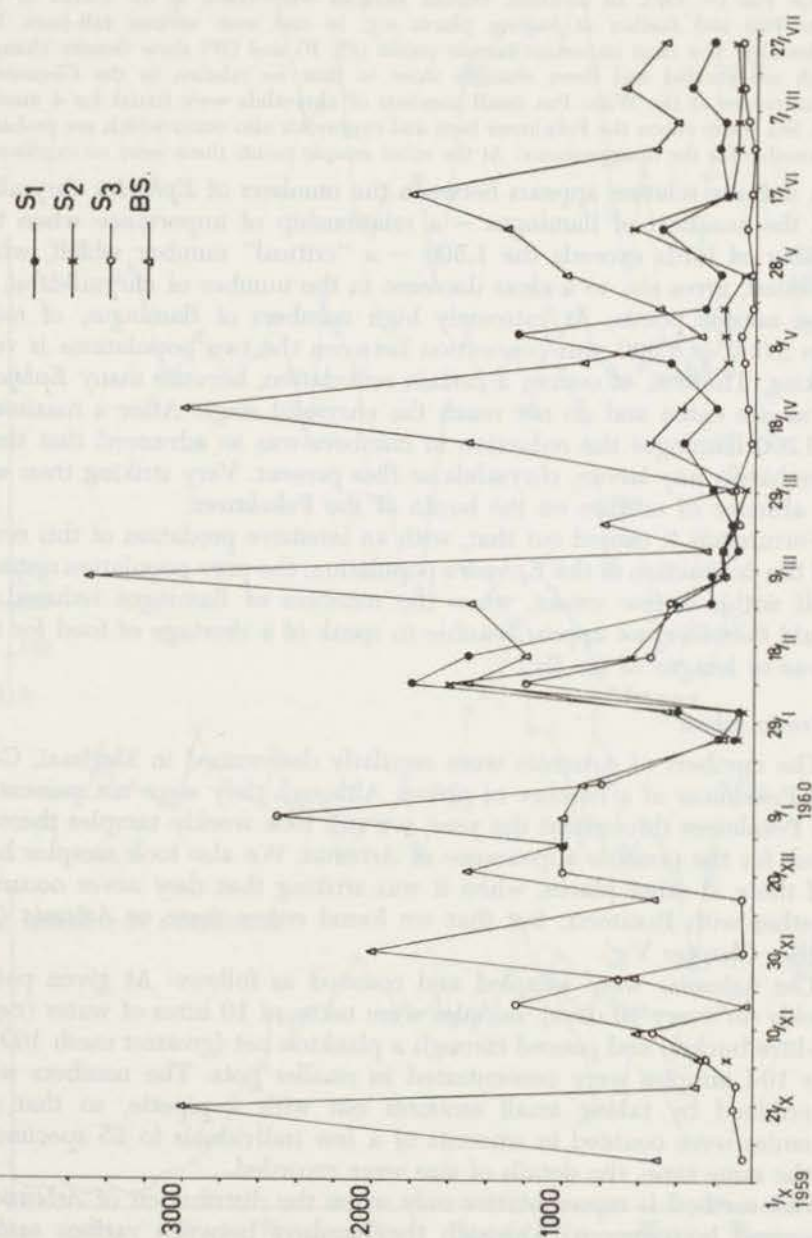
GRAPH 12. Fluctuations in the population density of *Artemia salina* at 4 sample points in Slagbaai. — Vertical scale the number of *Artemia* in a sample of 10 l water.

ARTEMIA in SLAGBAAI

this when red clouds of Artemias alternated with lower concentrations. It was then possible, in two 10-l samples taken one after the other at the same place, or close to each other, to have double the number of Artemias in the one bucket as in the other. This difference, which was also incidentally noticed at lower concentrations, appears to be correlated with the reproduction of the Artemias — the numbers of copulations in the cloud was striking. It did not occur often, however (i.e. we encountered this on the sample days only very infrequently), so that this hardly — if at all — influenced the quantative data. This is shown in the following table of double samples, which proves the reliability of this method of sampling.

TABLE III. NUMBERS OF *Artemia salina* IN DOUBLE 10-LITRE SAMPLES, from the same place, taken directly after one another.

Goto		Slagbaai	
17	18	107	127
36	37	185	200
42	44	330	360
50	54	370	390
50	58	520	550
62	72	600	625
66	70	675	700
72	85	1400	1600
102	108	2800	3200
132	137		

In 2 × 5-litre samples from S l a g b a a i were found 40—41 and 655—685 specimens.

The differences between these figures are so small that this method of sampling may be considered as reliable enough to give a representative picture of the fluctuations in the numbers of Artemias at the various sample points, the more since the 5-litre samples show a close agreement.

From the areas sampled only the salina of Slagbaai contained Artemias the whole year, Goto, the greatest part of the year and in Pekelmeer they were never seen. We will now consider the changes in density and the possible causes of this per area.

Slagbaai (Map 7)

At the beginning of October we began regular sampling at 2 places: BS and S3; at the end of January the number of sample points was increased to 4, with the addition of S1 and S2. In February a start was made in the differentiation of the Artemias into 3 size categories, i.e. > 5 mm, 1—5 mm, and < 1 mm — the latter we referred to as nauplii, i.e. still with one (nauplius) eye. Artemias larger than 5 mm are adult.

The changes in population density at S1, S2 and S3, although the numbers diverge, show a comparable course (Graph 12). The numbers at BS showed an entirely different picture, there was often a maximum when there was a minimum at other places.

There are, however, signs of a certain parallel course in the figures at other points. This difference between BS and S1, S2 and S3 may be connected with the differences in the Cl-content. We have seen in fact, that BS was the least salt, S1 and S2 salter and S3 the most salt (Graph 5 and Chapter IV d). The numbers of Artemias are, in general, largest at BS and smallest at S3, so that here also the difference in Cl-content may play a role.

We tested for a possible Cl-preference in *Artemia* in the following way. The numbers of animals from the four sample points were counted, summed and the percentage occurrence at each of the four points calculated. This gives a distribution, from which we can see that in the traject between 45 and 90 g Cl/l (Graph 13), the highest percentages occur. If we do the same for the three stages of development we have distinguished, it then appears that the group:

< 1 mm occurs most between 50–80 g Cl/l

1–5 mm occurs most between 45–85 g Cl/l and

> 5 mm occurs with no preference between 45 and 120 g Cl/l (Graphs 14–16).

This picture is emphasised when we consider the numbers of animals in this connection. To do this the percentages referring to numbers between 500–1,000, between 1,000–2,000 and between 2,000–3,000 are given separately.

We may conclude that the smaller stages of *Artemia* occur much less frequently

in areas with a high Cl-content. Whether one can speak of a real Cl (salt) preference or of other factors influencing this distribution, can be verified experimentally only. Under our circumstances on Bonaire this was, however, impossible.

MARIAN EMEIS carried out experiments on the salt-preferences of adult and nauplius Artemias in 1961 at the Caribbean Marine-Biological Institute in Curaçao. There was no clear preference to be seen in the adult specimens, but the nauplii showed a preference for high concentrations of salt (240⁰/oo). This last result does not at all agree with our field observations. We have in all probability a form of pseudo-preference in Slagbaai, where other factors play an important role in determining this distribution. There are indications that we may exclude migration, whether active or passive.

From the study carried out by MARIAN EMEIS, it appears that there is a difference in reproduction above and below a salt level of 85⁰/oo. The females lay eggs under this value which come out in water up to 85⁰/oo and these females may well have 50–60 eggs in the brood-pouch. Above the threshold value of 85⁰/oo, however, the females are viviparous and the number of nauplii observed in the brood-pouch varied between 1–15.

If there is really such a great difference in the numbers of (potential) descendants, we can then explain the differences in the absolute numbers between Boca Slagbaai

GRAPH 13. Percentual occurrence of *Artemia* (all sizes) at 4 sample points with different Cl' contents in Slagbaai. — Percentages referring to different sizes of numbers are differentiated.
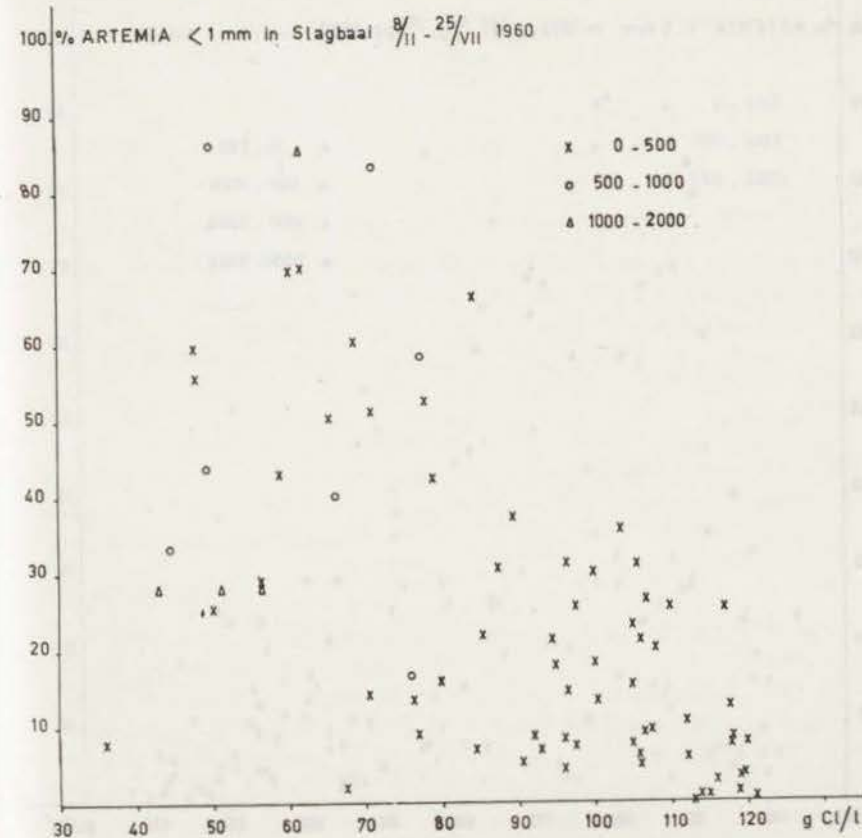
GRAPH 14. Percentual occurrence of *Artemia* < 1 mm (nauplii) at 4 sample points with different Cl' contents in Slagbaai. — Percentages referring to different sizes of numbers are differentiated.

and the other sample points S1, S2 and S3, since only at Boca Slagbaai we find these lower salt concentrations. During our study this varied between 36.3 and 84.5 g Cl/l (85°/oo is approximately 47 g Cl/l), and this value occurred frequently at BS. If this difference in reproduction is responsible for the pseudo-preference for the less salt area of the salina, we should also expect a larger percentage of adult Artemias in the lower Cl-content areas. This was not the case, however. The only reasonable explanation would appear to be, in my opinion, that in these less salt areas we find cyprinoids (see Chapter IVe — up to 75 g Cl/l or, as MARIAN EMEIS and I. KRISTENSEN observed on Bonaire and Curaçao, up to 135°/oo salt), which prey on the Artemias. According to MARIAN EMEIS the nauplii become adult in 10—14 days. This rapid development could lead to a heavier predation on the larger specimens than the smaller. It is also possible that the fish hunt only the larger specimens by choice and it is also possible that the higher Cl-contents at BS or in its neighbourhood could just act as a barrier for the cyprinoids, so that their predation locally and temporarily ceases.

In addition we must consider the flamingos which often foraged near BS and it is possible that during high concentrations filter-feeding directed against Artemia was carried out, whereby the larger specimens will suffer a higher predation than the nauplii.
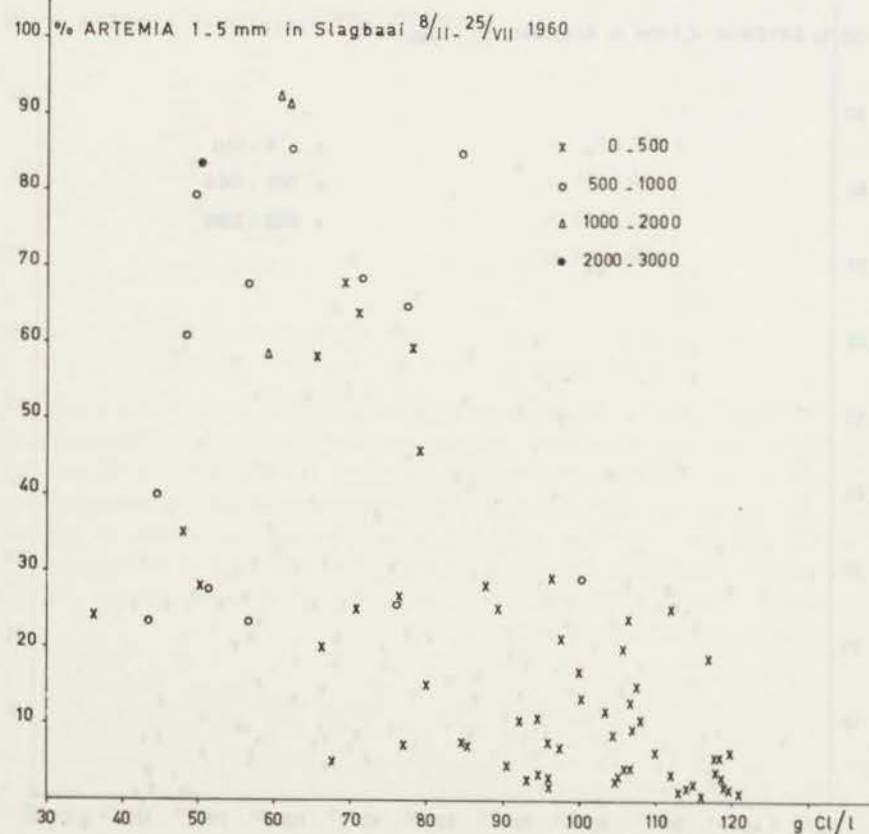
GRAPH 15. Percentual occurrence of *Artemia* 1—5 mm at 4 sample points with different Cl' contents in Slagbaai. — Percentages referring to different sizes of numbers are differentiated.

In general, however, there is in the entire salina no correlation between the numbers of flamingos and those of the *Artemia*.

Goto (Map 6)

In Goto the first Artemias were noted at the end of November, although in September, October and for the greater part of November they were absent. The changes in population density were more or less parallel for the three sample points, and with a few exceptions only, the actual numbers did not diverge widely (Graph 17). After the rise in December and January, large numbers were found at the beginning of February at all three sample points, but later such large numbers did not recur. We know nothing of the cause of this, although it should be mentioned that, since the advent of the Artemias the water became much clearer. It is possible that the food supply decreased so that the recurrence of high numbers was not possible. The cyprinoids play no role here, since they occur in the Boca only. Nor is it likely that the Cl-content is of importance — it changed little throughout the whole year. Predation by flamingos does not appear feasible either, since it was seen that these sought the Artemias only sporadically.

Pekelmeer (Map 5)

In the Pekelmeer there were no Artemias throughout the year (except in the pans).
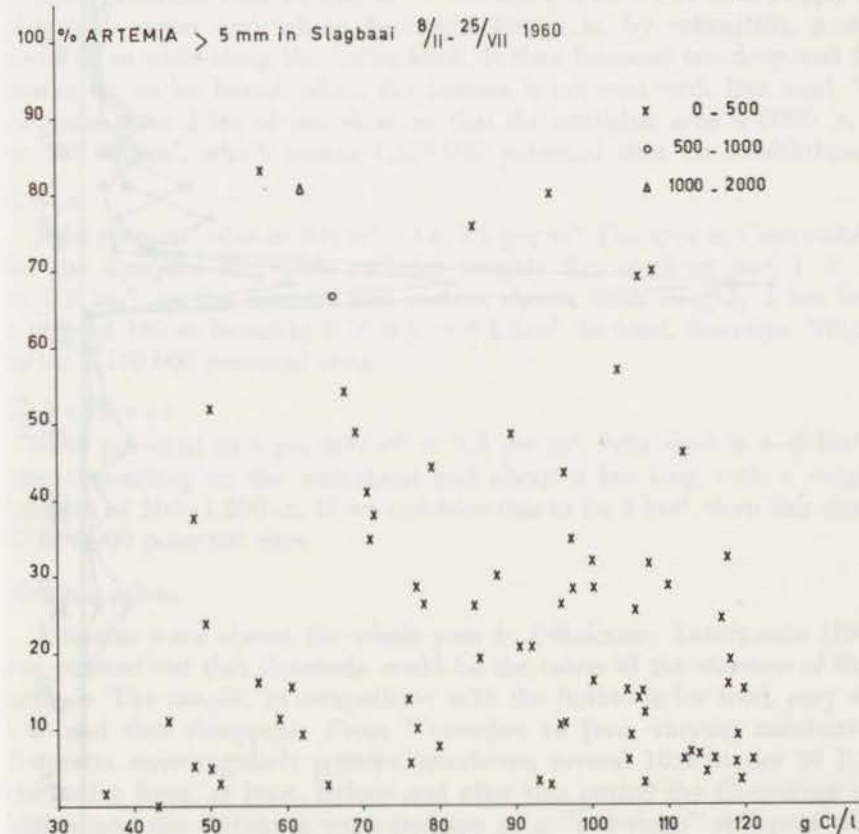
GRAPH 16. Percentual occurrence of *Artemia* > 5 mm at 4 sample points with different Cl' contents in Slagbaai. — Percentages referring to different sizes of numbers are differentiated.

ARTEMIA in GOTO

G₁
G₃
GN
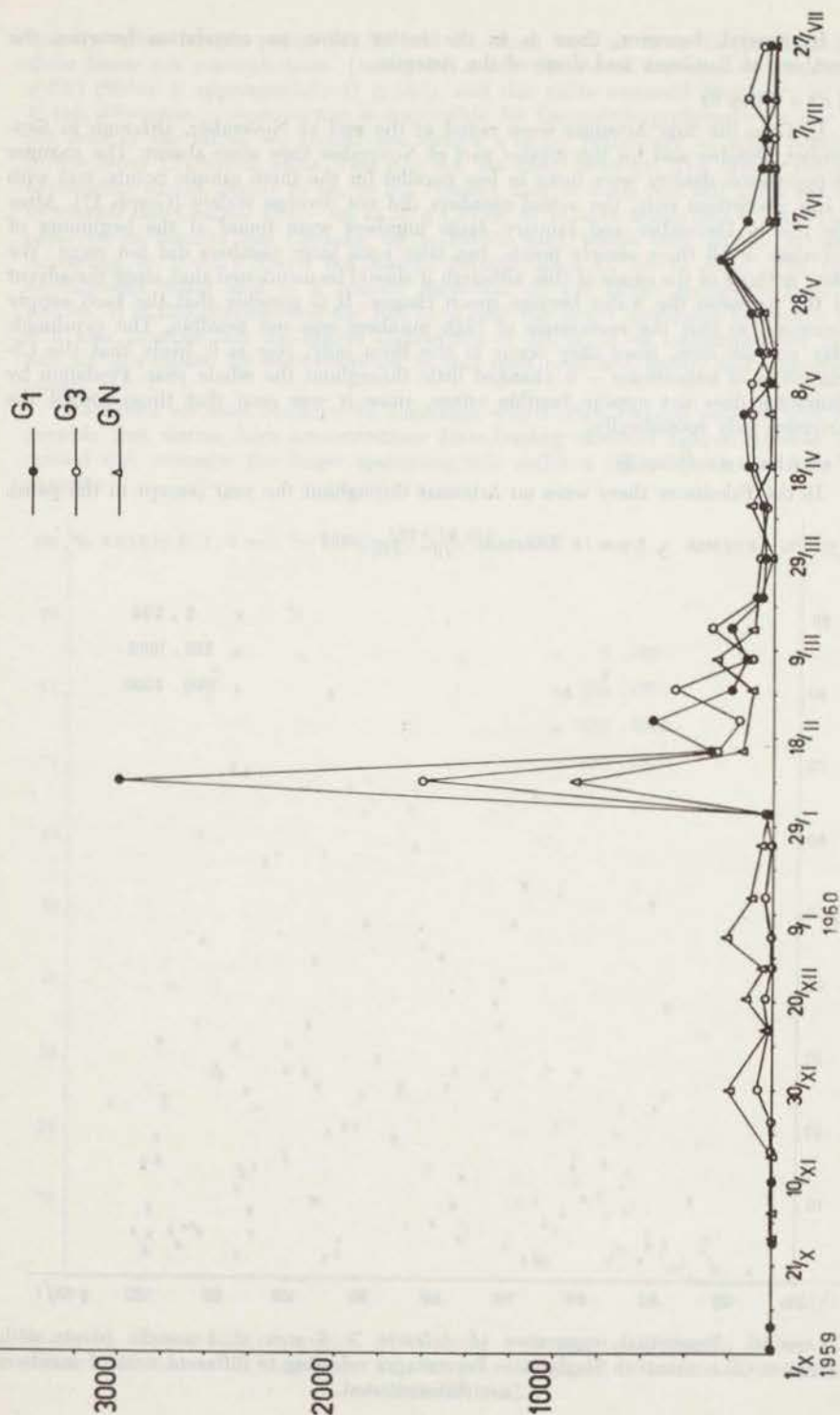
GRAPH 17. Fluctuations in the population density of *Artemia salina* at 3 sample points in Goto. — Vertical scale the number of *Artemia* in a sample of 10 l water.

3000
2000
1000

1/X 1959   21/X   10/XI   30/XI   20/XII   9/I 1960   29/I   18/II   9/III   29/III   18/IV   8/V   28/V   17/VI   7/VII   27/VII

g. POSSIBILITIES FOR THE ESTABLISHMENT OF EPHYDRA AND ARTEMIA

Ephydra gracilis

We have already mentioned that *Ephydra* metamorphose only when they have a hard substratum on which they can attach themselves. All types of stones and salt-crusts can help here on the bottom of the salinas. The possibilities for establishment may differ markedly in various areas per surface unit. Since the number of chrysalids is not directly to be established, as a large proportion of the stones are attached to the bottom, the number of stones and other potential sites were determined per surface area. This was done for 50 m² at the sample points with the aid of a wooden frame of 1 m². The 50 m² were taken at random and the same procedure was followed at other places, also. In Slagbaai, Goto and Pekelmeer 500 m² of potential sites were examined in this way and counted.

Slagbaai

4636 potential sites in 500 m² — i.e. 9.3 per m². The area where the chrysalids occur and where flamingos forage is, by estimation, a strip some 50 m wide along the entire bank. It then becomes too deep and few stones are to be found, while the bottom is covered with fine mud. We estimate some 3 km of shoreline, so that the available area is 3000 × 50 = 150,000 m², which means 1,395,000 potential sites for establishment.

Goto

1564 potential sites in 500 m² — i.e. 3.1 per m². The area in Goto suitable for the *Ephydra* chrysalids includes roughly the northern part $1 \times 0.5 = 0.5$ km²; on the western and eastern shores, both roughly 1 km long, a strip of 100 m breadth: $2 \times 0.1 = 0.2$ km². In total, therefore 700,000 m² = 2,170,000 potential sites.

Pekelmeer

3688 potential sites per 500 m² = 7.4 per m². Pekelmeer is 4–6 km² in size, depending on the waterlevel and about 6 km long with a varying breadth of 200–1,500 m. If we consider this to be 5 km², then this means 37,000,000 potential sites.

Artemia salina

Artemias were absent the whole year in Pekelmeer. KRISTENSEN (1963) has pointed out that Rotatoria could be the cause of the absence of these animals. The nauplii, in competition with the Rotatoria for food, may well lose and thus disappear. From November to June varying numbers of Rotatoria were regularly present (maximum several 10,000s per 10 l), in the active form, at least. Before and after this period the Cl-content was higher and the Rotatoria were perhaps as a "rest-stage" still present. It was striking that we found, at various places, either Rotatoria or Artemias, or the absence of both. So far as we investigated — with one exception — they did not occur together.

TABLE IV. OCCURRENCE OF ARTEMIAS AND ROTATORIA IN VARIOUS SALINAS

Salina	Artemias	Rotatoria	Numbers of 10-l samples	g Cl/l
Boca Bartool	+	−	2	61.1; 60.1
Slagbaai	+	−	144 at least	Graph 5
Goto	+	−	111 at least	Graph 4
Sal. Playa Lechi	−	+	2	14.2; 17.7
East Sal. Kl. Bon.	−	−	2	45.9; 47.6
West Sal. Kl. Bon.	1 spec.	+	1	64.0
Ven	−	−	3	22.7; 22.9; 25.5
Duinmeer	−	+	6	88.8; 92.3; 82.5; 65.7; 73.0; 70.2
Pekelmeer	−	+	135 at least	Graph 3
Ringmeer	−	+	5	55:6; 73.0; 114.7; 80.2; 72.7
Randplas	−	−	2	48.5; 31.2
Oranje Pan 1	−	−	2	141.5; 154.0
— — 2	+	−	2	40.0; 38.5
— — 3	+	−	2	42.5; 45.5
— — 4	+	−	1	58.9
Willemsoog	−	+	9	Graph 7
Witte Pan 1	−	−	1	47.1
— — 2	−	−	1	30.7
— — 3	−	−	1	52.1
— — 4	+	−	1	154.3

It is noticeable that at places where the Cl-content is higher, both species are absent, and the same is true for places with an extreme low Cl-content.

At one place only are both present – the western salina on Klein Bonaire. In this period groups of flamingos came regularly in the salina, so that it is possible that this was a chance specimen brought in by the birds. With the exception of this single specimen, no other Artemias were found in the water.

Seeing that the surrounding waters and salt pans of the Pekelmeer harbour Artemias and that flamingos forage in these, it may be expected that some transport to the Pekelmeer is possible. KRISTENSEN and MARIAN EMEIS found Artemias in the Pekelmeer in 1961 (250⁰/oo salt), while there were no Rotatoria, or at least no large numbers of them. According to WAGENAAR HUMMELINCK there was plenty of *Artemia* at Witte Pan in 1930 and 1932.

h. DIURNAL RHYTM

To gain some idea about the quantitative aspects of the food, it is necessary to know something about the time spent in searching for it. The numbers of food-searching flamingos in the Pekelmeer were noted during the counts made there. This was also done in Slagbaai and Goto, but since

the visits to these two localities were combined and were less frequent than those to the Pekelmeer, the observations are fewer and less distributed over the whole of the day. For these reasons we will not consider them here.

Since the data in question were noted *en passant*, we do not have a complete picture for the Pekelmeer either. In particular the early morning – when it was not so warm – was very suitable for observing the flamingo colony with field glasses, so that the observations on non-breeding birds for these periods are necessarily fewer. We have the impression, however, that the birds foraged chiefly in the early hours of the morning and at the end of the afternoon. This appears from Graph 18, where the percentage of birds searching for food during a given period is shown. Evening observations are given with a broken line, since only a fraction of the birds could be observed. Other, incidental, observations indicate that the birds forage a great deal at night (Klein Bonaire, Salina Playa Lechi). The trend in the graph is all the more striking since here observations are spread out over the entire period of study. With a large number of birds at nest, the partners search for food more frequently in the middle of the day; during food shortage, the birds also search for longer periods.

By approximation we may conclude that about 12 hours a day are used for searching for food. This is more or less a speculation since we observed the birds at night only now and then at full moon, when not everything could be seen. The flamingos that we did see, however, were in fact
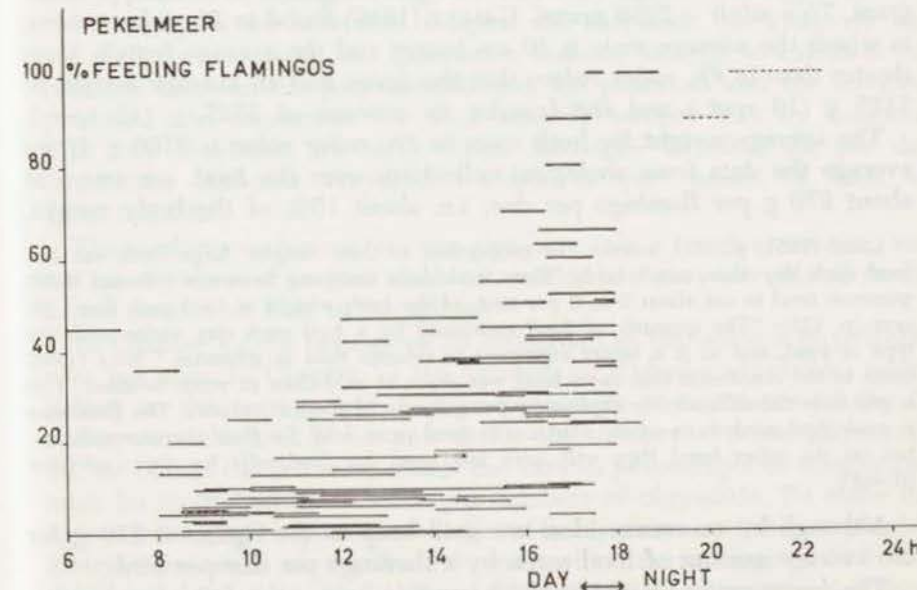
GRAPH 18. Percentage of flamingos feeding during the course of the day (and night). – See explanation in text.

searching for food. In the literature various authors have reported night feeding by flamingos.

Around midday many birds sleep and at the end of the afternoon (particularly after 16.00) many drink, bathe and preen, while the feeding then increases and part of the population disperses in a southern direction (see Chapter VII).

i. QUANTITATIVE ASPECTS OF THE FOOD

RATCLIFFE (1956) reported that flamingos need $^1/_2$–$^3/_4$ of a pound (= 225–340 g) of food per day. In the Zoological Garden of Rotterdam (Diergaarde Blijdorp) the feed is reckoned at between 200 and 300 g per day per animal (VAN BEMMEL, pers. comm.). BROWN (1959, p. 111) writes: "Accepting that a flamingos nearest relative is a domestic duck or goose, it may be reasonably assumed that an adult will eat at least 10 per cent of its body weight per day and probably more." He arrives at the figure of 310 g food per day for *Ph. ruber roseus.*

ALLEN (p. 9) gives two weights only of a male and a female handled by AUDUBON as 7lbs. 8 oz. and 6 lbs. 4 oz. that is, ♂ 3402 and ♀ 2835 g. In 1952 and 1961 VOOUS collected a number of specimens for which the following weights were recorded: 2 ♂♂ adult 2250 and 2743 g, and 4 ♀♀ adult 2235, 2400, 2160 and 2020 grams. We noted in *Ph. ruber ruber* the following body weights in grams: 3 ♂♂ ad. 3780, 2250 and 2600; 2 ♀♀ ad. 3500 and 2600 and 1 juvenile (a few months old) 1472,5. The combination of this data gives the following averages: 6 ♂♂ adult – 2837 gram, 7 ♀♀ adult – 2250 grams. GALLET (1949) found in *Ph. ruber roseus,* in which the average male is 10 cm longer and the average female 3 cm shorter than in *Ph. ruber ruber,* that the males had an average weight of 3425 g (13 spec.) and the females an average of 2525 g (12 spec.).

The average weight for both sexes in *Ph. ruber ruber* is 2700 g. If we average the data from zoological collections over the food, we arrive at about 270 g per flamingo per day, i.e. about 10% of the body weight.

LACK (1954, p. 131) writes: "In proportion to their weight, large birds eat less food each day than small birds. Thus land-birds weighing between 100 and 1,000 grammes tend to eat about 5 to 9 per cent. of the body-weight of food each day." He says (p. 132): "The quantity of food consumed by a bird each day varies with the type of food, and so it is better expressed in calories than in grammes." NICE (1938) came to the conclusion that more food was eaten in cold than in warm weather. This is precisely the difficulty in expressing the quantity of food in calories. The flamingos in zoological gardens in colder climes will need more food for their thermoregulation, but on the other hand they will have less need for foodstuffs for their activities (flying!).

Although by no means ideal we shall keep to the figure of 270 g for the average amount of food eaten by a flamingo per day per bird.

The investigation of the stomach contents gives the following results: Juvenile 1 and 3 gram; adults 14.5 – 16 – 16 – 9 and 6 g. MADON (1932) calculated that in *Ph. ruber roseus* the average content was 5.9 g (9 spec.)

with boundaries of 3.7 and 17.0 g. Not only the stomach but also the long intestines are filled with half-digested food. Since the stomach also always contains several hundreds of small stones, this is in itself an indication of the slight weight of the prey animals.

We have determined the weight of *Ephydra* larvae, chrysalids and *Artemia,* whereby they were first dried in filterpaper to remove water droplets. For the *Ephydra* larvae, the average weight was 5.3 mg (38 spec. 5–15 mm long). The chrysalids, which were on the average 12 mm long, had a mean weight of 8.3 mg (10 spec.). The specimens of *Artemia* (5–10 mm long) weighed on the average 0.2 mg each (45 spec.). There are, therefore, about 32,000 *Ephydra* chrysalids necessary to make up 270 g of food, and for the larvae this means about 50,000 specimens, while for *Artemia* some 135,000 specimens will be necessary.

In Chapter Vh we have seen that flamingos search for food for about one half day at a time. 32,000 chrysalids per flamingo means that they must catch 2650 per hour, roughly 45 per minute. When we see the way in which flamingos search for food, or imitate them in this, this figure does not seem unreasonable. As far as the larvae are concerned it would seem possible for flamingos with their specialised methods to catch some 4,000 specimens per hour – 60 per minute.

Should they eat only *Artemia* then, at a fairly high concentration of 1,000 specimens per 10 l water, it would be necessary for them to filter 1330 l water per 12 hours – 110 l per hour or 2 l per minute. This would also appear to be feasible seeing the way they search for their prey.

For *Ephydra* we have only sampled the chrysalids quantitatively and we shall, in a more or less speculative fashion, attempt to calculate the relations between the prey animals and the predators and the numbers produced and consumed. We shall simplify matters here by assuming that only chrysalids are eaten. 1,000 flamingos therefore eat per day 32,000,000 *Ephydra* chrysalids, which is, per month, a total of 1,000,000,000!

These enormous figures (we can give here only a rough estimation, and not exact values, of course) make us wonder how they are related to the actual reserves of food in the salinas.

In Chapter Vg we have given an estimation of the number of potential sites per area. In Chapter Vf the numbers of *Ephydra* chrysalids, which belong on the average with a given percentage of occupation of the 25 stones were checked. If we now divide the number of potential sites by 25, we obtain the factor by which the various percentages of occupations must be multiplied to estimate the numbers of chrysalids. To make the figures belonging to given percentages of occupation as reliable as possible groups were made of, e.g. 8–16%, from which the average of 12% was calculated from those of 8, 12 and 16%. We then obtain the following picture for the three most important areas (Table V).

perc. occup.	av. perc.	av. numbers	Pekelmeer	Goto	Slagbaai
8– 16	12	10.4	15,392,000	832,000	582,400
20– 28	24	23.6	34,928,000	1,888,000	1,321,600
32– 40	36	49.6	73,408,000	3,968,000	2,777,600
44– 52	48	74.8	110,704,000	5,984,000	4,118,800
56– 64	60	149.3	220,964,000	11,944,000	8,360,800
68– 76	72	478.5	708,180,000	38,280,000	26,796,000
80– 88	84	841.4	1,245,272,000	67,312,000	47,118,400
92–100	96	1605.9	2,376,732,000	128,472,000	89,930,400

With the same percentage of occupation, the Pekelmeer can have about 20 times the number of chrysalids as Goto and Goto about $1\frac{1}{2}$ times the number in Slagbaai.

Despite the difficulties that we know nothing of the population dynamics of *Ephydra*, nor the number of eggs laid by the flies, nor the age of the flies, larvae and chrysalids, we still wish to make an attempt to examine the reduction due to predation and the increase due to production in the three areas mentioned above.

In Slagbaai (Chapter Vf, Graph 9) we have seen that the small and varying number of flamingos had hardly or no, influence on the number of chrysalids. In the period when 200–300 birds were present, we had few data on the chrysalids, but in the period when 100 or fewer birds were present, the number of chrysalids remains fairly constant and varied at the two sample points around the 40 and 80% — an average of about 60%. The percentage of occupation of 60% (56–64%) corresponds with a total population of chrysalids of 8,360,800 in the whole of Slagbaai (Table V).

100 flamingos eat 3,200,000 chrysalids per day, so that this predation does not have the slighest effect on the numbers of chrysalids, since the percentages of occupation show no different picture than in the period when no flamingos were present. There would appear to be an equilibrium when about 38% are consumed (theoretically then, since in fact also larvae and fewer chrysalids were eaten).

In Goto we saw (Chapter Vf, Graph 10) that, at a number of 600–700 flamingos the density of the *Ephydra* chrysalids remained the same. The occupation percentage at the two sample points — at that time roughly between 75 and 95% — i.e. an average of 85% — means 67,312,000 chrysalids in the entire Goto area.

700 flamingos eat 22,400,000 chrysalids per day. There is therefore, at a theoretical predation level of 36% an equilibrium — and a rise in the

number of flamingos shows a decline in the numbers of chrysalids, there is thus an exploitation.

In Pekelmeer (Graph 11), when the original number of flamingos increases to about 1,500 the *Ephydra* population is more or less constant. At four sampling points the percentage of occupation is then on the average 60% and this means about 220,000,000 chrysalids in the entire Pekelmeer.

1500 flamingos eat per day 48,000,000 chrysalids and there is therefore still an equilibrium at a predation of about 22%. When we compare this with the situation in Goto and Slagbaai, then $\frac{1}{4}$ to $\frac{1}{3}$ of the population can be consumed (theoretically), but the total population remains then the same. This high predation must be compensated for by a high reproduction, which means that the period egg-fly-egg must be very short. Our observations in the Pekelmeer in July 1960 (see also Graph 11) indicate how rapid the turnover must be. On the 15th of July there was a minimum of chrysalids and very few flies were seen. On the 22nd of July there was not only an increase in the chrysalid population but also a striking increase in the number of flies. In addition, the number of larvae was also clearly much higher. On the 29th this increase in flies, larvae and chrysalids was even greater.

If the numbers of flamingos increase, then exploitation takes place and the number of *Ephydra* chrysalids is markedly reduced.

With 3,000–3,200 flamingos (a short period of a few days) a theoretical consumption of 100,000,000 chrysalids per day takes place. With an approximate occupation of 60%, there were 220,000,000 chrysalids in fact present and this signifies an exploitation. With about 2,000 birds, however, a recuperation of the fly population is possible, since this number of birds consumes 64,000,000 chrysalids per day. There was at this time an occupation of about 44% i.e. 98,000,000 chrysalids.

At the end of our study period there was, after a decimation, a recuperation of the *Ephydra* population. There were at this time an average of 1,500 flamingos present and these consume 48,000,000 chrysalids per day. The occupation was then around 32%, which means about 60,000,000 chrysalids in all.

During the period of recovery there appears to have been a predation of between $\frac{2}{3}$ and $\frac{4}{5}$ of the total population of chrysalids.

We may conclude:

1. That in these periods and situations, other food must be taken and/or another area or areas used (this agrees with field observations, see Chapter VII and VIII),

2. That the population of *Ephydra gracilis* has a greater reproduction at lower densities.

Also important here can be that the flamingos will search less for a given prey species when its numbers are very low and their hunting is not lucrative (see also TINBERGEN 1948, p. 224).

A quantitative approach to the predation of *Artemia* is of little importance, since these are eaten only incidentally.

We shall now consider the question of the e a t i n g of o o z e more closely. Four samples from the Pekelmeer (see Chapter V d) were examined for their organic content and were found to contain 21.1, 21.8, 20.1 and 20.1% dry weight organic material. The wet weight content was determined from the last two samples only as 10.8% in both cases. (In Salina Playa Lechi twice 15.5% dry weight and 4.9 and 4.5% wet weight.) If we take a 10% wet weight organic content for the ooze, then a flamingo eating this only, must (at least theoretically), if the 270 g food per day are to be obtained, consume 2,760 g of wet ooze, given that all useable material is extracted. If 50% can be used, it means 5.4 kg ooze, twice the body weight. If only 10% can be used then such a flamingo must eat 27 kilos of mud, which appears to be absurd and impossible.

The efficiency is probably much higher than 10%, seeing the length of the gut and the hard droppings which consist almost entirely of mineral material (Chapter Vd).

It would seem to me that the useability is more than 50% (between 50 and 100%) so that this method is still acceptable. In periods of food shortage at least, this method could be wholly or partly used. Considering the population changes in *Ephydra*, these periods will usually be short!

VI.   REPRODUCTION

PRELIMINARY REMARKS

Breeding sites

On Bonaire the flamingos breed in the three most important food-areas: Slagbaai, Goto and Pekelmeer (Plate III, VI, XII, XIII). The significance of these areas, both as feeding and breeding areas increases in this order also.

In S l a g b a a i in recent years there is only one observation of breeding by one of the owners, Mr. C. F. S. FORBES. In the course of 1958 a small colony settled here on the eastern side of the salina on a small dam separating the salina itself from the salt pans. The eggs were washed away at high water and were found near the Boca. The remains of some 30 nests, all more or less eroded, have been found (for details see Chapter VI d).

In G o t o breeding took place in 1959 and 1960 on small rocky islands, something not observed in 25 to 30 years. Between 1920 and 1930 the birds bred here regularly (GABRIEL 1938, VOOUS 1957). In 1959 we encountered young birds on the 3rd of September, the oldest being about $2\frac{1}{2}$ months old, so that the eggs must have been laid in the second half of May. The entire laying period was probably from the middle of May to the middle of June. In 1960 breeding took place from the beginning of January to July, but in small numbers, however (see Chapter VII-Numbers).

The shores of the P e k e l m e e r have throughout history been the most important breeding areas for flamingos on Bonaire. During our study large numbers bred here from the end of December 1959 to August 1960. The colony was visited four times for a short inspection of the numbers of nests, eggs and young and for collecting nest and water samples. Before the breeding period this area was also visited once.

Breeding Period

Contrary to other data, the breeding period appears to be extremely flexible. The months of September, October and November were the only in which breeding did not take place.

ALLEN (1956) gives a much more restricted period for the Bahamas and Yucatan — the beginning of March to the beginning of June and May to the beginning of July, respectively. In his comparison of other areas (other species also) it appears that the laying period is connected with the geographical position and it is in fact so that it is restricted to the spring and/or summer months in the Northern and Southern Hemispheres.

MOREAU (1950), SKUTCH (1950), THOMSON (1950), VOOUS (1950) and LACK (1950a, 1950b, 1954) all point out that in general birds breed in the most favourable period for feeding and rearing the young. In the tropics the breeding period is often connected with wet and dry periods, but this can hardly be the case for the flamingos on Bonaire since September is not and October and November are in the rainy season, but so are December and January when they do breed! (See Chapter IV b, where it is pointed out that the rainy season does not occur at all in some years.)

Reproductive behaviour

Because the West Indian flamingo is very shy the colonies were visited only a few times for short periods. It was possible, however, to observe much of the behaviour of the colony in some details from a distance, using 10 and 40 × glasses. The 40 × glass could be used with efficiency in the early morning and evening only, since the air-currents otherwise obscured vision. Pair formation and copulation could frequently be seen at a distance of a few tens of meters and it was often possible to see this from the car, to which the flamingos hardly reacted, if at all, if one remained seated. The birds could also be clearly observed at a distance of some 20—30 m from a hide near a drinking place.

Before we consider the reproductive behaviour, we shall first make some general remarks.

Sexual dimorphism

Apart from the difference in size, there is no dimorphism whatsoever. ALLEN (1956) gives the average total length for males as 162.9 cm (172.7—162.6) and for the females 149.2 (160.0—132.1). We found for 3 males a total length of 177, 174 and 174 cm and for 2 females 152 and 153 cm. This difference in size is clearly visible in the field and, as can be seen from the extreme figures, there is no overlapping in the sizes, so that mistakes in sexing are practically impossible.

Only the fully coloured birds take part in the pairing and further reproductive behaviour. We have never seen attempts at display by birds in various sub-adult stages, with the exception of a few times in Goto, where a few pale specimens, with some having the under part of the neck reddish in colour, were, in fact, displaying (see Chapter VI h).

From the difference in size we could make out that, with the exception of the copulation, both sexes show the same behaviour. This is contrary to ALLEN's observations, but it should be noted that we had the opportunity to study this behaviour many times and months on end, since it was an exceptionally good flamingo year, and could therefore describe this behaviour fully.

Display activities and Copulations

In Pekelmeer some 3,000 displaying flamingos were observed (30.X.1959 to July 1960), of which some 1,000 were in or near the colony itself and about 800 in the "Willemsoog". The remainder were spread at the back of the Pekelmeer, on the south (eastern) side, in Oranje Pan, South of P3 and even at P1 and P2. Those at P2 were furthest from the colony — at about 3 km distance — in which display behaviour was seen. The number of copulations about which notes were made was 60, of which 7 were in a group and 53 "solitary". These copulations were also widespread and also up to a distance of 3 km from the colony proper.

In Goto about 950 displaying flamingos were seen (middle December to June), of which about 340 on the breeding island and the rest spread along the shore on the north-western side, the northern and the north-eastern shores (shallow) at a maximum of about 1 km from the colony. Here 8 copulations were noted in detail.

In the other places where flamingos occurred, display activity did not occur, so that there would appear to be a certain attachment to the (future) nesting area.

ALLEN writes that they display at great distances from the future colony, but BROWN (1958) found that they displayed close to it. In the Tables VI—X some data are given on the reproductive or breeding behaviour.

TABLE VI. DEPTH OF WATER IN WHICH IS DISPLAYED.

depth (in cm)	Pekelmeer numbers	Pekelmeer groups	Goto numbers	Goto groups
0— 5	193	8	—	—
6—10	394	7	60	2
11—15	632	8	—	—
16—20	50	2	56	2
21—25	—	—	—	—
26—30	22	2	101	3
31—35	—	—	80	2
36—40	—	—	53	3
41—50	10	1	20	1
	1301	28	370	13

It is to be seen from Table VI that display takes places chiefly in shallower water. This is also evident from the fact that of the 3,000-odd displaying flamingos, some 1,000 were in the Pekelmeer in, or near the colony, and some 800 in the "Willemsoog", where the water is 5—15 cm deep. In Goto 340 from the 950 displaying flamingos were seen on the islands.

ALLEN (p. 154) supposes that for copulations the birds need deeper water: "possibly because the female is able to support the superior weight of the male more easily by dropping partially into the water." This view is not supported by our observations.

TABLE VII. DEPTH OF WATER IN WHICH COPULATIONS OCCURRED.

depth (in cm)	Pekelmeer	Goto
0– 5	2	–
6–10	9	–
11–15	4	–
16–20	8	–
21–25	9	2
26–30	6	2
31–35	1	–
36–40	1	–
41–45	–	–
46–50	1	–
	41	4

TABLE VIII. SEX-RATIOS IN DISPLAYING GROUPS.

Pekelmeer			Goto		
♂♂–♀♀	♂♂–♀♀	♂♂–♀♀	♂♂–♀♀	♂♂–♀♀	♂♂–♀♀
20–20	19–16	25– 25	15–15	25–25	4– 4
9– 9	10–10	4– 6	25–25	3– 3	3– 7
12–12	3– 3	20– 20	3– 2	25–25	3– 7
15–15	50–50	25– 25	5–10	3– 8	4– 7
5– 5	12–14	40– 40	8–15	10–10	3– 6
10–10	12–10	100–100	8–12	15–15	–
7– 7	7– 8	25– 25	10–10	20–20	–
11–13	9– 9	–	5– 5	3– 3	–

450 ♂♂–452 ♀♀ in 23 groups 200 ♂♂–234 ♀♀ in 21 groups

In total 650 ♂♂–686 ♀♀ in 44 groups

TABLE IX. TIMES AT WHICH DISPLAY AND COPULATIONS WERE OBSERVED.

	Pekelmeer			Goto	
time hours	display numbers	copulations groups		display numbers	copulations groups
6– 7	20	1	–	–	– –
7– 8	44	2	–	–	– –
8– 9	163	6	2	–	– –
9–10	570	12	1	37	3 –
10–11	137	5	2	174	9 1
11–12	227	6	5	426	14 3
12–13	258	7	14	176	7 4
13–14	195	6	8	115	4 –
14–15	280	8	5	–	– –
15–16	355	8	2	–	– –
16–17	714	14	8	–	– –
17–18	334	11	13	6	1 –
	3297	86	60	934	38 8

TABLE X. NUMBERS OF DISPLAYING AND COPULATING BIRDS IN PEKELMEER.

Maximum numbers observed on one day.

date		displ.	copul.	date		displ.	copul.	date		displ.	copul.
30.X	1959	17	–	5.II	1960	–	1	22.IV	1960	20	–
4.XI		40	–	8.II		10	–	23.IV		–	–
6.XI		–	–	10.II		–	–	24.IV		20	–
13.XI		–	–	12.II		30	1	27.IV		30	–
20.XI		40	14	19.II		14	1	29.IV		100	5
23.XI		–	–	24.II		35	2	1.V		+	2
27.XI		5	1	26.II		–	–	6.V		26	1
2.XII		30	–	2.III		–	–	8.V		+	1
11.XII		50	1	4.III		–	–	11.V		30	–
18.XII		100	–	7.III		–	–	13.V		80	1
21.XII		–	–	9.III		–	–	16.V		60	2
25.XII		150	–	10.III		–	–	18.V		–	–
31.XII		20	–	11.III		–	–	19.V		35	–
1.I	1960	150	–	18.III		–	–	27.V		10	1
4.I		–	1	23.III		–	–	3.VI		–	–
6.I		–	1	25.III		–	–	8.VI		–	–
8.I		30	2	28.III		–	–	10.VI		–	–
10.I		–	–	30.III		20	–	15.VI		40	1
12.I		100	4	1.IV		6	–	17.VI		50	2
15.I		25	1	6.IV		–	–	24.VI		40	4
17.I		–	1	8.IV		–	–	1.VII		80	–
20.I		60	–	13.IV		20	–	4.VII		30	3
22.I		24	2	15.IV		–	–	8.VII		200	3
25.I		–	–	17.IV		–	–	15.VII		60	1
27.I		–	–	18.IV		20	–	22.VII		50	–
29.I		30	–	20.IV		6	–	29.VII		15	–

The sex-ratio in the displaying groups appears to be more or less constant (Table VIII); sometimes there are more males, and sometimes more females, taking part. According to ALLEN only the males display, but BROWN (1958, p. 397) concludes that both sexes show the same behaviour.

Display times (Table IX)

Only the Pekelmeer data can give a true picture in this connection since Goto was visited less frequently and mostly between 9 and 14 hours, so that the absence of observations for certain times of the day prevents us from giving a total picture.

ALLEN found a minimum around noon and BROWN (1958) found a maximum around the same period and although there was no particular time when displaying did not occur, there would appear to be a certain tendency in this activity in the Pekelmeer. The early hours show little display behaviour activity, but this increases to a maximum between 9 and 10 hours and then a small number of birds display until a second maximum occurs between 16 and 17 hours. If we compare this with the

data for the frequency of food searching (Graph 18), it appears that the morning maximum is at the end of the feeding period and before the beginning of the resting or sleeping period.

The afternoon peak commences the increasing activity which, after the rest period, starts at about 16 hours. The drinking places are visited and it is here that the display activity often occurs. Much preening and bathing takes place here and it is possible that the many preening movements, some of which are seen in the display, have a stimulating effect leading to the display proper. During the preening and bathing when the wings are preened and allowed to dry, the high contrast of the red-black pattern on the wings is then visible. This is seen as a display during the following activities.

The time when the copulations take place is of little significance (Table IX) since there are only a few observations.

The data for the number of birds displaying in the course of the year (Table X) show that these activities all occur 7 to 8 weeks before the egg laying. It is strange that on 30.X.1959 the first display motions were seen since there was then a very small number of flamingos in the Pekelmeer. ALLEN (p. 152) writes: "Normally, pair-formation in the flamingo may be followed at once by nest-building and egg-laying. On the occasion described thus far, the next phase did not follow for some six weeks, for reasons that could not be determined. It was true, however, that not all of the Inagua flock took part in those initial displays or the pairing that followed. Possibly a lack of the stimulating effect of a great number of birds engaging in similar behaviour over a period of several days was responsible for the unaccountable lull."

The large numbers of displaying birds occur in general some time before the period in which the number of breeding birds increases once more. During March no displaying birds were seen and in this month the numbers of the other group decreased markedly and not until the end of April was there an increase once more, in both the displaying and breeding birds.

Pair formation and Copulation

During the display the pairing takes place and these couples then stay together until the brood period. Copulation then usually takes place during the normal foraging activity of the pair, without further ado. ALLEN (1956) and BROWN (1958) both report copulations from displaying groups but also in more or less isolated feeding pairs. We saw the first copulations 4 to 5 weeks before the first eggs were laid. ALLEN mentions a period of 6 weeks and BROWN saw copulations most frequently just prior to egg laying. For the description of the pair formation and the copulation we must first turn to a consideration of the agonistic behaviour.

In each of the following three paragraphs the description is followed by a discussion on the function, the causation and the origin of a number of d i s p l a y s. A satisfying analysis is possible only on the basis of many

quantitative observations and ours are, in this respect, insufficient since they have a more or less qualitative character. The context in which the various displays take place, however, does allow us, albeit more or less hypothetically, to make some remarks in this connection. TINBERGEN and a number of his pupils have shown that various displays are caused by
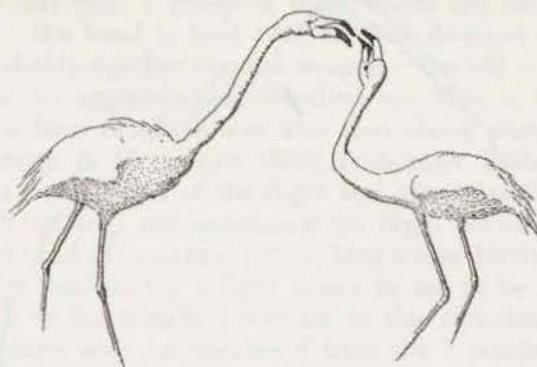
FIG. 10. Bill-fighting.

two or more tendencies (e.g. TINBERGEN 1959, BAERENDS 1960), such as flight and attack tendencies. By way of the circumstances under which the various displays occur, it is possible to state something of the relationships between the tendencies.

a. AGONISTIC BEHAVIOUR

Description

Although flamingos are often active in large groups — e.g. while searching for food, a small area exists in their immediate neighbourhood in which no other flamingo is tolerated. This is not a topographically defined place such as occurs in the colony, for example, and we cannot speak in this case, according to HINDE (1956) of a (food) territory. CONDER (1949), following HEDIGER and BURCKHART who used the term "Individualdistanz" in 1942 and 1944, writes of the "individual distance" and not the "individual area" ... "when the area has no topographical reference." HOFFMANN has also observed the "individual distance" and the accompanying aggressive behaviour in feeding flamingos (SWIFT, 1960). JACOBI (1959) also reports that the birds are "afstanddieren" or "distance animals".

If two individuals meet during their various activities or approach each other, the following situations can take place:

1. Both aggressive: they try to peck each other in the head, often with the result that they face each other with opened bills. They each try to seize the mandibles of the other and during this activity their necks assume all possible angles and shapes to avoid the opponent's bill (Fig. 10, Plate XIX*b* and *d*). The back and shoulder feathers are often on end. This

procedure is often followed by "food-searching" with the reversed head under water, after which a new attack can take place, followed once more by "food-searching" and so on. This searching is carried out always in the same fashion (Chapter V c 3), the birds remain standing, however, and rarely walk. After the fight a bird may assume the stretched position for
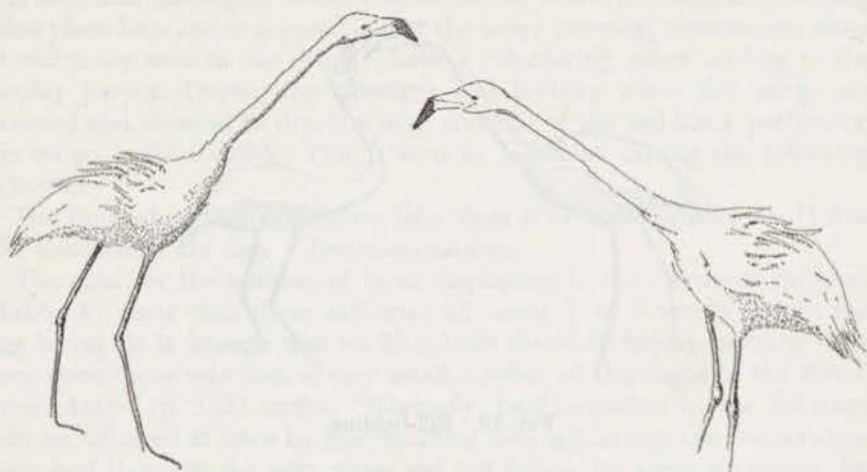
FIG. 11. Threatening.

many tens of seconds. In this case the neck is directed almost vertically in the air with the bill and head at a slant — the same position is assumed by alarm. During the fighting proper, one bird may turn his mandibles laterally away from the opponent (Fig. 17).

2. If one bird is more aggressive than the other, which has the tendency to flee, the latter is often chased away for several meters. The aggressor will try to peck at the back or tail feathers, but this may also take place under *1.* above. The escaping bird walks away with stretched neck and these long, pointed necks are also to be seen when the flamingos are alarmed by man, aeroplanes, pelicans, donkeys or goats. They often take off from this position as well.

3. The birds may threaten each other, so that the necks are directed slantingly forwards, or, more or less horizontally to the opponent(s) (Figs. 11 and 18). The bill is then often open and a growling noise may sometimes be heard. The whole procedure may change into fighting (*1.* above) or the turning away of the head. During threatening, the back and shoulder feathers are once more on end.

4. If a pair comes into contact with another flamingo or flamingos, then the male birds are the more aggressive — a female threatened by another bird, does not react to this at all or, at most, is hardly aggressive — the male reacts for the female. CONDER (1949) calls this the "mated-female distance" — "the male of a pair defends the area around the female, which is about twice the size of that delimited by individual distance."

Discussion

It is obvious that gradations occur between the four situations mentioned above and that one type of behaviour may change into another. Fighting is usually quite short and wounds are rare. Due to the communal habit of flamingos, bursts of aggression often flare up.

If an individual joins a group of birds which are bathing, preening, displaying etc., the head is held with the bill directed away from the group. This probably signifies that the weapon — the bill — is turned away, so that less or no aggressiveness is called up. This is thus a form of appeasement, a form of which was also seen above during the fighting proper (TINBERGEN & MOYNIHAN 1952, TINBERGEN 1953a). Threatening is apparently a combination of the flight and attack tendencies, whereby the attack (bill-fighting) and sometimes the flight (turning away of bill) gain the upper hand (TINBERGEN 1953b, MOYNIHAN 1955).

Searching for food during a fight seems to me to be a displacement activity since it is functionally irrelevant in this situation. It took place always in the same way, i.e. number 3 from the 7 possibilities observed on Bonaire. In these situations there will be a conflict between attack and escape tendencies, which inhibit each other, whereby an other behaviour pattern can be desinhibited (TINBERGEN 1940 and 1951, TINBERGEN & VAN IERSEL 1947, VAN IERSEL & BOL 1958). This searching for food may have an appeasement function since the bill (the weapon) is thereby hidden under water.

b. PAIR FORMATION

Description

Pair formation takes place at those points where many flamingos come together. This may be in or near the actual or future colony, but especially at the drinking-places, where — in the less salt water — preening and bathing also take place. Many of these preening movements are found in a ritualised form in the display.

The very beginning of the display may be as follows: A group of several tens of sleeping birds to several hundreds awake into activity. They begin by stretching their necks, but not fully as in the alarm attitude and as in the later display. In this attitude both males and females walk to and fro around each other; mutual agression is to be seen in the form of bill-fighting and pecking at the back and tail feathers of other birds, often followed by the turning away of the bill. A few minutes later a completely stretched attitude is assumed by the neck, so that this stands almost vertical and the head and bill are directed somewhat at an angle above (Plate XIIa). They then walk around in this streched attitude, sometimes all in one direction with "stiff legs", they then turn, more or less together, and walk back for several meters. Some birds may also walk in the opposite direction, so that they "slide" pass one another.
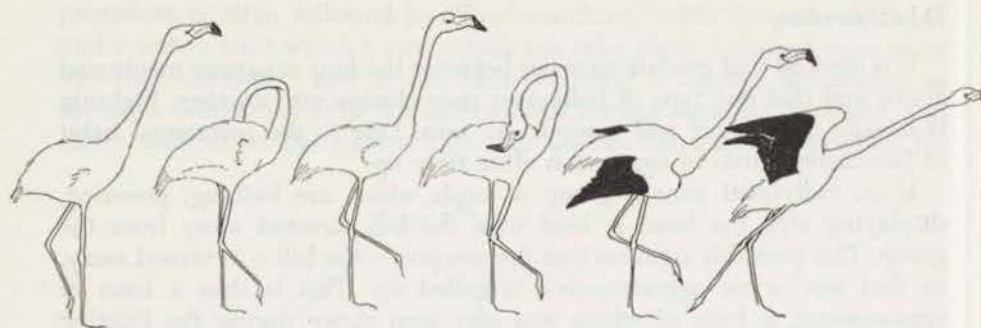
Fig. 12. Walking in stretched attitude alternated with wing preening, proceeding into flying.

This behaviour can last several minutes, being repeated time and time again, accompanied by a goose-like cackling and the "chogógo" call may also be heard. They may also stand still in this position and a number of birds spread the wings which are "displayed" for 2—4 seconds in a slanted fashion. The magnificent contrast of the bright orange-red coverlets and the black primaries is then obvious.

After this the birds may begin walking once more. The stretched position of the neck then alternates with a bent position, a movement which brings the bill for an instant in or on the back or shoulder feathers (Fig. 12). This movement resembles a short preening movement and is directly followed with the stretching of the neck into the "stretched attitude" described above. All these activities take place during the walking period, and alternate very rapidly — about 1 second neck stretching and about 1 second "preening" in the back feathers. This rhythmical movement proceeds via walking into flying when the goose-like noise is also to be heard.

After a number of minutes flight, the same procedure is followed; the spreading the wings is infrequent during the beginning of the display, but flying, on the other hand, is very frequent. The opposite is true of later stages in the display. The sight of circling flamingos may be interpreted as the increase in display activity, since flamingos do not, in general, fly very often or extensively.

After this introductory phase with much flying, the birds remain on the ground or, better, in shallow waters, where we see the following extension and change in the behavioural pattern: during the stretched position the head is very frequently rotated, i.e. the head and bill move from left to right and back through an angle of about 90° on the average (min. about 45° and max. about 120°; Fig. 13). One movement from right to left takes about 1 second while the repeated movement may take from a few seconds to a few minutes.

In this stretched attitude the wings are often spread in contrast to the introductory phase and this can last 2—6 sec. During the spreading of
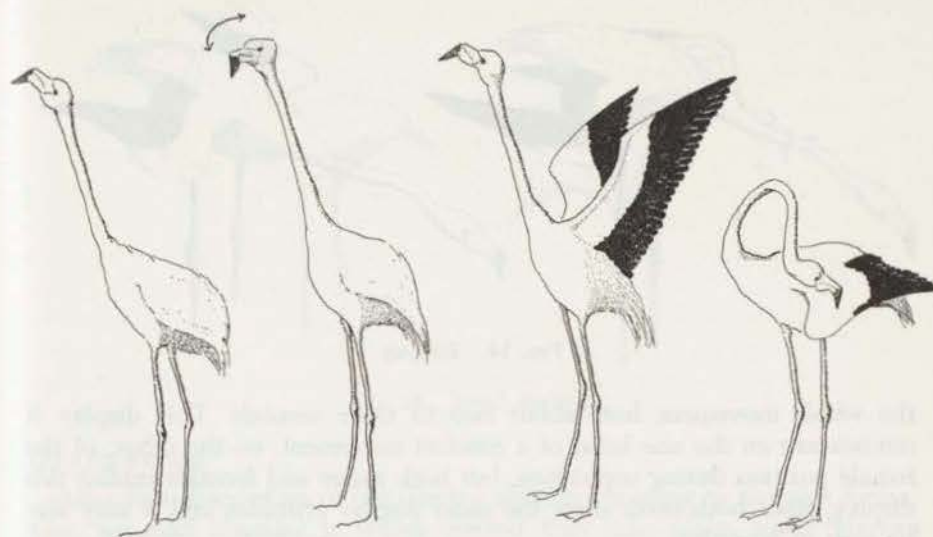
Fig. 13. From left to right: stretched attitude, stretched attitude with head rotation, stretched attitude with wing spreading, wing preening.

the wings no head rotation occurs. Wing spreading is nearly always followed by wing preening (Fig. 13).

In this stretched attitude, with or without head rotation, the flamingos spread their wings and carry out the preening movement all facing in the same direction that is, head-to-tail. One bird begins with the spreading of the wings and this is followed by several, or sometimes many, birds from the displaying group. The red and black pattern is very striking here, but this form of activity does not seem to be directed to any particular individual(s), although those at the back of the group will, of course, see those in front.

During all these movements, the same cackling noise may be heard, together with the "chogógo" and a number of grunting noises.

The contrasting wing pattern is also to be seen in the preening of the wings, which almost inevitably follows the wing-spreading activity (Fig. 13). This new activity does not appear to be directed at any one particular bird or birds, just as in the case of the spreading behaviour. Only one wing is preened — i.e. the bill "indicates" as it were the half hanging wing and there is no indication that under given circumstances the wing on one side or the other was "preened".

This behaviour is sometimes alternated with "bowing" a display in which the neck and head are directed at an angle downwards and forwards and both wings are half or quarter spread (Fig. 14). Here once again is the red-black contrast pattern visible. The head and bill remain, even when the behaviour takes place in deeper water above the surface and
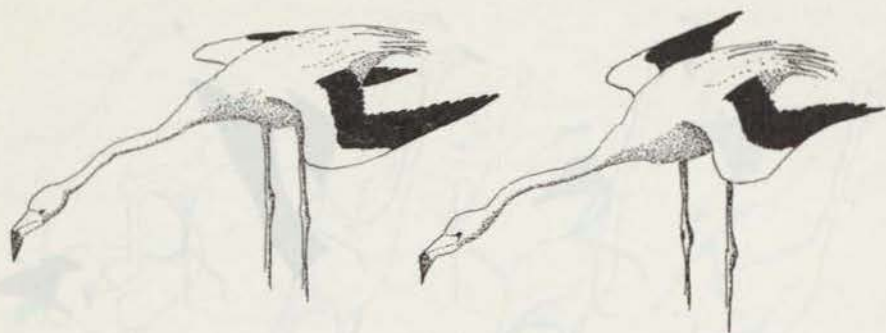
FIG. 14. Bowing.

the whole movement lasts about two to three seconds. This display is reminiscent on the one hand of a comfort movement, on the other, of the female position during copulation, but both males and females exhibit this display, since both sexes show the same display attitudes and it may also be seen in juveniles.

Another comfort movement — the one-sided stretching of one foot and one wing may also be seen between other display movements, although not so frequently, but all types of preening and comfort movements take place regularly. Especially after the stretched attitude, with or without the rotation the head, is head-shaking, and breast, neck, shoulder and back preening to be seen.

After preening the bill is regularly dipped for a moment in the water or just not i.e. only the intention movement. This is followed by head shaking. This head-shaking is different to the head-rotation (Fig. 15), although the one movement may be connected with the other. This shaking always takes place with a bent neck, whereby the head is situated in front of the lowest portion of the neck, or even somewhat lower. The head is then shaken to and fro 2 or 3 times a second, the whole display taking 2 or 3 seconds, so that for a total of 4 to 9 times the head is loosely shaken through an angle of 90°.

Head rotation takes place only with a stretched neck in a much slower tempo and with a more awkward, angular movement. This behaviour can also last much longer: tens of seconds or even several minutes.

In general the males are more active than the females during the display, showing the above display activities many minutes and sometimes a few hours. The females join in now and then with all these displays, but often search for food in the meantime. They do this in the same fashion always — standing or walking with the bill and usually the head under water. After a time pairs are formed from such displaying groups, but the way in which this occurs in not very clear, only that the group as a whole becomes smaller and the number of pairs increases. These paired birds remain together even during more or less loose communal gatherings, such as sleeping groups; during feeding they are also found together.
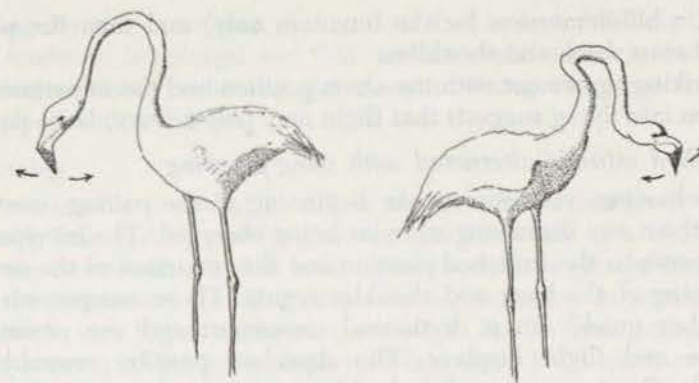
FIG. 15. Head shaking.

Discussion

After this description of the display activities leading to the pair formation, we shall consider in which context they take place, since this can tell us something about the relationship of the various tendencies playing an active role.

We saw the following activities during the formation of pairs:
1. Stretched attitude
2. Stretched attitude alternated with wing preening
3. Stretched attitude with wing spreading
4. Stretched attitude with head rotation
5. Bowing
6. Stretching of foot and wing on one side
7. Wing preening
8. Head shaking
9. Neck and breast preening
10. Back and shoulder preening
11. Bill immersion
12. Food searching

The aggressive and flight displays are not mentioned here since they have already been described for pair formation and may occur during all stages of the displaying period. Agonistic behaviour is especially common at the beginning of these activities.

1. Stretched attitude

This display takes place both standing and walking. It is preceded by sleep, searching for food, preening, bathing, bill-immersion, etc. Sometimes it is preceded by aggression — especially by the males — after which the stretched position may be taken up for a long time, followed by breast, back and shoulder preening. It develops sometimes into flying, which in turn may be followed by foraging and/or preening. It may also be followed by 2, 3 and 4. It may be followed also by bill-immersion or head-shaking.

once again bill-immersion (or the intention only) and then the preening of neck, breast, back and shoulders.

The striking agreement with the alarm position and the sometimes direct conversion into flying suggests that flight may play a (very) large part here.

2. Stretched attitude alternated with wing-preening

This behaviour, restricted to the beginning of the pairing, converts to flying without any disturbing stimulus being observed. The movement has two components: the stretched position and the retraction of the neck, and the preening of the back and shoulder region. These components follow one another quickly in a rhythmical movement and are preceded by aggressive and flight displays. The stretched position resembles that assumed by flamingos when disturbed by man, animals or aeroplanes, etc., and may indicate a high flight tendency.

We therefore have to do with attack (especially in the beginning) and flight tendencies and this is not surprising, since the flamingos go from a loose to a more compact grouping during this introductory pairing display. The preening of the back or shoulder region may then be a displacement activity. It is, in fact, functionally irrelevant with respect to attacking or flight displays. This activity may be a preening movement, which is present as an intention only, it is therefore a ritualisation in a quantitative sense, since there is no difference in form, only in the time, to normal preening. Due to fluctuations in the relative equilibrium of the two opposed tendencies attack and flight, the alternation of both behavioural components may be caused. During this behaviour the flight tendency in the group increases, the birds walking gradually more quickly and flying up at last.

3. Stretched attitude with wing spreading

This takes place in a stationary position only. It is preceded by the stretched attitude and usually followed by preening, restricted to one wing whereby the red-black pattern is visible. Momentary head-shaking may also proceed this at times, which may be followed by bill-immersion (or nearly — i.e. the intention only), once again head-shaking and then wing preening. A number of times we saw that the movement returns to *1* without the preening movements. The movement occurs in particular during active pairing behaviour.

4. Stretched attitude with head rotation

This can take place both standing still and walking. It is usually preceded by *1* (stretched attitude), sometimes also by bill immersion. Often followed by neck and breast preening, and then also sometimes bill immersion, in turn followed by wing preening. It is also possible that head-shaking may follow directly.

The movements *1, 3* and *4* are all three (also partly *2*) based on the stretched attitude. This would suggest a flight tendency, which is possibly stronger in *1* and *2* than by *3* and *4*, since both *1* and *2* may convert to

to flying. By the conversion of *1* to *3* or *4*, it is probable that the relative flight tendency is reduced and that conflict situations occur (with, e.g. an attacking tendency) whereby the many preening movements take place as displacement activities.

5. Bowing

This is usually preceded by one of the stretched attitudes *1, 3* or *4* and is usually followed by preening movements. Only one or a few in a group show this behaviour, which is never synchronous in a group. We sometimes have the impression that this occurs more frequently in situations where the attack and flight tendencies are high. It can also occur, however, during a series of preening displays, when there is no question of mating behaviour. It then occurs very often next to:

6. Stretching of foot and wing on one side

This occurs also during bathing and sleeping.

7. Wing preening

We see this during various of the foregoing displays; as a result occur: with *3* (stretched attitude with wing spreading) it follows always, sometimes preceded by head shaking.

with *4* (stretched attitude with head rotation), after which firstly other preening movements follow and only then, after head shaking, wing preening.

8. Head shaking

This may occur after *1, 3* and *4*, where after *4* it is sometimes preceded by neck and breast preening. It often occurs after bill-immersion. It is often followed also by the bill-immersion movement, or the intention only. Other preening movements always follow e.g. wing preening. This movement also takes place after drinking and foraging.

Under Chapter Ve we have described how head shaking serves, in all probability, to dislodge the salt excrement from the bill-point and from the nostrils and we see bill immersion taking place during and between these movements.

9. Neck and breast preening

This may be preceded by *1* and *4* (stretched attitude and idem with head rotation) and may be followed by head shaking or other preening movements. Naturally enough it occurs also after bathing and during preening bouts.

10. Back and shoulder preening

This occurs, albeit very shortly, during *2*, alternating with the stretched attitude or also after *1* (stretched attitude), *5* (bowing) and *8* (head shaking). It takes place (as do *5, 6, 7, 8* and *9*) after bathing and during other preening periods.

11. Bill immersion

This usually takes place after head shaking by displaying birds. It is followed by *1* and *4* (stretched attitude and idem with head rotation) or head shaking. In the latter case is often followed once more by bill immersion. At times, however, the bill is not really immersed, but the movement is stopped just above the surface.

12. Food searching

Food searching, with the bill or head under water, takes place during the other activities, always in the same way (Chapter V c no. 3), although there are various ways in which food searching can take place. It is often followed or preceded by aggressive activities: bill-fighting, threatening, pecking, etc.

We have already observed this behaviour under the agonistic behaviour and it occurs both before and after the copulation (see Chapter VI c). It would seem to me that it is displacement food searching as a result of an inhibition of the opposed tendencies of attack and flight. This occurs during the pairing activities more by females than males.

The first four movements show (partly) the stretched attitude, to which other components may be added and there are signs that the flight tendency may be high. This stretched attitude seems to me primarily an intentional movement for flying away (see also DAANJE 1950).

The wing spreading under *3* may perhaps also be brought down to an intention to fly away. Head rotation, it seems to me, is derived from head shaking a comfort-movement which has been ritualised. It may be preceded, just as real head shaking, by bill immersion (or its intention) when we see drops of water flying around. The orange-yellow bill with its black tip is, after immersion, striking colourful and shining.

Movements *5* and *6* seem to me to be normal stretching (comfort) movements, while *7, 8, 9, 10* and *11* resemble more or less ritualised displacement activities which may differ from real preening movements in that the movement itself is very short and rapid (e.g. the preening of the back during *2*) or incomplete (e.g. often in bill immersion) or markedly "exaggerated" (such as wing preening which resembles a wing display). These movements, whereby we often see striking colour contrasts are thus signal displays and may serve for the selection and synchronisation of partners (BAERENDS 1960).

ALLEN (1956) reported the following displays for the males: stretched attitude, the stretched attitude with head rotation, idem with wing spreading, the stretched attitude alternated with wing preening which he called "bobbing". He says (p. 145) that the females do not show these behaviours but "they walked along with their bills in the water, as if feeding, although this may have been merely a form of displacement activity". This is termed the pre-pairing phase by ALLEN. He describes the "pair-formation" as follows (p. 150): "At the start of this new phase of activity, the males resumed their typical male display, as previously described. The females were no longer bunched together, and the excitement of the earlier noisy huddles seemed to have passed. Instead, solitary quiet females were scattered about over the lake. They stood or walked very slowly along as if feeding in a desultory way. Perhaps this was merely a form of simulated feeding. Most of the females had their heads down, either in the water or with their mandibles rather indifferently dipping through the surface. Apparently the stage was now set for the accomplishment of pair-formation." On page 152, he writes: "Although the unpaired males continued to display without loss of vigor until a lull occurred towards midday, it was remarked that once an individual male broke away from a displaying group and singled out a solitary female, his manner altered and so far as we could see he did not return to any of the male displays. Thus, the break between the pre-pairing phase and the actual pairing is evidently quite abrupt in both sexes."

The description of the displays agrees in general with a number of the displays which we could distinguish. They differ in small details e.g. head rotation, which, according to ALLEN, takes place with the head moving to the left and then returning to the central position. We do not think that "bobbing" (= 2) takes place with spread wings, either and I disagree entirely with ALLEN that the females do not show these displays, although I did find that they were less active than the males.

These contradictions are perhaps caused by the fact that ALLEN was able to watch pair-formation a few times only, but it also possible that what he refers to as young males (p. 143–144) with a low social order, are, in fact, females. We never observed any traces of a social order in a group!

BROWN (1958) could distinguish the following displays in *Ph. ruber roseus*: stretched attitude, idem with head rotation (through 45°), idem with wing spreading (up to 4 seconds) ("wing salute"), bowing (called the "inverted wing salute" by BROWN, p. 396). "The bird bows forward and when in that posture partially opens its wings suddenly, exposing the scarlet upper wing coverts; the general effect is a flash of red. This manoeuvre is most often performed when in small loose groups, perhaps because of cramped space in a close-packed displaying flock. Allen does not record this for the West Indian race but Lomont (in litt.) tells me that he has seen *P. ruber roseus* perform the manoeuver in the Camargue." On the preening element of "head bobbing" he says: "This movement appears to be related to 'false preening' as the bird sometimes mandibulates the tail region."; bill immersion, sometimes accompanied by the preening of the bill with one foot, with the striking of the foot in the water (we saw this during the cleaning of the bill, but did not consider it a typical display activity); "Hooking" a threatening attitude, which agrees largely with that of *P. ruber ruber*. BROWN writes further (p. 397): "Allen seemed to assume that the display is performed exclusively by males, but in view of the numbers involved at times and their great variation in size, it appears likely that females might also take part; this impression was confirmed by R. T. Peterson in discussion at Lake Elmenteita."

We are able, therefore, backed by BROWN's observations, to conclude that ALLEN's opinion that females do not take part, is based on insufficient observations.

c. COPULATION

Description

The copulations take place very incidentally in the displaying groups. In the display areas, the pairs are formed in some way or other and they remain together (nearly) always and it is striking how, in a period before a new breeding wave, foraging takes place for the most part in pairs, as does sleeping. The partners stay together within the groups as well. The large number of paired flamingos seen on the the the 18th and 21st of December was notable reaching 70 to 80%! this a few days before brooding began in Pekelmeer. On the 4th of January the number of pairs was still large (60%), on the 8th of January and the 15th, this was declining
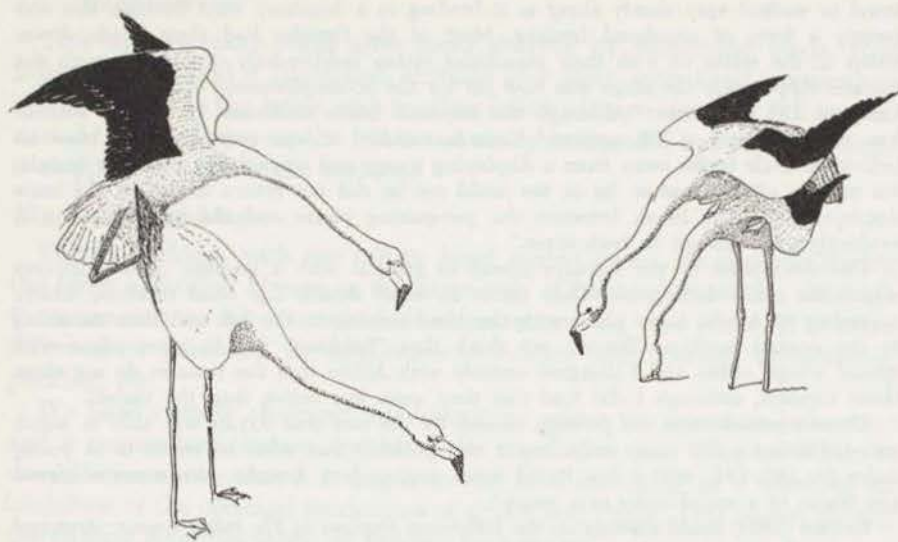
FIG. 16. Copulation.

and on the 5th of February this was 3% only, all outside the colony proper. On the 8th of July there were also many pairs — just before the new breeding wave!

Copulation takes place in these pairs without any further introduction. Of the 60 copulations observed in Pekelmeer, 4 took place in a non-displaying group, 3 after a group which we had disturbed settled dispersed, and 53 during foraging. The latter mode was also predominant in Goto.

Details concerning the places where copulation took place have already been given in the introduction to Chapter VI, in comparison to the displays. There follows now a description of the behaviour before, during and after the copulation, in the manner in which this usually takes place.

The female searches for food with the head and/or bill under water, the male walks behind and to the side of her; he walks then with his breast against the tail of the female, who then stands still and brings the wings out of the supporting feathers, raises them and turns them sideways. The male then mounts, whereby his feet are supported under the wings of the female on the body, so that his toes are visible at the origin of the female's wings (Fig. 16). The male sits with spread, and sometimes flapping wings to preserve his equilibrium, since he hangs over backwards, bending his tail downwards to effect contact between the cloacas. The female keeps the head under water during 80% of the copulations observed.

In one case it was noted that the male pushed the female's head under water by pecking in it and the neck. The mounting lasts some 2 to 10 seconds (average 6 sec.) after which the male flies off the female and stands in front and to the side of her as a rule. Very often they both have

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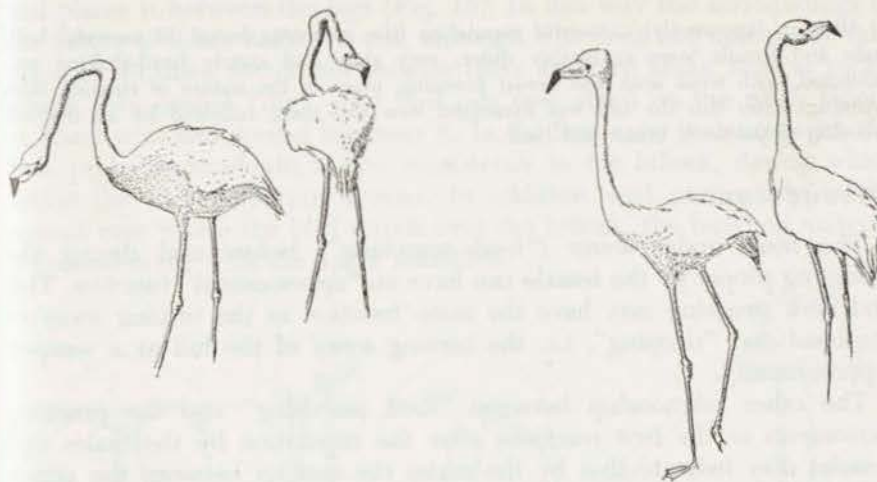
FIG. 17. Turning away of head and bill after agonistic behaviour and after copulation.

their heads under water and then begin preening. Sometimes they walk a short distance away from each other with turned heads (Fig. 17) and then begin preening, sleeping or searching for food.

activity	♀♀						♂♂					
	1st	2nd	3rd	4th	5th	6th	1st	2nd	3rd	4th	5th	6th
"food searching"	24	3	3	.	.	.	11	3	3	.	.	.
preening	12	4	3	1	1	1	12	6	3	2	1	1
turning away head	1	2	.	1	.	.	2	1	.	1	.	.
"sleeping"	1	.	1	.	.	.	.	.	1	.	.	.

The above are the noted activities following copulation and these are followed by some preening, and then often by sleeping or real food searching, whereby the partners remain close to one another (one to a few meters distance). The course of the activities which follow the copulation, which were noted in their exact sequence, agree with the general impressions which were often noted in a more sketchy fashion.

It is noticeable that the females have (or keep) their heads under water more frequently as their first activity and that the males show more preening in comparison. After the first reaction the then following activities do not diverge very much. The preening movements are directed in particular to the back, followed by head-shaking, then followed usually by breast and neck preening. Only once did we see wing preening and only once tail and cloaca preening (both by females). The turning away of the head occurred 8 times, and this is also to be seen when two birds (paired or not) approach each other, or when one bird joins a group.

After a failed copulation, where the female walked away from under the male, the male began head-shaking and became aggressive (pecking in the back) towards another bird. This is perhaps a case of "redirection activity" (BASTOCK, MORRIS & MOYNIHAN 1953).

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After an (apparently) successful copulation (the mounting lasted 10 seconds) both male and female were noticeably quiet; very slow and stately head-shaking was exhibited, with weak neck and breast preening, more in the nature of stroking than preening. After this the bill was immersed now and then, followed by an inactive preening of the neck, breast and back.

Discussion

The head under water ("food searching") before and during the mounting proper by the female can have an "appeasement" function. This and back preening may have the same function as the turning away of the head and "sleeping", i.e. the turning away of the bill as a weapon (appeasement).

The other relationship between "food searching" and the preening movements as the first reactions after the copulation by the males and females may indicate that by the males the conflict between the attack and flight tendencies is different, so that other displacement activities occur. Here a difference in the threshold value may play a role in the various movements. "Sleeping" is probably also a displacement activity since the eyes are not closed.

Other descriptions of the copulation in flamingos are to be found in ALLEN (1956), BROWN (1958) and SUCHANTKE (1959). These all agree in general, although SUCHANTKE believes that there is a difference between *Ph. ruber roseus* and *Ph. ruber ruber*, based on his observations in the Camargue, which he compares with those of ALLEN. I think that this difference can be explained by the fact that ALLEN also described failed copulations, where the male falls off the female, or the female is pushed under water for a time. In these cases, examples of which we also noted, it is probable that the preparedness of the female was not high enough. We see for example, that the wings are not spread, so that the male has insufficient foothold and therefore falls.

d. NEST BUILDING

Written data on nest building are scarce and somewhat contradictory. Before considering this further, we will first give our own observations.

In December and January and later in May and June, nest building was seen several times at the beginning of a breeding period, during which nest building activities also took place (for further details, see Chapter VI g). We noticed that the greatest activity was early in the morning, when tens of birds and sometimes hundreds, were building at the future nesting site. We did not see any signs of early building at sites where no later nest locality was situated, as can be seen in other bird species. There is much aggressiveness between the pairs during the building, but sometimes they sleep also.

It would appear that both males and females build, not at the same time, but alternating. The birds stand somewhat spread-eagled and use the closed bill as a trowel which scrapes up mud from the surroundings

and places it between the legs (Fig. 18). In this way the surroundings of the future nest are hollowed out, although this does not necessarily take place on all sides, sometimes because there are hard areas, such as rocks, where they cannot "dig". The bird can now stand on the small hillock or stand with widespread legs over it. In the first case, it stamps with the feet, probably to obtain a firm consistency in the hillock, during which action the bird may turn around. In addition, and particularly in the second case where the bird stands over the hillock, the building material is pressed home with the upper mandible.
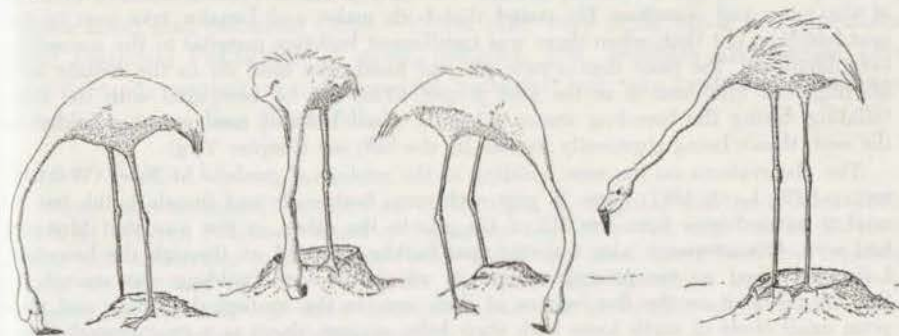
FIG. 18. Nest building, the bird on the right is threatening.

The time given to building was not very long (a few days only) in the northwestern and middle colonies, this being connected with the fact that the birds used nests from the previous year, and these were simply patched up and raised a little.

On the other hand, new nests were built in the South-eastern and Northern colonies, where much more time was necessary (Graph 19). The site was partly in the water (North-west colony) and partly near the water (North, Middle and South-eastern colonies — see Map 5). There were also older nests far from the waterline where the flamingos had used dry material for building, such as stones, sand, clay and salt.

The 1958–1959 nests were used in three breeding periods in 1959–1960, so that there were nests which had been used at least 4 times in about 1½ years.

Contrary to the statements of various authors, MACCANN (1939) and YEATS (1950) reported that *Ph. ruber roseus* used nests several times and this was supported by VOOUS (1957) for *Ph. ruber ruber* and by Messrs. MAYER and GERHARTS who, as inhabitants of Bonaire, have watched flamingos for a number of years. These observations agree therefore with our own.

CHAPMAN (1905) did not believe that the old nests were used, with the exception that "possibly when the governing conditions of any two years are alike, old nests may be repaired, but I saw no nests which seemed to have been rebuilt or added to." He saw reparations during the brooding only. At this time building material is collected, as far as possible, "at random" around the nest, but owing to the presence

of limestone, two or more excavations may be the only sources. The way in which this took place agrees with our observations. CHAPMAN's supposition that new nests are built in the same fashion is therefore correct.

GALLET (1949, 1950) describes the nest building as a somewhat changed food searching behaviour, whereby the "cônes alimentaires" are made. The detritus is removed with the bill from the runnel to the centre of the "cone" and trodden down. The movements are comparable with those where we saw that mud was collected from the surroundings and trodden down. McCANN (1939) presumes that the flamingos transport mud in the bill from small excavations in the neighbourhood.

ALLEN (1956) reports the observations of J. W. MORROW, who cared for the flamingos on the Hialeah Race Course in Florida for many years, and these agree with those of CHAPMAN and ourselves. He stated that both males and females take part in the nest building, but that, when there was insufficient building material in the immediate neighbourhood, the male digs a new pit and hands the mud on to the female with his bill, who then uses it as the nest proper. (This can be compared with the nest-building during the breeding season whereby small balls of mud are then added to the nest, theses being apparently formed by the bill; see Chapter VI g).

The observations on the nest building in the zoological gardens in Basel (WACKER-NAGEL 1959, LANG 1961) agree in part with ours; both male and female build, but no mud is handed over from the bill of the one to the other, in the way that MORROW had seen. WACKERNAGEL also reported that building carried on through the brooding. LANG described an exceptional manner in which the nest building was started. In this the birds sit on the flat bottom of their area in the zoological garden, and then prise small clods of earth loose with their bills, arrange these as a ring around themselves and then begin to tread this down.

ALLEN (p. 158) writes on the nest building: "In a small colony on Charles Island, Galapagos, Gifford (1913) saw one nest that consisted of a flat lava rock on which the egg had been laid, with mud scraped around it. There are other variations, each illustrating the fact that the birds use what is available by way of nesting material. Hartert (1893), at Bonaire, noted that the mounds were often built directly on the salt crust rather than on the actual bottom. According to Lloyd, quoted by Chubb (1916), mounds in British Guiana "resemble a large yam heap", and were made of "vegetable substances thrown up by the sea"."

"Gallet (1950) in the Camargue and Voous (1955) on Bonaire, speak of the mounds being of mud and "covered with a white mantle of salt." ... Except at Inagua, we found the mounds of the West Indian species constructed of marl of a stiff and somewhat sticky consistency. In Lake Windsor and the Upper Lakes, the mud is made up of a loose mixture of minute, ground shells and small particles of sand and clay. When wet it is reasonably adhesive, though not as successful in this respect as typical marl; but when dry it is almost powdery. Marl hardens and can withstand years of repeated flooding, but the shelly material on Inagua washes away quite readily. I saw marl nests on Abaco that were apparently more than ten years old. Mangrove shoots had grown completely through several of them, but their original forms were well preservered, and they were nearly as hard as rock. Inagua mounds, on the other hand, do not seem to survive as long as one year, so in this location there can be no question of using mounds again and again, as reported elsewhere."

Voous (1957, p. 80—81): "The nests in the Pekelmeer are the well-known truncated, cone-shaped mud structure, usually covered with a crust of salt and varying between approximately 15 and 30 cm in height and 25—30 cm diameter at the top. The nests were very close together, sometimes connected by low bridges of hardened mud, but in other cases separated by narrow channels of salt water. The nests seem to be used for many years in succession.... When we visited Bonaire in November 1951 we did not see anything of breeding flamingos; instead, we saw their mud nests rising out of the water of the Pekelmeer, between the Witte Pan and the Oranje Pan. By the end of March 1952, when the water level had risen, no nests were visible, so that

we assumed that all nests were inundated. Judging from the photographs taken by GABRIEL... of the breeding places in Goto, the nests must have been considerably lower there than in the Pekelmeer, apparently as the result of the lack of a sufficiently thick layer of mud. Many nests seem to have been lower than 10 or 15 cm!" BROWN (1958) also reported low nests on rocky islets in East Africa and Chili.

We saw not only fine mud being used as building material, but also pieces of stone and sometimes feathers, especially in Goto. At times there were the remains of a dead young bird from the previous season and these were not removed; the eggs were, on the other hand. The composition of the nests was very different at the various places: Slagbaai — especially black mud and pebbles; Goto — often only very little black mud, pebbles and feathers; Pekelmeer — mud, pebbles, grit, feathers and shells. One old nest-site contained much coarse material, but was built some distance from the water line (Plate VIa).

Size of nests

Nests were measured: in Goto on 11. IX. 1959; in Slagbaai (old nests from 1958) on 2. XI. 1959; in Pekelmeer (nests of the season Dec. 1958—Jan. 1959) on 13. XI. 1959. After this no further measurements were taken, the nests being used by brooding birds. In Slagbaai and the Pekelmeer the nests had, therefore, been exposed to erosion, so that they will have decreased somewhat in height, which made it impossible to determine the diameter either.

	Number	Height (in cm)	Diameter on top (in cm)
Goto I mud pool	34	26 (16—37)	30 (26—35)
II firm bottom	26	17 (10—25)	27 (22—31)
III rocky bottom	29	12 (4—21)	28 (25—31)
Pekelmeer	25	17 (11—23)	— —
Slagbaai	8	28 (24—34)	— —

The Goto nests show marked differences in height in connection with the substratum.

Where much nest material is present, high nests are made, while on the rocky bottom often only a thin layer of mud is sufficient. The nests on a firm substratum are intermediate in his respect.

In the Pekelmeer the nests were eroded (as explained above). It appeared later from the repaired (old) nests and newly built nests that the variation in height may be very large and that this is related to the amount of material in the direct surroundings of the nest.

In Slagbaai we found the highest nests and only those showing the least signs of erosion were measured. Black mud with some grit was present here on a dyke between the salt pans in sufficient quantity. But the eggs were, however, nevertheless washed away.

We have never seen the nests being raised during a rising water level in the Pekelmeer, which must be fatal for some of the lower nests. The function of these high constructions is clear at high water although the

literature often reports the flooding of colonies, despite the high nests. It is typical that the wader *Himantopus himantopus* which breeds along the shores of the salinas also makes such high nests! If we disregard the oldest observations from the literature, we find (according to ALLEN 1956, p. 159) a maximum height for the nests of 18 inches on Abaco, and a minimum of 4 inches, which is recorded from Bonaire. The Abaco maximum was therefore not equalled, but the minimum was certainly lower in Goto.

The hollow on top of the nest is usually very shallow, only one or a few cm deep. There were feathers in some nests and, with frequent usuage, sometimes a dead young bird and egg-shell remains.

e. COLONIES AND COLONY FORMATION

The difference between old and new colonies can be seen in the difference in building activity, as shown in Graph 19.

In the old colonies (dating also from 1960, being used for the 2nd or 3rd time) the building activities lasted only a few days to a maximum of 15 days in one large colony (North-west and Middle colony). In the new colonies the building activity was much higher and lasted about 24 days (especially in the large south eastern colony). The small Northern colony had few building days, as a result of the smaller number of nests (45) and probably because the beginning of the building activity was missed here.

Situation and size of the colonies (Maps 5—7)

In Slagbaai there were 30 nests, dating from 1958, on a small dam about 2 meters wide, between the salinas (Plate IIIa).

In Goto the colony was on a small island in the low-lying part. On 3.IX.1959 there were 200 nests, but on 25.VII.1960 there were only 48 remaining, the rest having been washed away by high water. It would appear that this erosion may be rapid: on the 20th of April 80 nests were still in use, on the 25th of July only the 48 were more or less intact (Plate VIb).

In the Pekelmeer a number of old colonies were met with, particularly on the eastern shore, often on the borderline between land and water, although some were at a distance from the water. This was particularly so for a colony dating from 1957, which was some distance from the water and consisted of high, dry nests made of coarse material (Plate VIa). A colony of 40 nests is known from a small dam between the salt-pans in the Witte Pan, dating from 1955. The other colonies, which we encountered, or their remains, or which we heard of from local information, were all on the eastern shore between Witte Pan and Willemstoren. With a single exception all these colonies were situated close to the waterline on a soft mud-bottom with much salt and sometimes also (in part) in the water.
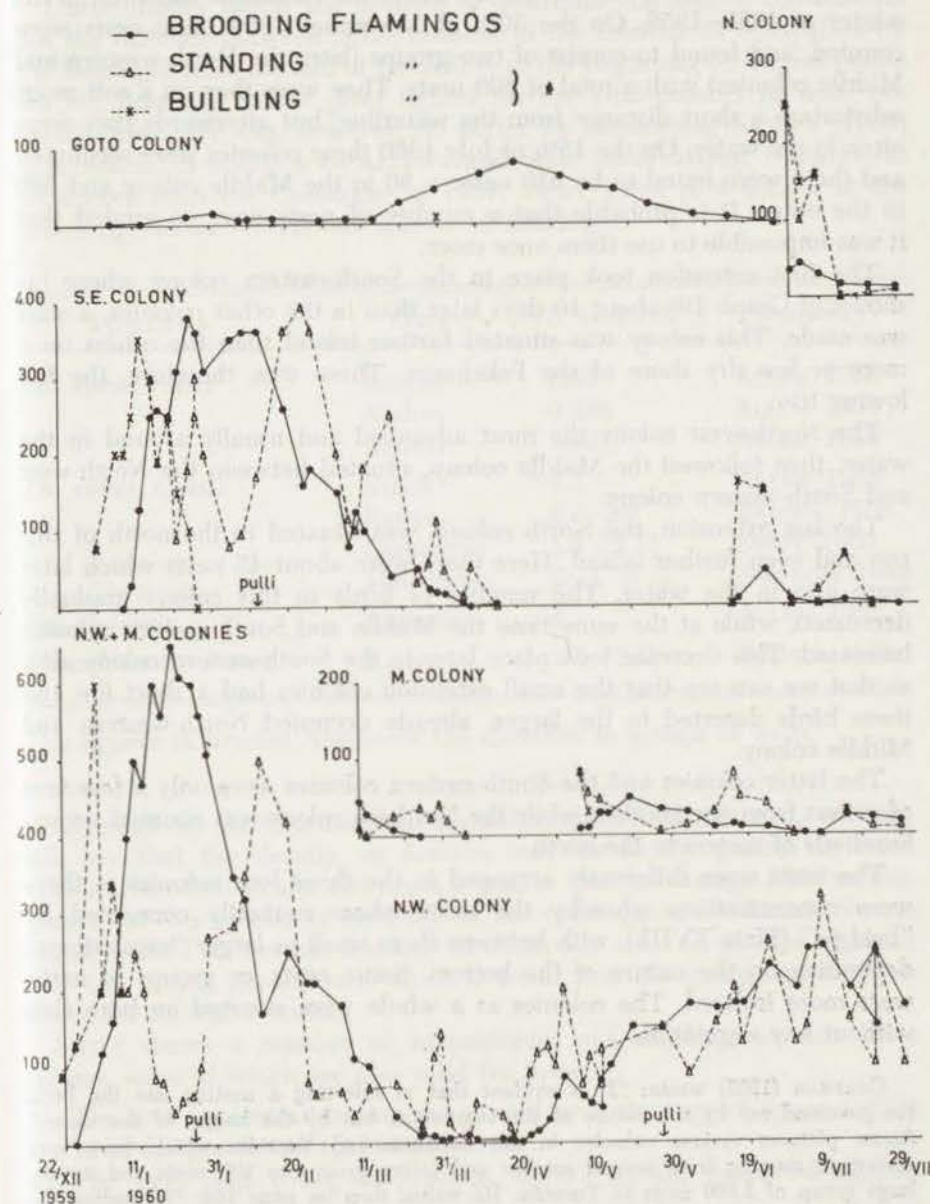
GRAPH 19. Activities of the flamingos in the Goto-colony and the different Pekelmeer-colonies: North-, North-West-, Middle- and South-East colony during the course of the breeding season.

Concerning the recent colonies in the Pekelmeer (Plate XIII): In the autumn of 1959 we found the colony where the flamingos had bred in the winter of 1958–1959. On the 30th of November 1959 these nests were counted, and found to consist of two groups (later the North-western and Middle colonies) with a total of 600 nests. They were then on a soft moist substratum a short distance from the waterline, but afterwards they were often in the water. On the 15th of July 1960 these colonies were recounted and there were found to be 640 nests — 80 in the Middle colony and 560 in the other. It is probable that a number of nests were so eroded that it was impossible to use them once more.

The first extension took place in the South-eastern colony where (as shown in Graph 19) about 10 days later than in the other colonies, a start was made. This colony was situated further inland than the others on a more or less dry shore of the Pekelmeer. There was, therefore, the following trio:

The North-west colony the most advanced and usually around in the water, then followed the Middle colony, situated between the North-west and South-eastern colony.

The last extension, the North colony, was situated to the north of this trio and even further inland. Here there were about 45 nests which later were also in the water. The number of birds in this colony gradually decreased, while at the same time the Middle and South-eastern colonies increased. This decrease took place later in the South-eastern colony also, so that we can say that the small extension colonies had a short life and these birds deserted to the larger, already occupied North-western and Middle colony.

The latter colonies and the South-eastern colonies were only a few tens of meters from one another, while the Northern colony was situated several hundreds of meters to the north.

The nests were differently arranged in the these four colonies — there were concentrations whereby the nests where mutually connected by "bridges" (Plate XVIIb), with between them small or larger "excavations" depending on the nature of the bottom. Some nests, or groups of nests, were more isolated. The colonies as a whole were situated on bare flats without any vegetation.

CHAPMAN (1905) wrote: "It is evident that in selecting a nesting site the birds are governed not by the nature of the vegetation, but by the height of the water." ALLEN pictures various colonies in the Bahamas and Yucatán, which were very divergent, ranging from several smaller and larger groups to 100 nests and 1 very large group of 2,000 nests in Yucatán. He writes then on page 164: "Excluding the remarkable total size and extent of the Great Rann and East African colonies, it can be said that those other sites whose overall areas are known, show a reasonable similarity. In terms of acreage, the largest extent reported is 1.16 acres (Horse Cay, Inagua) and the smallest is .50 acres (Porpoise Creek, Andros). The 1904 Andros site occupied about .82 acres and the Santa Fe location .62 acres more or less. The mean for these sites is .77 acres or .31 hectares, in other words about three-fourths of an acre."

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Nest Density

Unfortunately it was not possible to determine the area of the colonies nor the distance between nests, because of the continuous occupation by the flamingos from the end of December to the beginning of August (when we left Bonaire). ALLEN gives figures for the total number of nests per surface area. We can, however, do better by considering SWIFT's (1960) data which, in addition to ALLEN's and other observations, contains his own work from the Camargue in 1959. SWIFT 1960, p. 4 arrives at the following results for various species of flamingos:

Species	Place	No. nests/m^2	Authority
Ph. ruber ruber	Inagua	1.05	ALLEN 1956
	Andros	0.989	ALLEN 1956
	Andros	0.60	ALLEN 1956
Ph. ruber roseus	Kutch	1.3	ALLEN 1956
	Kenya	2.6–2.9	BROWN 1958
	Camargue	1.3 [2.7]	SWIFT 1960
	Mauritania	2–3, or 1	NAUROIS 1959
Ph. chilensis	Argentine	4	ALLEN 1956
Phoeniconaias minor	Kenya	1.7 [5.4]	BROWN 1958

The figures in brackets represent the densities in groups of nests.

Although we have carried out no measurements of this sort, we may still say that the density on Bonaire may be locally greater in some colonies, but then locally also much lower, so that the average from various places for this species is certainly of the order given by ALLEN. VOOUS found in 1961 on Bonaire a colony of about 500 nests on an area of about 800^2 (i.e. 1 nest per 1.6 m^2), which is lower that the group-figures given above for Ph. ruber roseus.

SWIFT draws a number of suppositions and conclusions from these figures, some of which are also valid for Bonaire:

1) The nest concentrations are not caused by a shortage of space and/or the need for protection against predators.

2) The eggs and young are hardly, or not at all, protected against predators.

3) The flamingos — seeing the nature of their biotope, are not likely to be surprised by predators and there the nests can be close to one another, because the birds walk away from the nests and then (not always) fly away, so that only a much reduced take off space is necessary.

According to SWIFT the most important cause of the high density of

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nests is the social stimulus which results in the simultaneous laying and hatching of the eggs. In this way, large groups of young birds (crèches) grow up together, which has a "survival value" against predators. SWIFT compares this with the similar behaviour of Sandwich Terns (*Sterna sandvicensis*), as described by CULLEN (1960). GALLET (1949), LOMONT (1954) and HOFFMANN emphasise this simultaneous reproductive behaviour of the flamingos in the Camargue.

Our experience does not agree, however, since on Bonaire there was in fact a very extensive breeding season from the end of December 1959 to August 1960! ALLEN (1956, p. 173) reported for Inagua a period with 3 overlapping breeding waves, which lasted a total of 110 days, and for Yucatán 2 waves, with a total of 2 months.

In addition to a mass start, it appears that a slow growth is also possible (Graph 19) for some colonies. In addition, new groups steadily appear and reproduce, so that more than 8 months continuous breeding was observed. This resulted in regular new groups of pullets (crèches), at times very small in size.

Small colonies may also be successful (see Chapter VIII) although we saw, in the latter weeks of June and in July small colonies which rapidly diminished, because the birds joined the larger groups (North-west and Middle colonies). These observations are thus partly in contradiction and partly in agreement with SWIFT's arguments.

f. EGGS AND CLUTCH SIZE

Eggs

The measurements of 24 eggs, which had not hatched in Goto, are (greatest length × greatest breadth to the nearest ½ mm):

87	× 58	91	× 57	95	× 58½
88	× 56	91	× 58	96	× 56
89	× 52	92	× 58	96	× 57
89	× 53	93	× 53	99	× 49
89	× 57	93	× 53	99	× 56
89½	× 54	93	× 56	104	× 58
90	× 52	94	× 58		
91	× 54	95	× 53	92.9	× 55.2
91	× 55	95	× 54	(87–104)	(49–58½)

Voous (1957, p. 81) writes: "The eggs are long oval in shape; the shell is chalky-white with broad pori and a rough texture; against the light a yellowish colour shines through." His measurements for 20 eggs from Bonaire are 87.4 × 54.2 mm (extreme length 82.6 and 97.4, extreme breadth 50.8 and 59.1).

Our average, particularly that for length, is therefore somewhat higher, as is that given by BENT (1926) for 41 eggs from various places in the Bahamas (91.3 × 55.4 mm; extremes 85.0 and 99.0, 51.9 and 59.4). ALLEN gives as the longest 103.5, collected by him on Inagua, while the shortest was 82.4 from Andros (CHAPMAN, 1905); the breadth extremes were 49.3 and 59.4 mm.

Clutch size

Voous (1957, p. 81) reports on this matter from Bonaire: "According to local information and the photographs presented to us by various people the nests in the Pekelmeer usually do not contain more than one egg, which, thus, is the full clutch-size. CHAPMAN (1905, p. 59—61), too, found in the rookery of nearly 2000 nests on Andros Island, Bahama Islands, only one egg per nest, except in two instances."

In the Pekelmeer we found twice two eggs in a nest and twice a pullet of 1 to 2 days old with one egg (Plate XV). The 2-egg clutches are there-fore very exceptional, even though ALLEN reports an observation by MAYNARD (1888) that 2½% of the total number of nests (2,000) had 2 eggs and in one case, 3 eggs. GALLET (1950) gives for *Ph. ruber roseus* hardly one per cent of the nests with two eggs. ALI (1945) found only one egg per nest for the same subspecies in India. BROWN (1958) found, in 900 nests, five 2-egg clutches.

Are the two eggs from the same female or is a nest, with an unhatched and deserted egg used for laying another egg? BROWN (1958) gave evidence for the laying of two females in the one nest by way of the difference in size, form and development. On page 401, he writes, how-ever, that "it is definite that the flamingo does lay two eggs on occasion, as in the second breeding colony between April and August 1957 a number of cases were noted where the same parent flamingo was feeding and tending two young about a day apart in age." The two cases of 1 egg plus 1 small pullet may then result from the fact that the pullets have climbed into the wrong nest after leaving their own nest. This is very possible, since the pullets are able to leave the nest very early and then return to it (see Chapter VI h). It is also possible on the other hand, that the egg has not hatched from a previous laying and that a new egg was laid next to it, and which has hatched.

The colony may be visited only with great care and this prevented us from checking the nests further, but we have never seen that a "lost" egg was rolled into (on to) a nest! GALLET (1950) is also of the opinion that this does not take place. We did see quite regularly, on the other hand, large numbers of eggs between the nests and also washed up here and there. This is probably a result of the habit of using old nests, whereby an old egg would be rolled out by the new owner. The eggs may also be washed away at high water, so that we found eggs washed up on the shore some 3 km away from the colony.

On 2.III, 9.III and 15.VII and 22.VII.1960, several tens of eggs were found regularly next to nests in the colony. In some parts this was not the case, however, e.g. on 15.VII in the Middle and South-eastern parts, although this was the case in the North-western colony.

After the breeding season in Goto the majority of the remaining eggs were near to the nests (about 30). They were probably removed by the parent and other birds, and partly by possible flooding of the nests.

It was observed that, at particular times, especially on the 2.III, 15.VII and 22.VII, there were fewer birds brooding, than there were eggs on nests. It was also seen that nests with eggs were left for hours during an alarm and that the birds in question did not return, not even in the following days.

LACK (1954, p. 31) writes: "It is considered that the clutch-size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food." (See also LACK, 1947). In this case, flamingos would be able to find sufficient food for one young only. They are capable of laying more eggs, if they desert one or loose it. Indications for this are given by a female shot in Goto which had three forming eggs of 30 mm diameter and the removal of flamingos from the smaller to the larger colonies, as we saw in June and July in Pekelmeer — the birds having already laid once in their former colony.

PEÑA (1961) reports for the Atacama Salt Lake in Chili that the flamingos there lay three times, due to egg collection. LACK (1954, p. 49) also writes: "In birds clutch-size is well below the physiological limit of egg-production."

g. INCUBATION

Duration

Our observations (Graphs 19 and 20) show that pullets were seen always about 30 or more than 30 days after the commencement of incubation. Since these observations were carried out at some distance, to avoid disturbing the colony, we probably saw the pullets a few days after they really hatched. ALLEN's statement that the incubation period is not less than 28 and no more than 30 days, would appear to agree with our observations. BROWN (1958) gives 28 days as the incubation period, and WACKERNAGEL (1959) reports 29 days for *Ph. chilensis*.

Nest relief

Both sexes incubate, as can be seen from the reliefs. CHAPMAN (1908, p. 180) wrote: "The bird on the nest was relieved late in the afternoon and early in the morning. The one, therefore, which incubated during the day, fed at night, and his or her place was taken by another which had been feeding during the day." CHAPMAN (1905) also states: "there was no relation between sex and the time of day occupied in parental duties, both sexes being represented during the day and hence, doubtless, during the night also." Our observations agree with this: the incubating birds are relieved in the early morning and at the end of the afternoon. The relieving birds generally fly from a drinking place near the colony, and the relieved birds also generally fly to a drinking place shortly afterwards. This often takes place in groups of some tens to a hundred birds.

BROWN (1958) reports that in the beginning of the incubation period a definite morning and evening peak is seen, which disappears later in the period, when the relief takes place throughout the whole day. He also saw the relieved birds going to drinking places. During the relief we often saw birds near the nests searching for food — probably a "displacement feeding" — since there is likely to be a conflict between two contrary tendencies, for example, incubation (to commence or to remain incubating) and for example, attack or flight, because the partners are so close to one another. By many birds we see in this situation a type of displacement nest building.

When the relieving bird starts brooding, the following ritual is usually to be seen. The bird (male or female) stands with the feet on the edge of the nest, often moves the egg, and then slowly folds its legs at the ankle and knee joints, coming with the breast on top of the egg. This is then followed by the "arranging" of the egg, sitting with a jerky movement, to arrange the egg against the incubation spot (on the breast). The legs are then doubled, next to the body, but they are so long that the tarsus and metatarsus can be clearly seen in the incubation position. The ankle joint often sticks out beyond the tail.

Behaviour

An incubating bird may, in addition to incubation proper, and sleeping, exhibit various types of behaviour: drinking, nest-building, standing up, and agonistic behaviour. It was observed several times that incubating birds drink while sitting on the nest. This occurred in the South-eastern colony only, were an "eye" of sea-water rose. Between the nests in the North-western colony we sampled water on 22.VII. 1960 and found it to contain 100.0 g Cl/l and in the South-eastern colony this was 41.5 g Cl/l. The waterlevel was fairly low (i.e. for the sea) so that the "eyes" provided little "fresh" water and it is clear that with a higher sea-level more "fresh" water (20 g Cl/l) enters through the eyes, and which is then potable for the birds. We also saw small cyprinoids swimming between the nests, which indicates less salt water. Is is also possible therefore that the flamingos eat a small fish, or something similar, while sitting on the nest. ALLEN (p. 175) saw nesting flamingos drinking after rainfall, and also that they brought water on to the edge of the nest or on to the egg.

During incubation nest-building also takes place, the results of which may be clearly seen, for example, at the base of the nest. The incubating bird then hangs over the edge of the nest and works with its long neck until some soft building material in the neighbourhood can be reached. The bill then takes some of this and, in some way or other, makes small clay balls of it, which are found in tens at the foot of the nest at the end of the incubation period; they provide hardly any increase in the size or strength of the nest, however (Plate XIV*a*). We must see this as "displacement building". Whenever there is a conflict situation between two antagonistic tendencies, such as remaining incubating or leaving the nest (or agression and/or flight after conflict with neighbouring birds), we may expect this behaviour to occur. This displacement building is known from numerous incubating birds (see, for example, BAERENDS 1959, MOYNIHAN

1953, VAN IERSEL & BOL 1958). ALLEN (1956, p. 175) has also observed this behaviour from the Bahama Islands.

If there is much wind, the incubating birds usually sit head-to-tail, with the head in the wind.

Agonistic behaviour between incubating birds often takes place in the colony, usually in the form of bill-fighting and threatening, during which the necks make turning and twisting movements to seize and avoid being seized. The feathers on the back and shoulders are then on end. GALLET and ALLEN believe this to be due to the wind, but BROWN (1958) and ourselves have seen this during calms and even against the wind (see also MORRIS 1956). CHAPMAN and ALLEN report bill fighting ("bickering") also, but ALLEN suspects that the Camargue flamingos are more agressive according to the descriptions of GALLET (1950) and YEATES (1950): GALLET giving a photograph of a wounded bird! This would appear to be contradictory to the greater density of nests in *Ph. r. roseus*, found in the Camargue by SWIFT (1960), in comparison with the lower density in *Ph. r. ruber*. A greater distance between nests can, in fact, indicate a higher aggressivity between birds. This is so, for example, in the series Sandwich Tern (*Sterna sandvicensis*), Common Tern (*S. hirundo*) and Little Tern (*S. albifrons*). The distance between nests increases in this order and the mutual aggression and also to predators follow parallel to it.

Now and then the flamingos rise from the nest, whereby the bill is usually employed as a third point of support, although the wings often assist also during this "three-point" elevation. At the start and end of the incubation period, many birds stand in the colony (Graph 19) and this happens regularly during the incubation proper. We had the impression that this occurred in particular just before their relief. It is possible that 1) the internal conditions were not very suitable for incubation, e.g. due to competition with other behaviour patterns or, 2) that the eggs were too warm, so that the incubation — due to the absence of the correct "feedback stimuli" (BAERENDS 1959) — is insufficiently activated. The eggs may also become overheated when, for example, the birds leave the nest in alarm. Our temperature measurements in nests in an old, deserted colony do not indicate that this may be the case, however.

On May 27th a maximum-minimum thermometer was placed in an old nest, with the following results:

27. V — 3. VI : 38.6 and 27.5° C   17. VI — 1. VII : 38.4 and 22.2° C

3. VI — 17. VI : 36.9 and 21.1° C   1. VII — 15. VII : 42.0 and 22.0° C

BAERENDS (1959) gives a number of figures for the temperatures of eggs during incubation — amongst others those of GROEBBELS (1937), from which it appears that the most usual temperature for eggs with normal development lies between 35 and 39° C. According to our observations the temperatures exceed this value only seldom and a bird standing above the egg will lead to its cooling-off. This behaviour is then probably caused by the "feedback stimuli" which then are absent, since the eggs are too warm.

Sleeping, naturally enough, often occurs during the incubation period.

During an alarm the birds stretch out their long necks and if the danger remains imminent they stand up and walk from the nests with extended necks and then leave the colony. In the case of a rapidly approaching danger (aeroplane) they then fly away and in the case of one which approaches slowly (e.g. man, goat or donkey) they walk away from the intruder. There is no aggression against such intrusions and neither the eggs nor the young are defended. On their return, the birds move the eggs. It was seen rarely that birds which had incubated much too long on an egg, did not return after an alarm, so that it is apparent that the incubation tendency was no longer very strong.

h. YOUNG

Hatching (Plate XIV)

Hatching takes place in the same way as for other birds, as can be seen from the descriptions of CHAPMAN (1905), GALLET (1950) and ALLEN (1956). BROWN (1958) reports that the young bird takes at least 24 hours to hatch and free itself from the egg-shell. ALLEN mentions 40—60 minutes to 2 hours for the same process.

During the hatching one of the parents is usually at the nest, but after this has happened, they frequently sit on the nest and the young often sticks its head out under the wing of the parent. Quite often it is fed in this position also, although this mostly takes place while standing.

First food

ALLEN (p. 178—179) writes on this subject: "Both Gallet and Yeates make something of a mystery of this initial food. Gallet (1950) describes it as "a simple viscid mucus" and wonders if it bears any similarity to "the delicate milk with which the pigeon supplies its young." He thinks that it may be a secretion of "sweet water" of a nourishing quality that is required by the chick's "embryonic organism" in the salt-encrusted regions in which flamingos are born. Yeates (1950) speaks of it as "a most indeterminate substance" and describes it as "a white liquid, which may be produced by some form of regurgitation". .... Chapman was more definite. He said that this food "consists of a blackish liquid, doubtless the juices of partially digested *Cerithium*".

LANG *et al.* (1962) examined this foodstuff in *Phoenicopterus ruber* in the Zoo in Basel: "These examinations revealed that this liquid is not regurgitated predigested food but a secretion produced by a yet unknown tissue. It is red, contains blood and a rich amount of carotenoids ... as to its nutritional value, it can be compared to the milk of mammals."

We could see that the first food provided was fluid, by the behaviour during feeding. After this was finished, the parent bird assumed a posture as after drinking, it would seem to allow the foodstuff to run back again! The composition of the initial food remained unknown to us, since we were forced to work at some distance from the colony.

CHAPMAN, GALLET and BROWN reported that the young consume the fragments of egg-shell in the nest; we have never seen this, however, and

have also found many fragments in and around the nests. We even found many remains in the nests themselves — and these nests had been used many years before! We do not have the impression, therefore, that this source of calcium is used to any large extent; it would seem that the older birds make little — if any — attempt at removing the remains of the eggs.

Leaving the nest

CHAPMAN (1908) writes: "The young stay in the nest until they are 3 or 4 days old. During this time they are brooded by the parents one or the other of which is always in attendance." GALLET (1950) remarks: "After a few hours the chicks leave the nest and become at once quite expert swimmers." BROWN (1958) saw them leaving the nest after 2 to 3 days, but they disliked swimming for the first 10 days.

Our observations agree with those of CHAPMAN, although we have seen (as he did) that younger birds of about 1 day old left the nest, since they tumbled over the edge, or because danger was in the offing.

CHAPMAN and GALLET write that, when there is danger (e.g. the approaching of people to the colony) all young, however small, leave the nests and walking or swimming, leave the area. We saw, however, that tens of small young of a few hours to several days old remained on the nests when we entered the colony, often pressing themselves down into it, or often sitting next to the nest proper (Plate XVIIb).

When the young have left the nest, they are able to climb back on to the (for them) relatively high nest-cone with the help of the bill, feet and wing stumps, and we have frequently seen this exhausting activity. CHAPMAN (1908) has also reported this.

GALLET has marked young birds with strands of wool around the feet and, after a disturbance, these were completely mixed with the others. On some nests there were 2 or 3 young and when the parents return they peck until only one young is present. According to GALLET, it is not important if it is the original young bird, or not! This contradicts CHAPMAN's remark (1908) where he says that the young birds are recognised by their parents, and that they are lured back to their nests by noises produced by the older birds: "the parents evidently recognised their own offspring and when a youngster lost his way his nape was promptly pinched by every old bird within whose reach he came, a method which was effective in keeping him on the move until he found his own home." He writes, however, that the young birds probably do not recognise their parents or their nest.

We have seen little signs of aggression against the pullets, who run around at first in a small area only, a few meters from the nest; during this period they do not suffer any attacks from older birds, as far as we could see. We also have the impression that they are left alone in this early stage and that this was possible, simply because there was no aggressive action from other birds. It is true, however, that both the parents and the young are sometimes mutually aggressive to one another.

The young, of a week's age, are able to "bicker", just like the adults and CHAPMAN interpreted this as mutual feeding, but we are convinced that this is bill fighting, as is GALLET, who has described the same from his observations.

After a few days the young birds wander between the nests, and then also come outside the colony. The older they are, the greater is their sphere of activity.

Leaving the colony

After about 4 to 6 weeks the young are seen several hundred meters outside the colony, although we do see birds of up to 2 months old which remain within the neighbourhood of the colony.

In the Pekelmeer they gathered usually along the eastern shore and only when they are 2—3 months old, are they to be seen along the western side and at other places in the Pekelmeer. In Goto they remained some 2 to 3 months on the breeding island, even though they are able to swim at an early age (1 day).

In the case of an alarm, they come together in various groups, while we see that these are formed of young of roughly the same size. In this way there arise 3, 4 or 5 compact groups of pullets of the same size, which disappear rapidly walking or swimming in different directions. Sometimes this was so for a large group of some 1000 pullets — with the largest in front and smallest (who could not keep up with the high speed of the older young) straggling behind. The larger young show much wing flapping at the same time, which may result in broken wings in the larger groups (see Chapter VIII). The groups usually walk into the Pekelmeer, although they may first traverse a distance along the shore. They remain active as long as there is danger, so that different groups may well pass through one another, with a resulting chaos of young birds. The young make no special attempt to approach the groups of parent birds which have left the colony and now nervously walk back and forwards some tens, or even sometimes hundreds of meters away.

We saw such reactions occurring whenever an aeroplane passed overhead, something that happened quite frequently. It also occurred when a Brown Pelican (*Pelecanus occidentalis*) landed in or near the colony. MIDDLEMISS (1958) reported also that young pelicans may disturb the flamingos. We have no indications, however, that these pelicans do any damage to eggs or young birds. When a pelican sat down in a colony, all nests in that area remained unincubated; fortunately, this did not happen very often. The flight reactions also appeared when goats or donkeys came into the neighbourhood of the colony. This does not happen very often, since there is nothing to eat in these salt flats. The reactions also took place each of the four times that we visited the colony.

If alarm stimuli occur rapidly one after another (with intervals of, say, a few tens of minutes), the flight reactions are then progressively weaker,

but after a long interval without an alarm, the reactions are once more strong and last longer also. These were, however, stimuli of comparable strength — e.g. aeroplanes, flying at the same height, etc.

A number of times we have experienced that there was a "leerlauf" flight reaction by the young birds (LORENZ 1937) or, what TINBERGEN (1942) has called "vacuum activity", since there were no alarming stimuli recognisable in the neighbourhood of the colony. This is probably an example of threshold value raising or lowering, respectively.

Older birds sometimes remain with the young and BROWN (1958, 1959) speaks of "nurse maid" adult and "aunties" just like those known in *Somateria mollissima*, the Eider Duck. These occur in a ratio of, in the beginning, one for 10 young, later one for several hundred young. We also saw this several times in Goto in particular, when the young — at our approach — left the island and swam away. Such groups were accompanied by an older bird or birds. It is not clear which birds play the role of "aunties" or accompanying birds — are they a number of parents, or are they birds which are not involved in reproduction? They are certainly fully coloured.

"Crèches" (Plates XVI*a*, XVII*a*)

The occurrence of large groups of young birds during an alarm and that of the numbers of accompanying birds as reported by e.g. McCANN (1939), ALI (1945), GALLET (1949), LOMONT (1954), ALLEN (1956) and BROWN (1958, 1959), are probably responsible for the introduction of the word "crèche" in flamingo literature. In connection with this is the problem how and if the parents can recognise their young and vice versa.

ALI (1945) believes that the young after leaving the nest, do not return to it, or to their own parents. He comes to the conclusion: "the community is run on a communistic basis, and adults feed young more or less indiscriminately. No other course seems imaginable."

SWIFT (1960) writes about this rearing of young in groups: "This synchronisation by speeding up nesting and enabling the young to be reared in large groups gives protection against predators, and thus has survival value. Few chicks hatched more than three weeks after the main group survive."

Other authors are also inclined to ascribe survival value to the crèche system, partly because isolated young will have more trouble from predators than the compact groups. When the young walk haphazardly during an alarm, the situation for a predator in the air is comparable with that of a sparrow-cloud for birds of prey — it makes concentration on one individual for capture much more difficult from the whole moving mass.

LACK (1947) says of crèches, such as those occurring in Tern colonies: "It may be tentatively suggested that the crèche habit is really an adaptation to a variable food supply and that, like asynchronous hatching in a hawk brood, it facilitates the survival of a proportion of the young during a food shortage, when otherwise many more might starve." Concerning the Emperor Penguin (*Aptenodytes forsteri*) in Anarctica LACK comments: "as Wilson's observations suggest, that, under these extraordinary conditions one chick is more than two parents alone can raise succesfully, and the crèche system results in the feeding of the chick by a group of adults." LACK further writes of the crèches seen by the Shell Duck (*Tadorna tadorna*) and the Eider Duck

(*Somateria molissima*): "In ducks the main function appears to be protection from predators, on the analogy of a convoy system. The larger the group, the smaller the length of perimeter which each parent (escort) has to patrol."

TINBERGEN (1953a) and VAN DEN ASSEM (1954) report for the Sandwich Tern, however, that it is their experience that, although the young assemble in larger groups, they are still fed by their own parents.

If we examine critically the crèche phenomenon in flamingos in connection with the possible advantages mentioned by LACK (1947), it appears: Firstly, that the hatching of the eggs is not necessarily synchronous and, Secondly, that protection against predators by the adult escorts does not occur and that there are often no escorts at all.

It remains possible that one young may be fed by a number of older birds. I doubt very much that this is true and believe that the young flamingos are fed by their own parents. In this way the value of the concept of crèche is dubious in the flamingo, since it would appear that none of the functions of a crèche-system are in fact present. The only function which now remains is that the reduction in the predatory potential from the air. It is striking in this connection how markedly both old and young flamingos are disturbed by passing aeroplanes.

Feeding of the young

ALI (1945), GALLET (1949) and ALLEN (1956) believe that the old birds feed every hungry and begging young and that they do not recognise their own young. CHAPMAN (1908) states that the parents do recognise their young and BROWN (1958, 1959) also has evidence for this and is supported by HOFFMANN.

BROWN (1958, p. 411—412) writes: "On 1 September the adults arriving to feed young between 5.30 and 6 p.m. came in small and large flocks, which, on arrival, did not alight together, but split into smaller flocks and groups and alighted in particular parts of the colony. Individual adults were not importuned by large numbers of young as one would expect if feeding were indiscriminate, but appeared to walk purposefully up to a particular chick and feed it. One in particular walked up to an outlying broken-wing casualty and fed it. Even more striking, on 8 September 1957, at close range from my hide, I observed a very large adult, probably a male, alight near a herd of some 800 young, and begin to call loudly as it walked towards them. None of the large herd of young paid any attention to it, but an isolated young one feeding among another group at least a hundred yards from the adult started to hurry towards it, answering the adult call for call as it came. This calling young one ran right through the flock of 800 other young, and was at once led out into open water by the adult, which then delivered a feed lasting 18 minutes. Other observations on the same day confirmed that at this late stage of the chick's life, just before they became independent immatures, the adults did not indiscriminately feed any chick that solicited."

We too have evidence that the adults feed their own young: 9.III - During feeding a second young came begging, but was not fed. The adult went on feeding the same young, and the other then went away. 27.V-15.00 h. - One juvenile begging with a bent neck (see Fig. 20). He is already quite large, about 1.20 m. He keeps begging by the same male. The young makes a high-pitched rolling and chirring noise, presses his

head, neck and back against the neck-base of the adult. Once in the begging position, he seizes the bill of the male adult who then walks backwards, being followed by the young. The older bird sometimes walks quite a distance away, but the young is able to find it between 290 adults and 275 subadults in various plumage stages, with 130 young in one group. The older bird flies away over the young, which once more follows and appears to continue begging in flight to judge from the noises made.
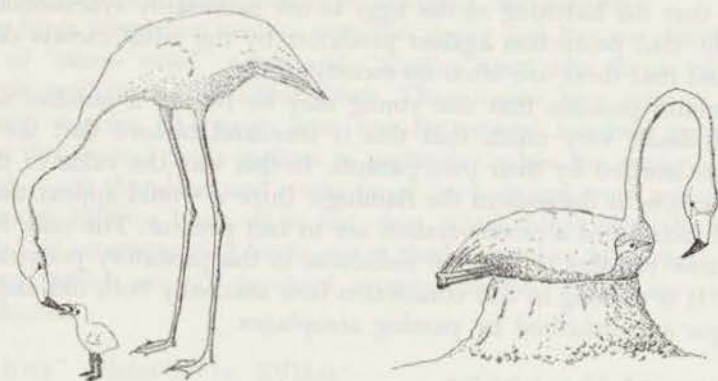

FIG. 19.   Feeding of pullets.

WACKERNAGEL (1959) reports that a young *Ph. chilensis* in the Basel Zoological Gardens was fed by its parents for 6 months, and that no other birds showed any tendencies to feed it. LANG (1961) reported further on these flamingos in Basel where in the meantime *Ph. ruber roseus, Ph. ruber ruber* and mixed pairs between both subspecies were reproducing. These young were also fed by their parents only, and also until they were about six months old. A hungry young walks calling through the whole troop of birds until it finds its parents and then begins begging. In the case of the Basel *Ph. ruber roseus*, the first 3 weeks the young received a red fluid.

Begging is carried out as follows: The young make a high chirring noise, when the wings (at first the wing stumps) are moved up and down, the birds facing each other often. The young stretch their necks, and in the later stages the head, neck and back are pressed against the neck-base of the adult bird and against the breast by way of an alternating raising and falling of the head (Fig. 20). The parents must at first to all intents and purposes place their bill nearly on the ground to be able to feed the young, or — better — to allow the young to "wedge" its bill points around the top of the adult's bill. When the young reach 120 cm (about 4 months old) feeding sometimes still takes place; here the adult does not have to bend its neck and it can feed the young while standing up straight (Fig. 20).

In contrast to the begging situation, where parent and young may stand differently with respect to each other, in the feeding position, the situation is always the same. The older and younger bird always stand parallel and

in the case of very small birds, it may stick its head out under the parent wing while the bird sits on the nest, and be fed in this position. CHAPMAN called this "breakfast in bed" (Fig. 19). Even in the case of these very small birds, however, feeding may also be observed in the standing position, whereby the adult bird towers above the young.
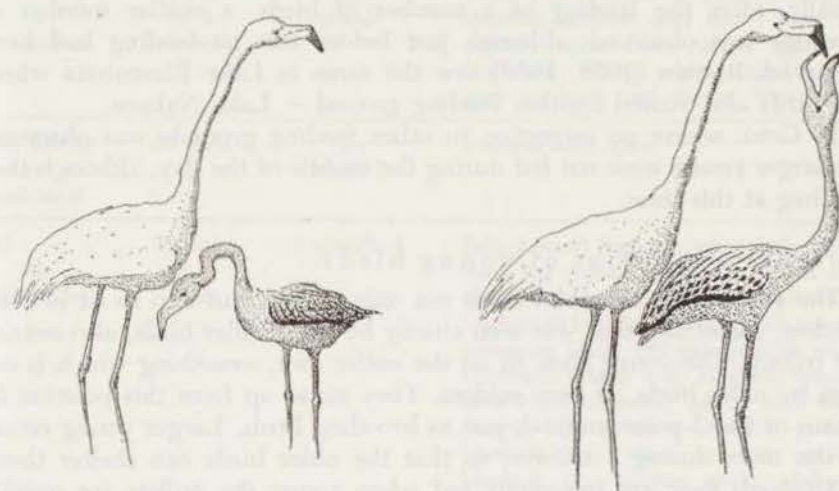
FIG. 20.   Begging (left) and feeding (right) of juveniles.

Only if the parent and the young are parallel to each other is it possible for the older bird to bring the food from its curved bill into that of the young. If the older bird and its young were to face one another, the point of the adult's bill would indicate itself as it were, and the young could never fasten its own bill on to it. This method is still successful, when the young's bill begins to curve also (after about 3 weeks.)

Duration and frequency of feeding

Very young birds (a few hours to a few days old) are fed very frequently sometimes 7 times in 5 minutes. One feeding then lasts a few to several tens of seconds. BROWN (1958) saw feeds which lasted 5—15 seconds at this stage. The feeding frequency falls off rapidly with time and we had the impression that for pullets of a few weeks, they were fed twice only per day and later once only. If they are 2 to 4 months old, then the feeding rate seems to be once in every few days, but these feeds take longer; juveniles of about 6 weeks of age (ca. 75 cm long) the feeding proper lasted 8—12 minutes, with a maximum of 15 minutes. BROWN (1958) noted for older young 11—18 minutes; LOMONT (1953) also noted once a feed of 18 minutes for a young already capable of flight. LAND (1961) mentions 12—15 minutes.

When the young bird is somewhat older, the number of feeds in the daytime is reduced. There are then two definite feeding periods, i.e. early morning (between 7 and 10 o'clock) and in the late afternoon (after 4

o'clock). It is not certain if this is universal, since in this period with larger young, many older birds leave at about sundown, returning in the morning, or leave in the morning, returning in the evening, probably visiting the feeding grounds in Venezuela (Chapter VII). When one of these returning groups approaches, the begging noise in the colony is much amplified and usually, after the landing of a number of birds, a similar number of feedings was observed, although just before this no feeding had been observed. BROWN (1958, 1959) saw the same in Lake Elmenteita where the birds also visited another feeding ground — Lake Nakuru.

In Goto, where no migration to other feeding grounds was observed, the larger young were not fed during the middle of the day, although they did beg at this time.

Further activities of young birds

The young visit the older birds not only to beg, but also to sit in their shadow, something that was seen chiefly by the smaller birds, also outside the colony. The young then sit on the entire foot, something which is not seen by older birds, or very seldom. They stand up from this position by means of the 3-point method, just as brooding birds. Larger young return to the nests during a shower, so that the older birds can shelter them.

Although they are frequently fed when young the pullets are quickly able to fend for themselves and during the first few weeks of life, when the bill is still straight, they use this as a seizing instrument. We have also seen small juveniles using the methods of food-searching — circling around the bill and stamping with their feet (Chapter Vc 4–5). The young birds gradually are forced to search more and more for their own food, simply because the feeding frequency of the older birds decreases.

Flying

The first attempts at flying are seen when the young are about 6–7 weeks old and about 80 cm long. They carry out a number of springing movements whereby they beat with the wings. They are fully able to fly when they are 2–2½ months old and the final migration begins after 3 months (Graph 21, Chapter VII).

LOMONT (1954) reports that they are fledged between 65 and 75 days, although BROWN (1959) mentions 62–75 days for *Ph. ruber roseus*. WACKERNAGEL (1959) gives 12 weeks for *Ph. chilensis*.

Plumage and moult

The data given by CHAPMAN (1905) concerning the first plumage of the young birds agree with our own observations (Table XI).

We would add to this, that in the 1st stage for at least the first few weeks, the bill, legs and feet are orange and that at the end of this stage and in the 2nd, this becomes greyish brown, while in the 3rd stage the legs and feet are brownish black and the bill is then light brown with,

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TABLE XI. DATA ON THE MOLTS according to CHAPMAN and ALLEN (p. 14).

Plumage	Approx. age	Approx. duration	Description
1st downy or natal	birth to 1 month	one month	thick down released from waterproof sheaths; uniform over body; lores and orbital region bare; upper half tibia feathered; snowy white tinged bluish-gray on back and crown. This varies.
2nd downy or post-natal	28 days	two weeks ?	uniform ashy gray.
3rd or juvenile	35 days to adult	7 months ?	fully formed feathers; when fully developed the colour is grayish brown with tinge of pink on under parts and wings; feathers of back have black shaft streaks; primaries black; tail pale pinkish white, externally edged with blackish; secondaries black internally edged with white except tip; primary coverts pinkish, blackish tip; other coverts pinkish, blackish tip; axillars pink; abdomen pinkish washed with brown.

in particular at the base of the upper mandible, a trace of yellow and the beginning of the black bill point (Plate XVIII*a*).

In addition to the juvenile plumage we could distinguish the following subadult plumages:

Juvenile, with a transition to the greyish white plumage, which has itself a transition to the plumage we called "à la Camargue" since it resembles *Ph. ruber roseus* so closely. This stage has another transitional form to the fully-coloured adult plumage. In addition to these there was also orange brown variety.

The juvenile plumage agrees with CHAPMAN's description (see above). As far as we could see, the young birds retain this until they are 6–10 months old. After 6 months the grey areas gradually lighten so that after about 10 months a lighter form can be seen, which we have called the "grey-white". The bill is somewhat pale rose, and there are large white patches. The back, wings, neck and head are still light grey, however.

In this variety, various light grey areas slowly change into white or very pale pink. The body and wings have little of this colour, being still grey-white. The head and neck are no longer grey, however, but white to pale pink. The legs and feet, which were still grey-brown in the grey-white stage, now become pink. The bill is now pale rose with a black tip.

The "à la Camargue" stage now follows, whereby the grey-white is replaced by pale rose patches, while the pink on the wings gradually darkens.

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This is then followed by the transition to the adult plumage, the pink on the wings becoming orange-red. The lower half of the neck becomes first red, while the rest of the feathers remain pink, as are the bill, legs and feet. This is thus the *Ph. ruber roseus* plumage, but with an orange-red "collar". .

In the a d u l t plumage the pink feathers are finally replaced by orange-red, and orange appears in the bill between the yellow base and the black tip. The legs and feet are a dark pinkish red.

In this series we therefore see a gradual transition. In addition to this, however, we could distinguish another plumage, that of the b r o w n-o r a n g e t y p e. The head, neck, breast, back and under parts are brownish with an orange-red underlay. The wings may, however, be of a fine orange-red and black, as in the adult birds, but it is also possible that in the red areas on the wings, dark and light patches can be seen. The legs and feet may be grey-brown, brown-black and sometimes pink as well. The bill is yellow, orange and black as in other adult birds, and the iris is yellow.

It is difficult to place this plumage in the series with transitions mentioned above. It is possible that these birds are adult, but are about to moult completely, although the colour of the feet would suggest a younger stage, but this does not agree in turn with the fully coloured bill. These birds were not endemic in Bonaire, and did not stay long there either (Chapter VII), so that we did not see any possible changes in the plumage.

Apart from this latter type, the gradual transition between the other types would indicate that here is no general moult. We have seen a more or less symmetrical moult in the primaries in spring. McCann (1939) supposes also that there is no general moult, but a general colour-change from the bottom of the feather shafts. Bent (1926) reports a "continuous molt from the juvenile into older plumage, which is unmistakably immature. This transition plumage might be called the first winter or the first nuptial plumage, for it covers both seasons, but it represents a constantly changing progress toward maturity." He continues further: "During the summer a complete molt takes place at which time the young bird assumes the adult plumage, or closely resembling it, in which a few signs of immaturity may be retained in the way of dusky shaft-streaks or dusky tips in some of the wing coverts." The latter is the only description in the flamingo literature in which we can make a comparison with the brown-orange type. There is nothing (or next to nothing) to be found in the whole literature concerning the other plumages between juvenile and adult. Brown (1959) writes: "All that one can say so far about the nuptial moult in flamingos is, that it may not occur at all and if it does it can equally well before and after breeding. Could anything be more contrary?"

Lang (1961) reports that the young *Ph. ruber roseus* at one year have black patches on the back feathers and when they are two years old, they still have traces of brown back feathers. Their legs and feet are then still

dark and the bill and feathers less coloured than in the older birds. In the third year, *Ph. chilensis* is still not fully in colour. It is, in the absence of ringing data, very difficult to make out the age at which the various subadult plumages appear. Allen (1956, p. 72) writes: "The flamingo attains its adult plumage by the end of the first year and probably is capable of breeding during its second year."

On the basis of the various subadult stages with gradual transitions between them and the age at which the juvenile plumage still occurs (6–10 months), after which the grey-white plumage is seen, we must disagree with Allen's views on this matter. We suggest that several years are necessary before the birds are fully coloured and can begin reproduction. We saw fully coloured birds only engaged in reproduction. The data given by Lang (1961) for captive birds also indicate that several years are necessary before they reach full colour. According to him, a specimen of *Ph. chilensis* was at three years old still not fully coloured. Ring data collected by Hoffmann (1957) in the Camargue suggest for *Ph. ruber roseus* that they are sexually mature at 5 to 6 years old. It would seem to me on the basis of the foregoing, therefore, that this is the most likely for *Ph. ruber ruber* also (see further Chapter VIII).

VII. NUMBERS AND MIGRATIONAL MOVEMENTS

From the beginning of September 1959 to the end of July 1960 the numbers of flamingos in the Pekelmeer and neighbourhood, in Goto and in Slagbaai were counted differentially as to adult, various sub-adult stages, juveniles and pullets. Other areas were visited incidentally e.g. Salina Tam, Playa Frans, Boca Bartool, Playa Lechi, Lagoen, Lac and the salinas on Klein Bonaire. These areas were not, however, so important for the flamingos, although in most of them birds will be seen at times: in small numbers and for short periods only.
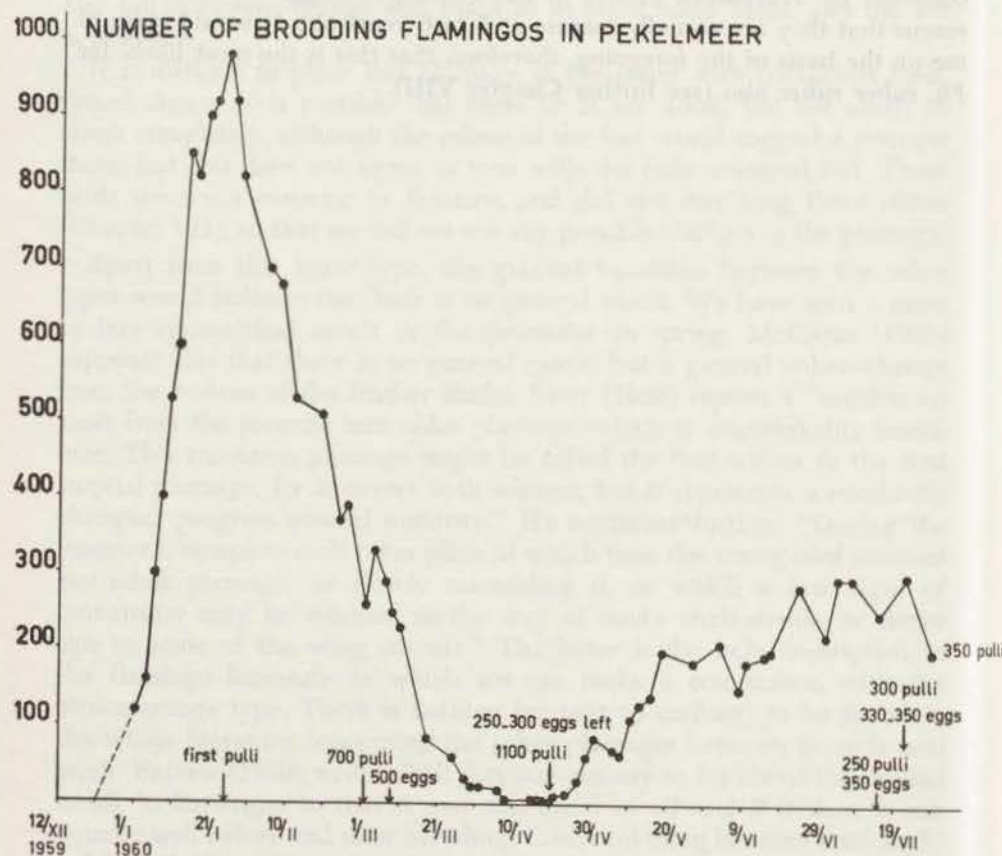
GRAPH 20. Number of brooding flamingos in Pekelmeer. — The numbers of pulli and eggs, which were checked during the short visits in the colony, are indicated.

Graph 21 gives the number of adults and juveniles for Goto and for Slagbaai as one figure in each case, since the number of juveniles was never large. The number of pullets in Goto has not been given separately since on the scale used, they would hardly be noted. In the case of the Pekelmeer the number of young has been reported, with a differentiation between the young from the first breeding period (from the end of December to beginning of April) and those from the second (which began at the end of April). This arrangement is somewhat artificial, since in fact breeding was more or less continuous from December to August. There is, however, a definite minimum between the beginning and the end of April (Graph 20) and this enables us to differentiate between the young of the two periods mentioned, a necessary procedure in connection with the migration of the juveniles. In Graph 21 the adults and subadults are summed; the occurrence of subadults was chiefly restricted to the period from the end of April — details are given in the text.

From time to time the three most important areas were visited on one and the same day. Thus we could obtain a total figure for the flamingo population of Bonaire. In daytime resettlement from one area to another was never observed, so that the possibility of double counting was excluded.

By summing in Graph 21 we see that the total population fluctuated between a minimum of 440 flamingos (with 410 adults) to a maximum of 4,130 (3,000 adults). With the use of large glasses and re-counts, it was possible to reach a high standard of reliability. It is often possible to count such large birds individually and the agreement between counts was striking.

After considering the total counts, we shall also examine the subdivided counts for each area.

ADULTS

In the Pekelmeer we see that after beginning with 400 adults, a gradual decrease took place to 146 birds on 13.XI.1959. This decrease was even more marked in Goto, where on 26.X.1959 a minimum of 16 adults (and 9 juveniles) was reached. In Slagbaai the number of birds in September and October was relatively constant and then decreased rapidly from November to the middle of December and in February they were totally absent. After this the flamingos return very gradually, when the number hardly passes the 100.

The decrease in September and October is then to be found in all three areas.

In the course of November there is an increase to be seen in Goto once more which continues with a number of fluctuations until the 25th of May 1960 with a maximum of nearly 1,100 flamingos is reached.

The Pekelmeer shows from the middle of November a fairly marked increase, which with a number of fluctuations reaches a maximum of 2,300 adults on the 19th of February 1960. After this maximum figure we see a

NUMBER OF FLAMINGOS

3000
2000
1000

Pekelmeer ad.
  "   juv. 1
  "   juv. 2
Goto   ad.+juv.
Slagbaai ad.+juv.

31/VIII 1959
20/IX
10/X
30/X
19/XI
9/XII
29/XII
18/I 1960
7/II
27/II
18/III
7/IV
27/IV
17/V
6/VI
26/VI
16/VII
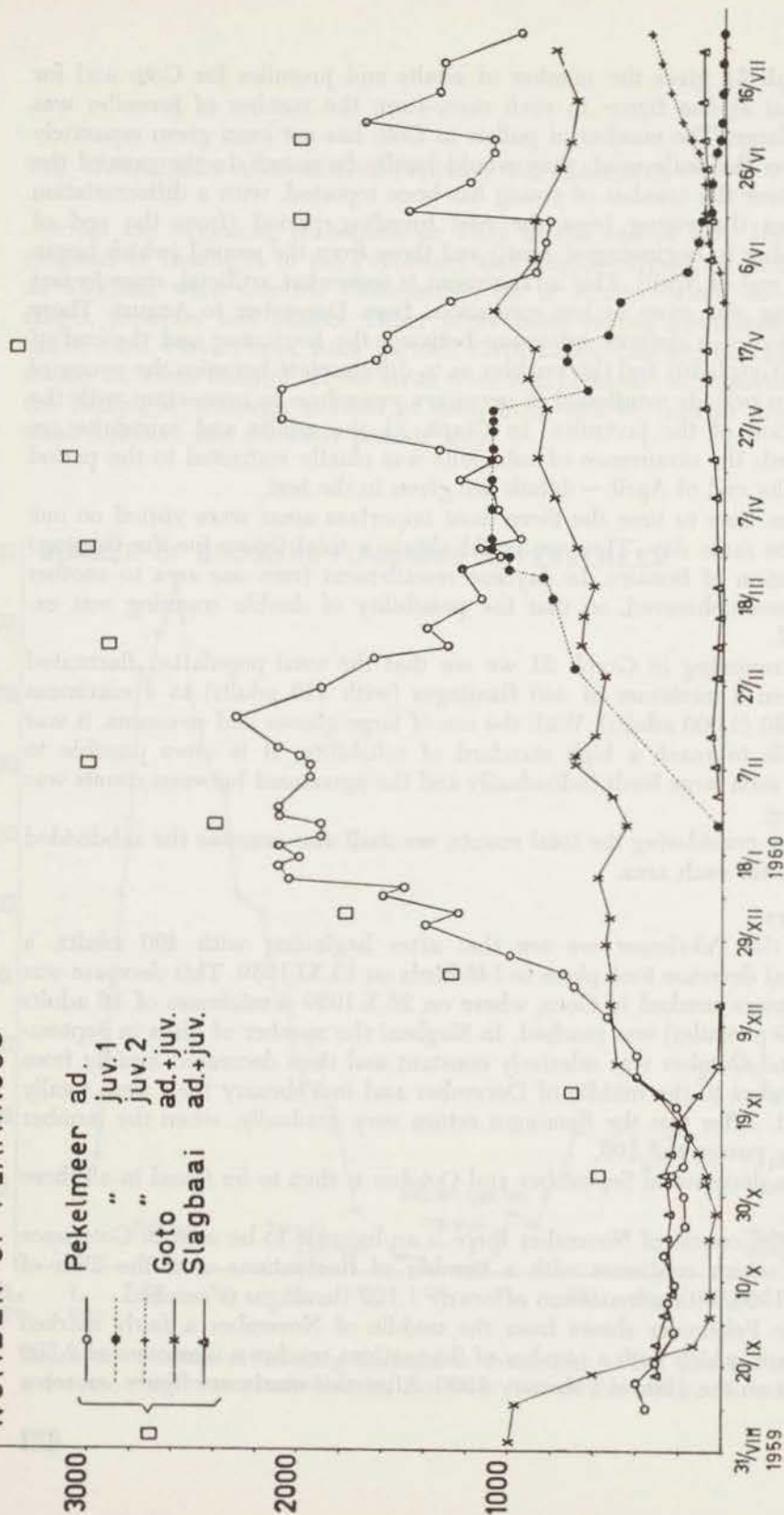
GRAPH 21. Number of flamingos in Pekelmeer, Goto and Slagbaai. — Total numbers of Bonaire and the young birds of different ages in Pekelmeer are indicated separately. The curve from 0—700 should probably have a steeper slope (cf. Graph 20), as a result of the difficulties of counting the young when they stay between the nests.

sharp decrease, reaching a minimum on 1.IV.1960 with 960 adults. After a number of fluctuations a second maximum is reached in the period 29.IV.1960—6.V.1960, with a total of 1,600 adults (the Graph gives 2,100, but this includes 500 subadults). There is then once more a decrease followed by two small peaks — 17.VI.1960 with 1,350 adults (150 subadults) and 8.VII.1960 with 1,660 adults (40 subadults).

The first maximum of 1,900—2,300 adults coincides with the great breeding activity of maximal 980 pairs. The following peak (end April—begin May) is very high in comparison to the 200 breeding birds then seen here, while the juveniles were not being fed to any large extent and were partly already away from the colony. The two lower peaks in June and July are also high, in comparison with the maximum of 300 breeding birds.

In the first period there were few or no flamingos which did not take part in the reproductive activities and during the last three maxima there were many flamingos present, which did not take part.

Apart from the fact that we have to do here with both emigration and immigration in the population, there is also a food-migration (Chapter VI h), i.e. there are birds which either in the early morning or the late afternoon reach Bonaire over the sea in a southern direction and which usually fly directly to the colony and begin feeding the young. On the other hand, we also saw — especially at the end of the afternoon and once in the moonlight — that several tens or hundreds of birds left in a southern direction via the southern point of the island. We suspect that these birds search for food in Venezuela and seeing the southern departure and arrival direction, it would appear reasonable to assume that this is an area in Venezuela due south of the southern part of Bonaire.

We know from correspondence with Messrs. W. PHELPS and G. YÉPEZ (Caracas), that the flamingos in Venezuela have been seen for example in an area due south of that part of Bonaire in a mangrove swamp near Tucacas in the area Chichiriviche. This area is situated about 140 km to the south of Bonaire. We have measured the flying speed of flamingos with a car — once only — and found a value of 50—60 km p.h. with side-wind. ALLEN (p. 35) reports two observations on the flying speed (without wind), one from Switzerland of 60 km p.h. and one of about 40 miles p.h. from the Bahamas (i.e. slightly more than 60 km p.h.). It can be seen therefore, that the flamingos could cover this distance in 2 to 3 hours leaving from a period of 12 hours about half or more for foraging. Before setting off the flamingos can often be seen bathing and drinking. It is striking that the chief flight activity was noted after about 15.30 hours.

In the 40 times that we were present at the southern point after 15.30, we saw departure 27 times. The directions were usually S, twice SW and once SE. It is possible that these three groups veered around after to S, but always the direction was followed some time over sea. The birds hesitate as they cross the sea wall, they then ascend, circle for a time and fly some distance from the coast. The group usually splits and part of it,

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TABLE XII. OBSERVATIONS AT THE SOUTHERN POINT OF BONAIRE

(the only departure point that we saw) on days when we were present after 15.30 hours and the time at which there was activity or not. — In addition, incidental arrivals are noted with times and directions plus a number of movements on the island.

Date 1959—1960	Time of observation	Number	Direction of departure	Direction of arrival and movement on the island
18.XII	15.30—17.00	40	SW	
16.IX	appr. 18.00	75	SW	21.30 heard over Kralendijk
21.XII	16.30—17.15	—		
1.I	16.15—16.50	127	S	
4.I	16.30—17.30	—		
6.I	16.30—17.00	40	S	
7.I				9.55 50 from S
10.I	16.00—17.00	—		
12.I	16.30—17.00	40	S	
15.I	17.15—17.30	125	S	
17.I	15.30—17.30	148	S	
20.I	15.30—17.30	—		
22.I	16.30—17.30	24	S	
25.I	appr. 17.00	—		
27.I	16.15—16.45	90	S	
29.I	15.30—17.30	165	S	
3.II	15.30—18.00	departure	S	
5.II	16.00—17.30	80	S	
8.II	17.20—18.00	—		
10.II	16.30—17.40	100	S	
12.II				8.00—10.00 30 to S (no return)
19.II				8.15 150 from SSE (relief)
25.II	17.00—18.30	—		
7.III	16.30—17.15	—		
10.III	16.00—17.30	—		
18.III	17.30—18.00	130	S	
28.III	17.00—18.00	—		
30.III	appr. 17.30	60	S	
1.IV	15.30—17.00	150	S	
9.IV				occurring on previous days on Klein Bonaire
18.IV	15.30—17.30	200	S	
20.IV	17.00—18.00	—		
23.IV	16.30—17.45	125	S	
24.IV				9.30—12.00 115 from SE + 200 from SW
25.IV				9.10 near Lac, 60 from ESE
1.V	16.50—17.35	240	S	17.20 50 from S, feed young

Date 1960	Time of observation	Number	Direction of departure	Direction of arrival and movement on the island
8.V	appr. 17.00	—		
11.V	17.00—19.30 full moon	350 among which juveniles	S	
13.V	15.00—17.35	110 idem	S	17.10 30 and 1 juv. from S, feeding
16.V	17.00—17.30	—		
18.V	16.30—17.15	departure	S	many tens to N at Kralendijk in evening
21.V				100 to N at Kralendijk in evening
22.V	16.30—17.00	departure	S	
5.VI				regularly (chiefly juv.) at Kralendijk to N
17.VI				10.40 25 adults from E
20.VI				2 juv. near Lac, Flamingos at Playa Frans
21.VI	17.00—18.00	departure	S	
24.VI	16.00—17.00	20	SE	
4.VII	17.30—18.10	90	S	18.00 5 form E
		30	N	spreading over island, often S to N last days
				23.00 100 flamingos in Pl. Lechi
9.VII				6.00 19 ad. & 1 juv. Playa Lechi
29.VII	16.55—18.00	15	S	

sometimes the whole group, returns to the Oranje Pan, or the Pekelmeer. One part, and usually the half or two-thirds, flies on, low over the waves in a southern direction.

It is obvious that these movements are not concerned with food migration only, by which is meant that when the birds return to Bonaire, they feed young birds, or they relieve brooding partners. The number of times that we saw flamingos arriving from a southerly to easterly direction was fairly small, in fact 9 times only, six in the morning and three in the late afternoon. The absolute data for the food migration are, it will be seen, not very numerous, but are strenghtened by the indications from the Pekelmeer, where — in a period of increase — it was seen that birds left 12 times in a southern direction (as against 6 times when none left). This was probably not emigration. The observations from 19.II to 18.IV, a period of decrease, show 4 departures and 4 with no departures. In the period 18.IV—6.V, once more a period of increase, there were 2 departures and 1 without departures. From 6.V—15.VI, in which period there was

an increase, there were 4 departures and 1 non-departure. After this, in a period of decrease, we see departure every time.

BROWN (1958) also saw food migration (Chapter VI h); the flamingos in Lake Elmenteita searched for food in Lake Nakuru about 20 km away. ALLEN (1956, p. 99) reported for the U.S.S.R., where according to data from *Birds of the Soviet Union*, the old birds fly daily 30—60 km in search for food.

The cause of this food migration might well be food shortage, but it also takes place in periods when there does not appear to be any (Chapter V f). Under these circumstances the long-distance foraging of part of the birds may have a "survival value", since then more food remains for the young, growing birds. In this connection it is striking that we have no indications that the same took place in Goto and Slagbaai. These areas were richer in food in relation to the number of flamingos present. It is peculiar that only in middle May, when the food supply in the Pekelmeer due to the large numbers of flamingos reached a low, we saw departures over Kralendijk to the north. This, on the 18th and 21st of May coincided with an increase in Goto of 200 adults (from 16.V—25.V !). Only then was there an increase in the terrain used by the birds (also by young birds) for food-searching, to Klein Bonaire, Playa Lechi, etc. In Goto an increase was seen to the end of May, but thereafter a gradual decrease in the number of flamingos.

SUBADULTS

In Goto subadults were seen only after 20.IV.1960, and in the Pekelmeer after 22.IV.1960 in several tens. Before this, with the exception of a few grey-whites and a number "à la Camargue", no subadults had been seen. This changed at the end of April, and on the 29th of the month there were 500 subadults in the Pekelmeer. They remained more or less in the Pekelmeer. In Goto and Slagbaai we saw chiefly birds in their first juvenile plumage, which had probably been hatched in Goto in the summer of 1959.

From these changes in occurrence we see that for the recognisable subadult forms it is a question of "va-et-vient"! It would also appear from the late occurrence and the changing numbers in the subadult groups that here, just as in the Camargue (pers. comm. HOFFMANN), they do not remain in the breeding area or in the colony, but roam between the breeding area and the winter quarters. There is no seasonal migration, but the birds probably wander around in the area of the Venezuelan coast and the offshore islands.

The maximum of 500—300 subadults was in the period 29.IV—22.V, a peak arising immigration, giving a population much greater than the breeding population. In this period the number of "à la Camargue" birds remained constant, the grey-whites decreased somewhat and the number of brown-orange was reduced to half. A large number appear to have left with the general emigration wave. In the following peak period 17.VI the

TABLE XIII. SUBADULT GROUPS WHICH HAVE BEEN OBSERVED IN THE PEKELMEER

Date	Total subadults	brown-orange	grey-white	à la Camargue
29.IV	500	250	150	100
6.V	500	250	150	100
13.V	400			
16.V	several hundreds			
19.V	300			
27.V	350	125	125	100
3.VI	110	30	40	40
10.VI	90	30	20	40
15.VI	40	10	5	25
17.VI	150	60	ca. 10	75
24.VI	25			ca. 20
1.VII	40	15	5	20
8.VII	40	0	16	24
15.VII	ca. 30	several	13	13
22.VII	25	0	+ overlap type +	
29.VII	several	0	+ overlap type +	

gradually reduced numbers of brown-orange is increased once more to 60, and there is a small increase in the numbers of grey-whites and a marked increase in the "à la Camargue" type. Following this, there was once more a gradual decrease.

It would appear that, for part of the population, from time to time there is a migration from the Venezuelan coast to Bonaire, whereby subadult birds also arrive.

With the departure from Bonaire, the brown-orange specimens are the first to leave, followed by the grey-whites and the "à la Camargue" type remains the longest (having perhaps already some tendency for reproduction).

The cause of the departure is very probably food shortage (Chapter Vf).

JUVENILES

The oldest group in this class are juveniles hatched in the winter months of 1958—1959 in the Pekelmeer. Here on 28.VIII.1959 there were still some grey young present, probably from the breeding period 1958—1959. In the middle of January 1959 300 young were hatched, so that these were about $7\frac{1}{2}$ months old; later they left the area.

In addition to these there were young from the summer of 1959 — some 150 pullets, hatched from the middle of June to the middle of July in Goto, and these remained there up to and including 18.IX (they were therefore 2—3 months old), but on the 25.IX their numbers had decreased to 83 and to 6 on 2.X. After this, a few young (varying between 4 and 12)

remained to 2.V.1960 in Goto. They were then on the average 10 months old and were at that time indistinguishable from the grey-white stage. The varying number of between 4 and 12 from 2.X can be explained, at least until the end of November, from the similarly fluctuating number in Slagbaai (5—20 specimens) and in the Pekelmeer where, from 21.IX to 2.V.1960 the number of young varied between 0 and 9. This means that from the 150 juveniles at the end of September (about 3 months old then) the majority left, but also that up to 2.V.1960, a number of birds, then 10 months old, still remained in the breeding area.

For the breeding period (begin January 1960 — begin July 1960) in Goto we may distinguish 3 separate breeding periods, i.e.

begin January — end February: 12 pairs — 8 pullets
begin March — middle April: 6 pairs — 5 pullets
end March — begin July: ca. 90 pairs — 58 pullets.

From the first of these periods a number of juveniles remained up to and including 4.VII in Goto, with an age therefore of about 5 months and from 11.IV to 25.VII sometimes 1 of this generation was present in Slagbaai. From the second and third period there were the full 63 juveniles present on 25.VII, varying in age between 1—3½ months.

The departure from Pekelmeer can be read off in Graph 21: from the Christmas to April breeding period this is clear, but the fate of the 2nd generation occurred after our departure. Between 1.V and 6.V 450 young left and we found them nowhere else on the island. Later, on the 11.V and 13.V we saw juveniles accompanying adults to the south. On 13.V we saw 1 juvenile returning with a small group of adults. This is possibly part of a large-scale movement which would explain the small increase on the 13th and 16th of May. In June we also saw migration over Kralendijk to the north, when they were subsequently found in the salinas of Playa Lechi, but during June and July juveniles were also seen in various other places. Their number gradually reduced, so that on the 29th of July only 1 juvenile was still to be seen in the Pekelmeer.

The main group left, therefore, the breeding grounds at an age of about 3 months.

It occurs regularly in Bonaire that the young, walking and/or flying, leave the Pekelmeer in a northern direction to be found later in Kralendijk, and it is reasonable to suppose that this is caused by food shortage. These "stranded" juveniles are then returned to the Pekelmeer by the police and others; in the summer of 1961 this was also the case (GERHARTS and VOOUS, pers. comm.) when there was probably a food shortage in the Pekelmeer.

VIII. REGULATION OF NUMBERS

The factors causing the fluctuations in density are reproduction, mortality and migration, and we shall consider these three factors and their causal affinities in more detail in this chapter.

REPRODUCTION

We have seen in previous chapters that in both the Pekelmeer and in Goto extensive breeding takes place and we shall now examine the production of young birds per colony (or breeding period, where it is possible to distinguish these). We can assume that the clutch size is 1 egg per pair of adult birds (Chapter VIf).

Goto

We encountered the last phases only of the breeding period from May to July in 1959 and on the 3rd of September we found 200 nests, 150 young, about 30 unhatched eggs and about 10 dead young. We may also assume that a number of unhatched eggs were broken, or washed away. It is dangerous to estimate the number of breeding pairs in a flamingo colony on the basis of the number of nests only, when the whole breeding and brooding process has not been followed from near by — see, for example, Pekelmeer where the same nests were used several times. Observing the slight differences in sizes between the young birds, we may safely conclude that about 200 pairs bred here, and these produced then 150 fledged young, with a subsequent loss in eggs and young of the order of 25%.

The following brood period in Goto, which we could follow at regular intervals, lasted from the beginning of January to the beginning of July 1960. Our figures for this period concern the number of brooding birds, pullets and growing juveniles, since the colony was not visited in this period for fear of disturbing the nests. Although brooding was continuous in this period, there were three visible waves whose production of young can be given. The calculation of the total number of brooding pairs in such a long period, with overlapping, is best done by drawing a line in a graph parallel to the line representing the numbers of brooding birds, but this 40 days later. Although the brood period is about 30 days, experience has shown that, in Goto at least, the pullets are mostly seen when they are 7—10 days old since the older birds sit on the young, for a great deal of the day.

We can say therefore that in period I (begin Jan.—end Feb.) 12 pairs bred and gave 9 juveniles. That for period II (begin March—middle April), 6 pairs bred and had 5 juveniles and that for period III (end March—begin

TABLE XIV. NUMBER OF BROODING PAIRS AND JUVENILES OBSERVED IN GOTO

Date		Pairs	Pullets/Juveniles
4.I,	13.I	several	
25.I,	1.II	12	
8.II		5	4
10.II		6	5
17.II		9	3
29.II		4	8 length 50– 70 cm
7.III		6	8 length 50– 80 cm
14.III		6	9 length 50–100 cm
21.III		28	9
30.III		44	4(9)
11.IV		65	8 [and 1 juv. in Slagbaai]
20.IV		80	14; 9 large, largest appr. 125 cm, 5 small light grey of about 1 week old
2.V		60	18; 8 large, of 120–140 cm, 10 small, 20–40 cm [1 of 140 cm in Slagbaai]
9.V		48	34; 30 pullets and 4 juv. (1st batch) [none in Slagbaai]
16.V		45	32; 28 pullets and 4 juv. (1st batch) [none in Slagbaai]
25.V		24	30 pullets, no juv. [1 juv. in Slagbaai]
6.VI		11	53; 52 a few days-a few weeks old; 1 juv. first batch [and 1 in Slagbaai]
15.VI		7	55; 53 pullets, 2 juv. first batch [none in Slagbaai]
27.VI		1	61 of 25–90 cm, 1 juv. (first batch) [none in Slagbaai]
4.VII		1	65 of 25–90 cm, 2 juv. (first batch) [none in Slagbaai]
13.VII		–	63 pullets – juveniles [1 in Slagbaai]
25.VII		–	63 juveniles [1 in Slagbaai]

After this was finished we found 48 nests, heavily eroded, in which 5 eggs were to be seen, one per nest.

July) about 90 pairs bred and gave 78 juveniles. In total some 108 pairs bred with a resulting 72 juveniles, that is an efficiency of 67%. For each period there were 75%, 83% and 64% of young, respectively.

Pekelmeer

Although various colonies have been distinguished, it was not possible to determine the number of young for each colony separately, since when they are very small and run around between the nests, they cannot be counted with any accuracy. This is possible only later when they leave the colonies proper more, but then we have the difficulty that young from various colonies are mixed together. The periods when 700, 1100 pullets, etc., are mentioned in Graph 20 are somewhat late for the same reasons,

and these figures were reached in all probability some two weeks before the date given.

We are able to determine the number of young for each different period, however, just as has been done in the case of Goto. We find then a period running from the end of December to the end of April and from the end of April to the end of July. Brooding still took place after this. Our studies had to finish then, but we are able to make an estimation for this last group based on the other production figures for young birds, to obtain a total figure for the Pekelmeer and for Bonaire.

At the end of both brooding periods 2 short visits were made to the various colonies when the number of eggs and dead young was noted. In addition, 35 eggs and 6 dead pullets were found in February, which had been washed away and later stranded on the western shore. In June 75 eggs and 2 dead pullets were washed up on the western shore and at the beginning of July 2 dead juveniles with broken wings were found.

The possible error of double counts at the end of the second period, of eggs which had been left over from the first period, could be avoided to a large extent, since then only eggs on nests were counted. Seeing the low number of 2-egg clutches we can assume that the eggs which remained behind were removed.

By means of a combination of all these facts and figures we come to the following result:

1st period 1450 pairs, 1100 juv. (76%), 310 remaining eggs (21%), 40 dead pullets (3%).
2nd period 500 pairs, 350 juv. (70%), 135 remaining eggs (27%), 15 dead pullets (3%).

If we take the first group of 200 brooding pairs into consideration then, comparing these to the other results, we come to the following final results:
3rd period 200 pairs, 145 juv. (72.5%), 45 remaining eggs (22.5%), 10 dead pullets (5%).

As a total for the Pekelmeer we then arrive at the following for the period December 1959 to August 1960:
2150 pairs, 1595 juv. (74%), 490 remaining eggs (23%), 65 dead pullets (3%).

For Goto in the period January to the beginning of July, we obtain the following:
108 pairs, 72 juv. (67%), so that from September 1959 to August 1960 the

total for whole Bonaire is:
2258 pairs, 1677 young, giving 74% turnover.

If we take the summer of 1959 for Goto and add this to the above this means that in slightly more than one year, the breeding of 2,500 pairs (exact 2,458), more than 1,800 (exact: 1,817) young were produced, a turnover of 73%. This figure of 1,800 young birds is the number that actually fledged and was not lowered in any considerable fashion by mortality under the juveniles, since this was, after the pullet stage, very low and has been included in the pullet mortality. The latter has been taken on the high side; from the first and second period 30 dead pullets and 6 juveniles were found, while the figure used for the loss was estimated at 55.

Naturally enough these figures are not all equally accurate and the result is an estimation that approaches the actual situation as closely as possible. Bearing this in mind, we arrive at the following figures for the reproduction in the various colonies (or breeding periods):

Goto 1   12 pairs   75% young grew up
Goto 2   6 pairs   83% young grew up
Goto 3   90 pairs   64% young grew up
Pekelmeer 1   1450 pairs   76% young grew up
Pekelmeer 2   500 pairs   70% young grew up

The reconstruction for Goto before the study period — 200 pairs and 75% young and the estimation for Pekelmeer after our departure — 200 pairs and 72.5 young — have been left out of consideration here.

There is no definite trend in this series of reproduction figures indicating that in smaller colonies fewer young grow up than in the larger. ALLEN (1956) and SWIFT (1960) report that smaller colonies (up to several hundred pairs) are less succesful than larger. ALLEN mentions a colony of 2,000 nests as being typical for the West Indian flamingo and reports that a normal nest mortality (i.e. loss of eggs and small young) is about 25% and that this may be much lower in very large colonies. The low nest mortality of 20% and less in Yucatán would appear to ALLEN to be explainable from the synchronous breeding behaviour.

LOMONT (1954) gives for the Camargue a loss of eggs and young of 30–33%. BROWN (1958) gives as the percentages of grown young, 21%, 31.5% and 74%, with an average of 51%; disturbance by Marabus (*Leptoptiles crumeniferus*) and the predation of the Fish Eagle (*Cuncuma vocifer*) account for the first two low figures.

On the basis of these figures the results observed on Bonaire were average to good, but they are lower than those given by LACK (1954) for various species of birds, with the exception of a number of crevice dwellers. The low predation on the eggs and young of the flamingos probably accounts for this.

BROOD FREQUENCY

Having seen something of the reproductive results, it is interesting to examine the frequency of brooding at various places, including Bonaire, the entire Caribbean, the Camargue and East Africa, since only from these areas are there observations of several years standing.

Bonaire

In the period before 1940 the flamingos bred more or less regularly on Bonaire, but we can say no more than this. In 1941 they bred and 500–700 young grew up. The next following information is of the disturbing of the birds by the American airforce in 1943, and it was 1950 before they began once more (See further Table XV.)

TABLE XV. BREEDING FLAMINGOS AT BONAIRE SINCE 1950

Year	Pekelmeer/Goto	Succes	No. of pairs	No. of fledged young	Time of year
1950	P	+	1,000	600	August
1951	P	+	1,000	?	summer
1952	P	−	young and eggs washed away by heavy rains in July		
1953	P	−	no brood		
1954	P	−	no brood		
1955	P	+	1,400?	800	March-May
1956	P	+	?	3,000?	February-March
1957	P	+	?	3,000?	February-March
1958	P	−	?	?	February
1958–1959	P	+	700	300	December-January
1959	G	+	200	150	May-July
1959–1960	P	+	2,150	1,600	December-August
1960	G	+	108	72	January begin July
1960–1961	P	+	1,200?	?	November-April
1961	P	−	1,000?	150?	May-July

In 1961 VOOUS found 850 eggs: 250 on the nests and 600 between them. There was a high mortality under the young.

He presumes that, owing to food shortage, the brood activities of 1961 were ended, when most of the adults and the fledged young left Bonaire. There were no more than 400 fully coloured birds and 180 pink sub-adults and 150 first-year young (a total of about 730 birds) in July 1961. A great number of eggs were deserted (100% of the last concentration of 850 nests). The growing birds have had a miserable existance, so that long journeys both walking and flying over the island led to the death of even more. The best food areas on the island at that time — Goto and Slagbaai — gave refuge to the majority of the birds — about 390 ($^2/_3$) of the adult birds. (All according to VOOUS).

Brood activity shows no relation to the rainfall.

The small numbers which reproduced in 1958 and 1959 may be the result of the bad years 1952, 1953 and 1954, when no brooding took place or when the eggs and young perished. We have already seen in Chapter VI h that flamingos are probably reproductive only when 5 or 6 years old and the absence of a given year-class is therefore felt a number of years later in the breeding population. In the same fashion it is possible to explain the excellent results in 1960 and 1961 as a result of the favourable circumstances in the years 1955 and 1956 (See Table XVI.)

ALLEN (1956, p. 73) gives a survey of the reproduction of the total population of *Ph. ruber ruber*, to which should be added that the population he refers to as "Caribbean" covers Bonaire and the coast of Venezuela

TABLE XVI. AN ESTIMATE OF NUMBERS (after ALLEN 1956, p. 73)

Peak numbers = theoretical peak attained by sum of maximum adult numbers and surviving young-of-the-year.

Population unit		1952	1953	1954	1955	totals 1956
INAGUA	breeding adults	16,816	17,860	14,588	14,071	14,000
	young	5,102	500	4,000	–	
	production rate	.60	.06	.55	–	
	peak numbers	21,918	18,360	18,588	–	
YUCATÁN	breeding adults	4,000	4,160	4,327	4,500	4,500
	young	1,600	1,664	1,730	–	
	production rate	.80	.80	.80	–	
	peak numbers	5,600	5,824	6,057	–	
CARIBBEAN	breeding adults	2,000+	4,150	3,000	2,400	2,400
	young	0	0	0	–	
ABACO	breeding adults	300	306	305?	304?	300
	young	110	100?	100?	–	
	production rate	.75	?	?	–	
	peak numbers	410	?	?	–	
GALÁPAGOS						300?
TOTALS	breeding adults	23,416	26,776	22,520	21,575	21,500
	young	6,812	2,264	5,730	–	
	peak numbers	30,228	29,040	28,250	–	
	nests built	11,554	3,226	9,457	–	

TABLE XVII. BROOD RESULTS IN THE CAMARGUE

1949	Colony not found			LOMONT 1954
1950	ca. 3,000 nests	2,000 pullets		LOMONT 1954
1951	ca. 3,000 nests	2,000 pullets		LOMONT 1954
1952	ca. 2,400 nests	1,800–2,000 pullets		LOMONT 1954
1955	3,000–4,000 pairs	400	fledged young	HOFFMANN 1955a
1956	3,000–4,000 pairs	700–800	fledged young	HOFFMANN 1957
1957	4,000–5,000 pairs	2,200–2,500	fledged young	HOFFMANN 1959a
1958	"échec complet" storm gradually reduced number of brooding birds			HOFFMANN 1960a
1959	3,650 pairs	585	fledged young	HOFFMANN 1962a

and its islands, the coast of Columbia to the Guianas; Bonaire is the most important breeding area within this group.

The low number of breeding birds in the beginning of 1955 (when no more observations were made), in comparison to 1952 is, according to ALLEN due to the poor brood results on Inagua in 1953. It seems to me that this is very doubtful, when we see the age at which the birds become reproductively ripe.

Camargue

GALLET (1949) surveyed the period 1914 to 1947 – in 34 years the flamingos bred 16 times and the colony was disturbed 5 times, either completely or partially. In this period 18,000 young grew up, with an included loss of 8–10%.

East Africa

BROWN (1959) reports that the Small Flamingo (*Phoeniconaias minor*) bred in East Africa in 1954, 1957 and 1958, and probably not in 1955 and 1956.

The picture obtained for the various (sub)species in the areas mentioned above is similar: in some years there is little or no breeding activity at all and when breeding does take place the results are often very variable. Despite this erratic reproductive activity GALLET (1949) and LOMONT (1954) write that the population is in equilibrium. HOFFMANN (pers. comm.) believes that in the Camargue poor years are compensated for by years in which a large number of young grow up. BROWN (1959) assumes also for the Small Flamingo in East Africa that there is an equilibrium.

It appears from the foregoing that with a variable and often low productivity rate, the mortality must be low and the average age high, if this population is to remain in equilibrium.

MORTALITY, AVERAGE AGE AND POPULATION EQUILIBRIUM

We have seen above that the West Indian flamingo's colony mortality reaches 20–30%.

In the Camargue and East Africa this may well be higher, and is explainable for a large part as predation. HOFFMANN (1959) reports that in 1957 at least 20 pullets per day were killed for about 1½ months (a loss of nearly 1,000 pullets) due to the activities of the gull *Larus argentatus*. HOFFMANN (pers. comm.) suspects that foxes (*Vulpes vulpes*) may also be important for their damage here. In the Rift Valley, as we have seen (BROWN 1958, 1959) eagles and Marabus act as predators of the eggs, and the Marabus are also able to kill adult Small Flamingos. The eagles appear to seek out isolated young in particular.

McCANN (1939) and ALI (1945) mention Scavenger Vultures (*Neophron ginginianus*) as a predator in the Rann of Cutch (India) but the predation level was not so very high.

ALLEN (1956) mentions for various parts of the Caribbean area, the Turkey Vulture (*Cathartes aura*) as the bird of prey, but there is nowhere mention of a serious predation.

ALLEN (p. 197) writes: "On other islands, Hispaniola and Cuba, for example, the mongoose (probably *Herpestes auropunctatus auropunctatus*) was introduced some years ago. In Haïti and the Dominican Republic it may have been a factor in destroying the former flamingo nesting colonies. In Cuba, according to Westermann (1953), it seems

to be confined to the western provinces, and thus may have had no part in the flamingo losses in that country."

There are no predators on Bonaire which attack either the eggs, young or adult birds, and it is therefore striking that we have seen so few dead birds, with the exceptions of the pullets and young birds already mentioned.

In Slagbaai, two "grey-whites" were found and one fully coloured specimen and the latter was, for some time before we found him, seen to be solitary, which means — according to local flamingo experts — that they are ill and/or are dying.

In the Pekelmeer one fully coloured specimen was found.

During a period of 11 months, when every important flamingo area was regularly visited (including all the banks of the salinas) we found only 4 dead birds. This would suggest, with such a large adult and young population, a very low mortality rate.

BROWN (1958, 1959) also noticed the small number of dead birds in East Africa, while — according to his data — the remains are visible for some 6 months. He writes (1959) that, for the Lesser Flamingos, a population of 1,000,000 in Lake Hannington lost at most 2,000 birds per year to predators and he found that in a population of Greater Flamingos of 9,500 birds only 3 dead adults. In a breeding population of about 3,200 birds he found in the course of two months 1 victim only, and from a population of more than 15,000 flamingos, 4 dead adults, also in a couple of months. BROWN (1958, p. 413–414) writes: "The adult Greater Flamingo, unlike the Lesser Flamingo, seems to have almost no enemies in nature." He connects the small number of dead birds found and the reproduction for both species and estimates the average age: "From all the evidence available it seems that adult Greater Flamingos have a low mortality rate, and while casualties are sometimes heavy among the young, once the latter have reached about 40 days old the casualties from natural causes appear to be low. It is possible to calculate that if the 20,000 — odd flamingoes which bred on Lake Elmenteita had an average life expectation of ten years, the death rate should be about 55 per day. Mortality on this scale certainly did not occur among the adults at Elmenteita, and it would therefore be reasonable to assume that the Greater Flamingo must be a long-lived, bird, a conjecture which is borne out by all that is known of its existence."

BROWN (1959, p. 104) gives further a calculation of the average age of the Lesser Flamingo, based on reproductive data. He estimates the entire East African population at 3,000,000 specimens. In 7 years about 1,100,000 young were reared, an average of more than 150,000 per year — in some years no breeding took place, but in 1957 and 1958 together 800,000 young were reared. He considers the number of young reared per year in connection with the total population and then arrives at an average age of about 20 years. Based on the number of dead specimens that he found, BROWN surmises that this must be even much higher, and concludes that to keep the population steady, only a small number of young are necessary, a conclusion supported in other areas. Years without reproduction are then plausible.

ALLEN's approach to the problem of mortality and population equilibrium is as follows (p. 72): "The flamingo attains its adult plumage by the end of the first year and probably is capable of breeding during its second year. The normal clutch is one egg per pair. A study of life tables, productivity charts and the breeding characteristics of the flamingo suggests that, assuming certain mortality rates, a stable population level will be maintained if each potential breeding pair produces .67 young annually.

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According to Hickey (*Survival Studies of Banded Birds*, 1952), the mortality rates that would govern such a situation are 40% for the first year of life and 20% as an overall adult rate. Testing these figures with a sample unit of 2,000 breeding pairs, we find that on this basis, 1,340 young are hatched of which approximately 800 survive the first year, while adult losses over the same period equal 800. Thus, at these rates, losses and gains balance each other exactly."

From the data for the West Indian flamingo (Table XVI) ALLEN (p. 73) concludes: "The long-term trend at present appears to lie below the point of equilibrium, on a slight downward grade, and may so continue unless the current protection program results in a gradual improvement in the productivity average. On a basis of actual performance, this now seems to be about .63 young per pair, and would be more hopeful if it could be moved above the .67 rate that may be needed for stability."

My objections to ALLEN's views are as follows:

1. The flamingos are certainly not fully coloured at the end of their first year and do not reproduce in their second. The ring data of HOFFMANN (1957) show that they are ripe after 5 or 6 years only.

2. The assumed mortality is too high, both for the first year (after the nest mortality) and in the following years, seeing the low mortality noted by both BROWN and ourselves among large numbers of flamingos during long periods. On the other hand, we know nothing of the mortality outside the breeding areas and during migrations.

3. The assumed production rate of 0.67 young per pair per year necessary to keep the population stable, is too high. Despite the irregular breeding, with years in which few or no young are produced, there is no definite decline in the Camargue, on Bonaire or in East Africa.

It is possible that the data given for the captive flock, at Hialeah, Florida cited by ALLEN (p. 65), give in fact indications against his own theory, although there is a danger that captive birds behave differently to those in the wild. In this group of 750 birds 65 young are reared annually. He assumes that there are 250 potential breeding pairs and arrives at a production rate of 0.25 young per pair. It is possible that an average of 0.25 young per pair per year is more correct than one of 0.67 young per pair per year. On the other hand, it is also possible that 0.25 is too small because this group contains less than 250 potential breeding pairs. This is very probable seeing the late age at which the birds are reproductively ripe. The Peak numbers given by ALLEN in Table XVI are also too low, for the same reason, since the subadults have not been taken into account. HOFFMANN (pers. comm.) can conclude from his ring data that the flamingos which are sexually immature remain in the winter quarters (N. Africa) during the breeding season or roam around the western Mediterranean. There is no winter quarter in the Caribbean, but we do have evidence that the subadults roam around (Chapter VII). This

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is shown by the invasions of hundreds of subadults which suddenly appear and, after a short stay, depart once more.

For the exact calculation of the mortality and the average age, sufficient ring data must be available and only in the Camargue does these occur on a large scale. These data (HOFFMANN 1955b, 1956, 1959b, 1960, 1962b) show an atypical picture at the moment, however, since the ringing was begun in 1950 only. In addition there was no ringing in some years i.e. in 1951, 1955 and 1958 and in the years 1950, 1952, 1953, 1954, 1955, 1956, 1957 and 1959 a variable number of birds was ringed, so that certain year-classes are not yet represented. The oldest reported flamingo was in 1963, as might be expected, 13 years old (HOFFMANN, pers. comm.). On the basis of zoological garden records and other sources we can safely assume that they may reach a much higher age. WACKERNAGEL (1959) reports a case of *Ph. ruber roseus* 44 years old (Philadelphia) and in Basel there are a few flamingos 27 and 21 years old. LACK (1954, p. 106) writes: "The annual death-rate is 40—60 per cent in various song-birds, ducks and gallinaceous species, 30—40 per cent in various wading birds and gulls, 20 per cent in swifts and 10 per cent in a penguin." On p. 93 he states: "The highest average age may be expected in birds such as the larger petrels or eagles with a clutch of only 1 egg and several years of immaturity." This would also be valid then for flamingos. LACK (p. 83) also says: "After the juvenile birds have become independent of the parents, they do not at first survive so well as adults."

When we compare the flamingo mortality data and ages from various areas with LACK's conclusions for a large number of bird species, we obtain a rough picture for the flamingo. ALLEN's data of 20—30% losses of eggs and pullets would seem reasonable for the West Indian flamingo, and in Africa and in the Camargue this may be higher, due to predation. A first year mortality of 40% and a second year mortality of 20% and for following years the same, as accepted by ALLEN, would seem to me to be on the high side and on the basis of the foregoing a first year rate of 20% and a 10% rate in following years would seem to me to be closer to the facts. If these figures are correct, this means that after 5 to 6 years about half of the fledged young are still alive and after 20 years, some 10%.

Since we may assume that *Ph. ruber ruber* — just as *Ph. ruber roseus* — can breed after 5 or 6 years, this calculation shows that about one half of the young that are fledged in one year, will reproduce finally. The number of adult birds is thus reduced by one half after 6 to 7 years and we can, therefore, on the basis of this hypothesis make the following conception of the population-history.

In a given year there are n breeding pairs; with a 30% nest mortality (on the high side) these will produce $0.7n$ fledged young and these become adult after 5 to 6 years when they are reduced to one half — $0.35n$. The $2n$ breeding birds are reduced to a half after 6 to 7 years — n. If the $2n$ birds breed 3 times successfully in 6 to 7 years, $3 \times 0.35n = 1.05n$ sexually mature birds are added to the population. If our mortality figures are correct, this means that the population will be stable if there are 3 successful broods in every 6 to 7 years. This agrees with the facts in several colonies where, without any reduction in the numbers we find that sometimes no or unsuccessful breeding takes place for one, two or sometimes three years. In areas where the predation is high, (e.g. the Camargue) or

where for other reasons the nest mortality is higher, more frequent breeding will be necessary and this does, in fact, occur there. If the flamingos continue breeding with a favourable result, then an increase in the population will take place.

For the sake of completeness a number of c a u s e s o f d e a t h follow here, which have already been taken into consideration in the nest mortality and predation figures considered above.

Parasites and Disease

There is little mention of possible deaths due to parasites or disease in the flamingo literature. Of the 7 specimens examined by us, one — the juvenile specimen shot on 11.XI.1959 — contained tens of intestinal parasites at 50—100 cm from the cloaca. According to ELISABETH VAN DEN BROEK (Utrecht) these were very probably Hymeno-lepidae (Cestoda). In addition, on all the flamingos shot we found harmless Mallophaga which were identified by THERESA CLAY (1962) as *Colpocephalum heterosoma, C. salimalii, Trinoton femoratum, Anaticola phoenicopteri* and *Anatoecus keleri*. The first four species are also found in the European *Phoenicopterus*, the last one is only known from Bonaire.

Warmth and Drought

The combination of these two factors would, in some places, appear to be fatal in *Ph. ruber roseus* for the pullets. ALI (1945) believes that in the colonies in the Great Rann of Kutch, the heat is chief cause of death for the pullets. At 11 o'clock in the morning a temperature of 116° F has been measured.

In comparison, our temperatures on Bonaire give no reason to assume this as a cause of death there. ALLEN also writes that this is not important in *Ph. r. ruber*.

Floods and Storms

ALLEN (p. 198—200) writes: "Floods are a major threat to the successful nesting of flamingos particularly, it would seem, in the Bahamas and Yucatán. High waters are caused either by heavy rains or by high storm tides, the most violent disturbances being caused by the West Indian hurricanes, which, in addition to the destructive force of the wind, combine both extreme rainfall and unusually high tides. F. M. Chapman (1905) believes that "aside from attacks by man, the heavy rains of the tropics are doubtless the chief cause of mortality among Flamingos" ". — "A nesting attempt on historic Bonaire Island, in the Netherlands Antilles, was washed out by heavy rain and high winds on July 6, 1952. The following September, with S. F. Briggs and Richard H. Pough, the writer saw well-grown chicks, possibly one month old, strewn along the low shoreline of Pekelmeer, where the waves had deposited them."

In 1958 the eggs were washed away from the small colony in Slagbaai. On Bonaire these are unfortunate exceptions, partly because the island is outside the hurricane zone. Certainly, the situation on Bonaire is more favourable than in other places in the Caribbean.

Accidents

BROWN (1958, p. 414) writes: "In the later stages of their lives the chicks suffered some casualties from broken wings, probably caused by accidents when fleeing from Marabus or Fish Eagles in panic; these casualties however, did not exceed 1%".

We found 2 dead juveniles with a broken humerus and suspect that these were caused during panic reactions, by aeroplanes, for example, when flapping their wings in dense groups.

Migration

After the mortality factors we shall now return to the migration and distribution, whereby we shall also consider the food supplies.

We have already seen in the chapters on the food, the distribution of the young, and the numbers and movements, that the food supply has a great influence. Food shortage acts here as a limiting factor i.e. that the mortality does not necessarily increase, but that it is the cause of the distribution of the birds over the island and their departure from it. In Chapter V i we have also seen that the predation percentage (i.e. food usage expressed as a percentage of the population size of the prey species — TINBERGEN 1948), for the chief prey (*Ephydra*) is often 30% and cannot in fact exceed this by very much.

In comparison to a number of other bird species such as *Sturnus vulgaris* (KLUYVER 1933), *Accipiter nisus* (TINBERGEN 1946), various tits (*Parus* spp.) (TINBERGEN 1949), and *Phalacrocorax carbo* (VAN DOBBEN 1952) this percentage is exceptionally high, and this is caused by the fact that the flamingos on Bonaire are practically monophagous, in contrast to the foregoing species which are all polyphagous.

With larger numbers of flamingos the predator-prey equilibrium is disrupted (see Chapter Vf) resulting in a marked decrease in the *Ephydra* population. Not only are there then few larvae or chrysalids but also very few imagos of *Ephydra* to be seen along the shores of the Pekelmeer. This marked reduction in the prey may cause the dispersal of the birds over and away from the island.

On the other hand we saw in the middle of June to the middle of July 1960, that when the food supply was at a minimum, flamingos nested and began brooding. It is true that after this, when many birds had left, a reasonable increase in the prey population took place. VOOUS noted in 1961 on Bonaire that the colony (with many eggs!) was deserted, that there were a few (weak) young and hardly any adults in the Pekelmeer. He ascribes this to food-shortage: there were few *Ephydra* flies along the shores and very few larvae or chrysalids on or under stones.

It is possible that the great breeding activities of 1960 and 1961 had exhausted the food supply. It is also possible, however, that some abiotic factor may have caused this desertion — man and/or aeroplanes, may also have been responsible. The disturbing influence of the latter is very marked and has been noted in 1944 in the Camargue (ALLEN, p. 213), in the Bahamas (ZAHL 1951, ALLEN 1956), and in 1943 on Bonaire (WESTERMANN 1953). There are protectory measures but these are not always sufficient.

IX. PROTECTION

From early times man has had a great damaging influence on the flamingos, by way of the disturbing of the colonies, the collection of eggs and the hunting of young and old birds (see e.g. ALLEN 1956).

The flamingos on Bonaire have been protected since 1931 and in Venezuela since 1944 (WESTERMANN 1953). Fortunately protection includes also a number of other places in the areal of the West Indian flamingo. Often, however, it is very difficult to check the protective measures in these remote areas, so that locally the flamingo is still subjected to human activities.

For Bonaire, in addition to the prohibition of egg-collecting, catching and hunting, the colonies themselves should be protected.

Since the construction in 1959—1960 of a circular road around the southern part of Bonaire the breeding places are accessible with little difficulty, especially on the eastern shore.

An efficient protection will be attained only when the Pekelmeer and surroundings are designated as a reserve with sufficient guard especially during the breeding season. These measures need in no way hinder the tourist trade, since the flamingos are easily visible from the road along the western shore of the Pekelmeer. It is possible, in fact, to see the flamingos from a car at a distance of some tens of meters, and the advantage of remaining in a car is that the birds are not disturbed and remain closer than when one leaves it.

In addition we have the disturbing influence of the aeroplanes flying over the Pekelmeer; for Slagbaai and Goto this is less frequent. There are airspace restrictions over Bonaire in connection with the protection of the flamingos. Flying is permitted only above 6,000 feet with the exception of a circle with a radius of 3 nautical miles around Flamingo Airport south of Kralendijk. This is not strictly observed, however, and we often saw K.L.M. and Venezuelan aircraft, and also sport craft below the 6,000 foot limit over the Pekelmeer colony. The low-flying aeroplanes are particularly dangerous in causing great panic among the flamingos.

A stricter supervision is necessary to prevent a re-occurrence of the 1943 disturbance — then the flamingos did not return until 1947 and it was 1950 before they commenced breeding once more!

X. CONCLUSIONS

From our field observations on Bonaire, and from the literature, it appears that flamingos are capricious birds.

The breeding grounds, breeding periods and frequencies can all be very variable. The breeding grounds are not particularly restricted to muddy building material, although this is probably preferred. The breeding periods are, outside the tropics, more restricted than in them and on Bonaire only the months September and October showed no breeding activity. The breeding frequency is not very high and in various places there are indications that years with poor results are compensated for by years with good breeding successes.

On Bonaire there is no predation of the eggs, young or adult birds.

Flamingos can reach a high age, whereby even though breeding is with varying success, the population can still remain stable. This is possible, however, only when man does not interfere and the birds and their habitat are left in peace.

The habitat selection does not appear to be directly influenced by the food supplies. Large numbers of birds and/or lengthly breeding activities on Bonaire can decimate the food supply, with as a result the dispersal of the flamingos over the island and a more or less *en masse* departure. It is important in this connection that the flamingos on this island are practically monophagous and that *Ephydra* larvae and chrysalids form the most important item of diet.

Their preference in habitat selection for extreme physical and/or chemical circumstances enables them to occur in such large numbers. The biocoenosis is here poor in species but rich in individuals but these supplies of food are not inexhaustible and this is probably the origin of the roaming behaviour seen in the flamingo. This changing of feeding grounds allows the temporarily deserted areas to recuperate their food supplies.

Influences due to mankind may be extremely destructive and it is therefore necessary that a strict protection of the birds, breeding grounds and feeding areas should exist.

The great reduction found by ALLEN (1956) for the last decades, is not continuing on Bonaire. ALLEN (p. 73) mentions for Bonaire in 1952, 1953 1954 and 1955, 2,000, 4,150, 3,000 and 2,400 breeding birds respectively. From June 1959 to August 1960 about 2,500 pairs bred and 1,800 young were reared on Bonaire. In addition hundreds of adult birds, which were non-breeding, and several hundreds of subadults, were also seen. There are no indications in the literature that flamingos breed more than once

per year and we can therefore say that this 2,500 pairs represent a population of about 5,000 breeding birds. In comparison to ALLEN's figures we may have to speak in fact of an increase.

Taking into consideration the number of birds which did not breed, the subadults and juveniles, we can estimate the total Bonaire population of flamingos at several (5—10) thousand.

There is no question of a decline in the flamingo population on Bonaire in this case.

XI. SUMMARY

The problem leading to this investigation was that of establishing if the West Indian flamingo on Bonaire (Neth. Antilles) was on the decline and, if this was the case, what the possible causes of this could be. To this end a study was made on the island from August 1959 to August 1960 of the environment, food, reproduction and the numbers of birds.

In the description of the habitat in Chapter IV much attention has been given to the water management of the salinas, since these form the biotope of the flamingos. It appeared that even in extensive droughts the salinas retain a certain waterlevel. This is caused by the entry of sea-water, the salinas being somewhat below the average sea-level. The rate of entry is determined particularly by the seasonal fluctuation in the sea-level, and the water-level in the salinas follows this more or less parallel; the Cl-content shows an opposite fluctuation.

The extreme physico-chemical circumstances in the salinas ensure the occurrence of a biocoenosis, with few species, but the number of individuals of these species may be very great. This is probably one of the reasons why the flamingos show a preference for these areas.

In Chapter V food-searching and the food itself was considered both qualitatively and quantitatively. Seven clearly different methods were described, and imitation of these indicated the type of food searched for under the given circumstances. From this it appeared that the food was chiefly the larvae and chrysalids of *Ephydra gracilis*. Less frequently were *Artemia salina* and the molluscs *Batillaria minima* and *Cerithidea costata* taken as food. Under certain circumstances the eating of organic ooze was noted. Exceptionally attempts were seen at eating the fishes *Cyprinodon dearborni* and *Mollienesia sphenops*.

The examination of stomach contents confirmed that on Bonaire the staple diet was formed by the larvae and chrysalids of *Ephydra gracilis*.

A quantitative approach was given to the effect that the flamingos have on the food supply, whereby the number of *Ephydra* chrysalids acted as a standard. If $1/4$ to $1/3$ of the *Ephydra* chrysalids are consumed per 24 hours (theoretically, since larvae are also taken), the number of chrysalids remains more or less constant. With an increasing predation percentage, exploitation occurs and the number of *Ephydra* chrysalids decreases. The flamingos then switch to other food and/or leave, so that the *Ephydra* population is then able to recuperate.

In Chapter VI the reproductive behaviour was described. Both males and females show the same behaviour during pair-formation. During paired foraging is copulation most frequent. The partners build the nest together.

The height of this depends on the amount of building material in the immediate neighbourhood of the future nest. The time given to the building is very variable, sometimes old nests are used and these are simply repaired a little.

Brooding lasts about 30 days. In the Pekelmeer continuous brooding took place due to the overlapping of various groups from December 1959 to August 1960. Partly in connection with this long period, during which both large and small young were present in and around the colony, the occurrence of crèches was examined critically. On Bonaire it appeared that none of the typical functions of the crèche were to be found. The young were, as far as could be established, fed by their own parents. The feeding frequency decreases during the growth of the young, but the duration increases. Young of 4 months age were sometimes fed now and then.

Various sub-adult plumages could be distinguished after the juvenile plumage, with gradual transitions between them. There was evidence that it is several years before the birds have a fully coloured adult plumage.

In Chapter VII the numbers and movements were considered. In addition to emigration and immigration to and from the South American continent, food migration was also undertaken to Venezuela.

During the study period a minimum of 440 and a maximum of 4,130 flamingos were present on Bonaire.

In Chapter VIII the reproduction and mortality were considered. In something more than one year nearly 2,500 pairs bred and reared more than 1,800 fledglings, i.e. 73%. The breeding success in small and large colonies showed no striking differences. There is no predation on Bonaire of the eggs, pullets, juveniles or adult flamingos. The mortality of eggs and young is on the average 25–30%: 20–25% for the eggs and 5% for the young. Since mortality figures for other stages and life-classes in the West Indian flamingo are absent, it has been shown, using data from other areas, that the population probably remains constant in size if successful breeding occurs 3 times in 6 to 7 years.

It is a fact that, although there have been years when little or no breeding took place, the present South Caribbean flamingo population, with its breeding ground on Bonaire, shows no signs of a decline. It is possible that there has been a slight increase during the last 5 to 10 years.

It is very necessary for the conservation of the flamingos on Bonaire, however, that both the breeding and the feeding grounds be protected and given the status of a reservation.

APPENDIX

TABLE XVIII. WEIGHTS, MEASUREMENTS, ETC. OF THE SPECIMENS COLLECTED

	31.XII.1959 ♂ adult	21.I.1960 ♂ adult	27.VI.1960 ♂ adult	24.III.1960 ♀ adult	23.VI.1960 ♀ adult	11.XI.1959 juv. 4–5 mnth.
Total weight (g)	3780	2250	2600	3500	2600	1472.5
pH Stomach	7–8	7–8	7	–	–	7–8
Size stomach (mm)	85 x 55 x 40	76 x 85 x 35	61 x 43 x 23	60 x 50 x 25	52 x 40 x 33	–
Length gullet (cm)	85	84	–	70	–	48
Length gut (stomach-cloaca) (cm)	ca 300	ca 300	370	>300	ca 300	255
Length of 2 caecae (cm)	11	9 and 8.5	15	8 and 13	15	9.5
Total length (cm)	174	174	177	153	152	110
Upper mandible, length (cm)	15	15	16	15	13	14
Neck, from bill base to clavicles (cm)	74	74	72	60	57	34
Wing, from shoulder to tip (cm)	83	77	70.5	65	64	69
Wing, from hand to tip (cm)	42.5	42.5	41	39.5	40.5	–
Foot, from knee to sole (cm)	72	67	74	63	61	46.5
Tibiotarsus (cm)	38	36	39	33	32	25
Tarsometatarsus (cm)	34	31	35	30	29	21.5
Middle toe (cm)	10	9.3	8.5	9	8.5	9.5
Testes (mm)	{ 26 x 18, 27 x 18 }	{ 23.5 x 19, 18 x 9 }	{ 10 x 6 x 6, 10 x 6 x 5 }			

♀ 24.III.1960: more than 18 eggs of one to several *mm* diameter, and 3 of about 30 *mm* diameter.

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PLATE I

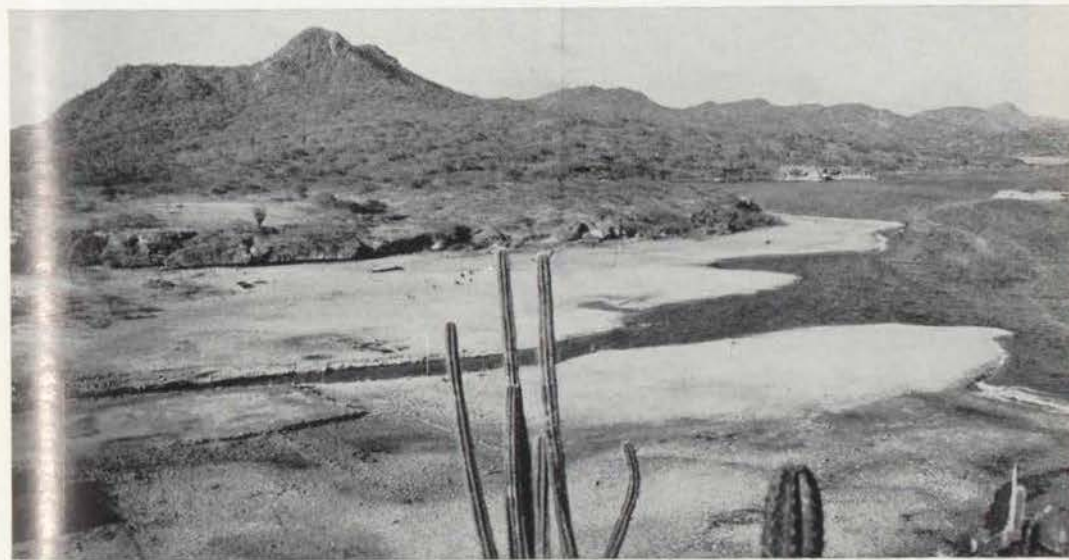I. Eastern part of Salina Slagbaai with saltpans and Brandaris.

PLATE II

PLATE III

IIa. Small "canal" at Boca Slagbaai.

IIIa. Nests of 1958 in Slagbaai, on dam between salina and saltpans.

IIb. View of Slagbaai from the south-east. — From left to right: Caribbean Sea, wall of coral debris with plantation buildings and the end of the small "canal".

IIIb. View of Slagbaai from the south-west. — From left to right: the small "canal", seepages (the dark patches) and the salina.

PLATE IV

PLATE V

IV*a*. View of Goto from the south-east. — The white stripe to the left of the Brandaris is the breeding island.

V*a*. View of Goto from the south.
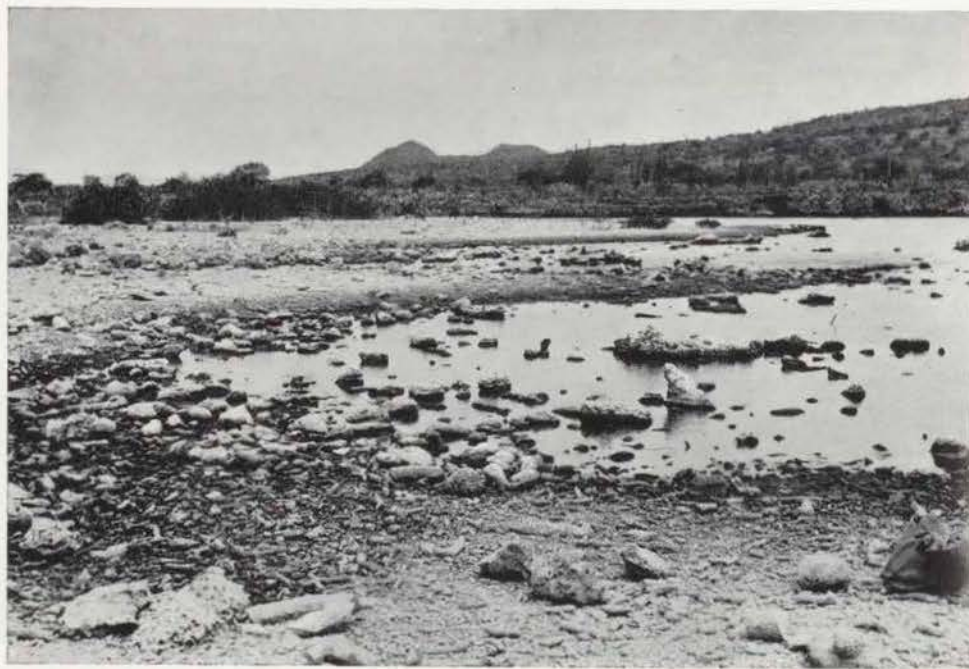
IV*b*. Boca Goto. — The inside of the wall of coral debris with seepages.

V*b*. Boca Goto. — The outside of the wall of coral debris.

PLATE VI

PLATE VII

VI*a*. Nests of 1957 far from the border of the Pekelmeer made from dry and coarse material.

VII*a*. "Duinmeer" from the east.
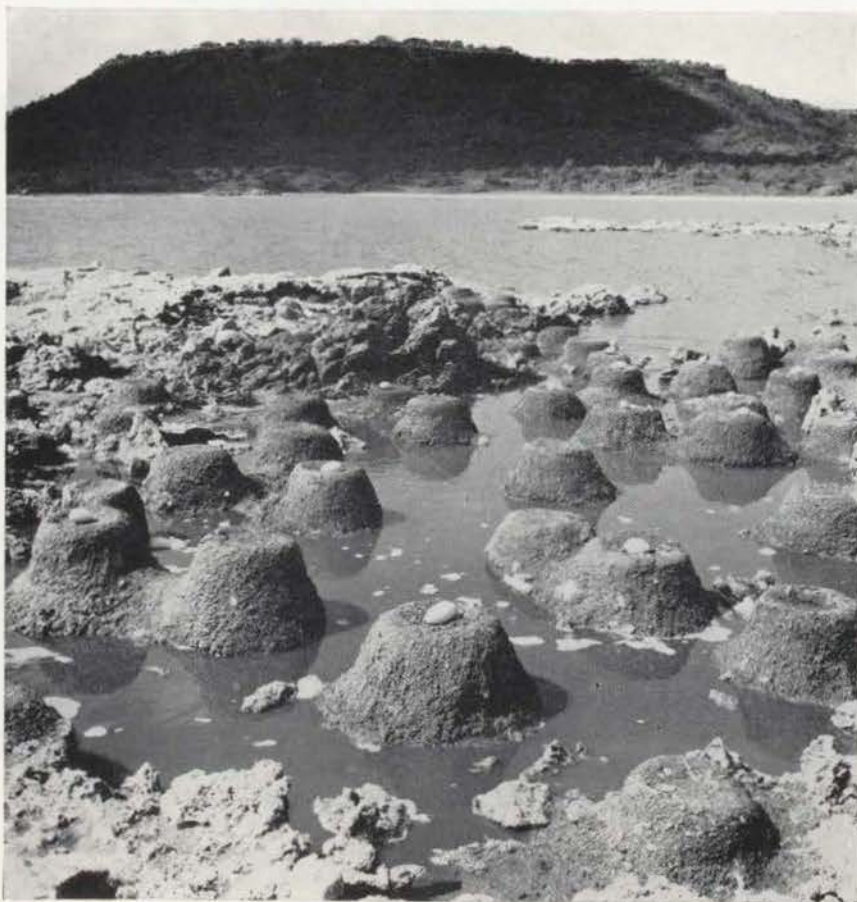
VI*b*. Nests in the mud pool on the island in Goto.

VII*b*. "Ven" from the west, with remains of feeding by stamping, describing a circle around the bill as centre: small round mounds with grooves around them.

PLATE VIII

PLATE IX

VIII*a*. "Oog" (eye) with green algae.

IX*a*. Small canal and saltpans at Oranje Pan.

VIII*b*. View of Pekelmeer at Witte Pan to the north-east.

IX*b*. View of Pekelmeer at Witte Pan to the south-east.

PLATE X

PLATE XI
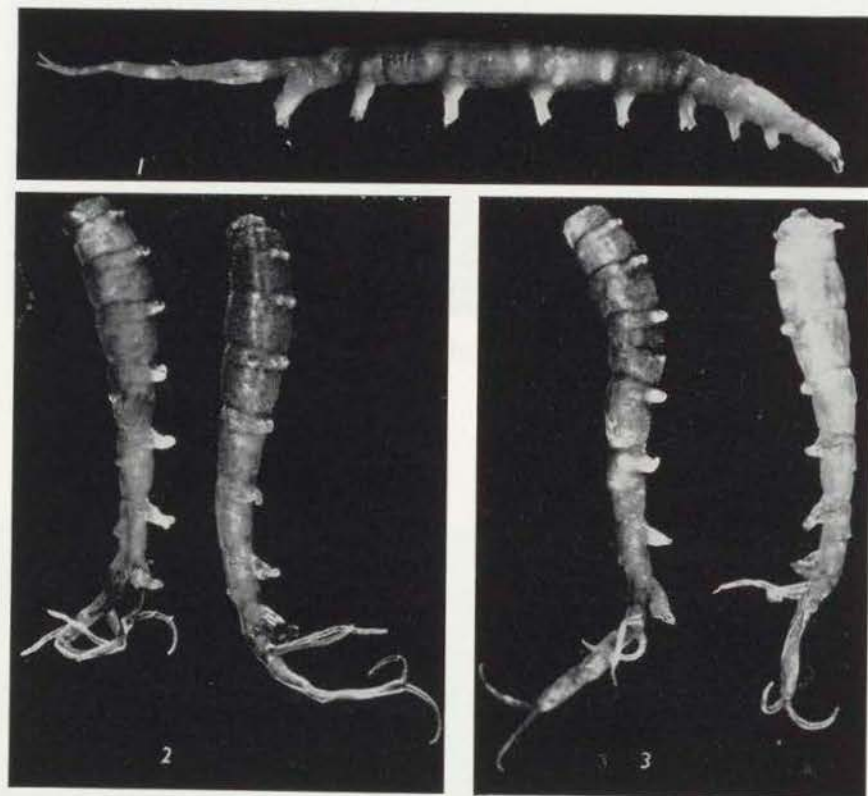
X. *Ephydra gracilis:* 1. larva; 2. pupae; 3. empty puparia.

XI*a*. Flamingo bill. — The ridges of the filter and the spines on the tongue can be seen.

XI*b*. Tracks of the bill and feet after eating organic ooze.

PLATE XII

PLATE XIII
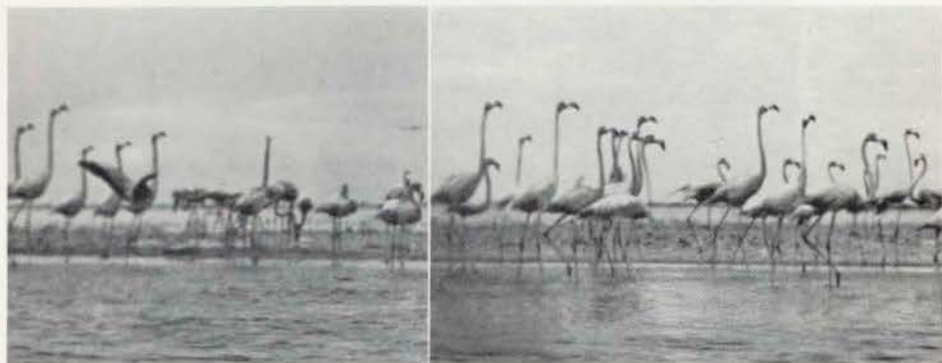
XIIa. Stretched attitude with and without wing spreading.

XIIb.-c. A small part of the S.E.-colony.

XIIIa. N.W.-colony.

XIIIb. S.E.-colony.

PLATE XIV

PLATE XV

XIV*a*. Hatching.

XV*a*. An exceptional clutch of 2 eggs.

XIV*b*. Just hatched.

XV*b*. The exceptional situation of 1 egg and a chick in one nest.

PLATE XVI

PLATE XVII

XVIa. Alarm: a compact group of pullets is leaving the colony, the largest at the front and the small pullets in the rear.

XVIIa. Escaping group of pullets of the same age.

XVIb. Group of pullets leaving the colony.

XVIIb. Pullet between the nests. — The smallest ones remain behind in the colony.

PLATE XVIII

PLATE XIX

XVIII*a*. Juvenile, about 6 months old.

XVIII*b*. Pullet, about 10 days old.

XIX*a-d*. "Willemsoog". — *a*: bathing and preening; *b*: drinking, with the characteristic slanting of the neck (the left bird), and to the right bill-fighting; *c*: rising by tripod method (in the centre) and drying of the wings (left); *d*: bill-fighting to the right.

PLATE XX

XX. Departure for migration near Oranje Pan. — Salt heaps and old factory buildings in the background.