FALKLAND ISLANDS DEPENDENCIES SURVEY

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No. 6

THE EMPEROR PENGUIN

Aptenodytes forsteri Gray

I. BREEDING BEHAVIOUR AND DEVELOPMENT

By

BERNARD STONEHOUSE

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CONTENTS

Section 1. INTRODUCTION

THE material for this paper was collected during studies of Emperor Penguins in a newly discovered rookery on the west coast of Graham Land. The rookery was found on the Dion Islets (Lat. 67° 52′ S., Long. 68° 43′ W.) in Marguerite Bay (Fig. 2) during a sledging journey made by the author and three companions. Sea ice conditions at the time (October, 1948) made it necessary for the party to withdraw almost immediately towards the safety of the coastline, and very little work was possible in so short a visit. In the winter of the following year a second party, consisting of the author and two companions, spent two and a half months on the rookery during the breeding season. The breeding behaviour was studied in detail, and a series of embryos was collected throughout the incubation period. The party returned to its base on Stonington Island in mid-August, taking a number of captive birds as material for further study.

Although the Emperor Penguin has been recognised as a distinct species for over one hundred years (Gray, 1844), its range and habits have made detailed study of its natural history particularly difficult. Known to the earlier voyagers only as a summer wanderer among the pack ice, its breeding haunts and habits remained a mystery until 1902, when the first rookery was discovered at Cape Crozier. Dr. Edward

Wilson, of the British National Antarctic Expedition, subsequently visited the rookery; his observations and captivating illustrations are incorporated in a report (Wilson, 1907) which remains, in the words of Dr. Robert Cushman Murphy, "the most important single study of the Emperor Penguin". (Murphy, 1936).

Astonishing facts were disclosed by Wilson's studies. He found the birds assembled on the sea ice below crumbling ice-cliffs, with chicks held firmly on their feet and no nesting sites. From the state of development of chicks seen in September, 1902, he was forced to conclude that incubation had taken place during the coldest period of the Antarctic winter. By a careful count of deserted eggs and chicks he found that the death rate of the year's brood was no less than 77%. He watched the extraordinary migration, on drifting ice floes, of the adults and down-covered chicks, and concluded, with some justification, that the habits of this bird were "eccentric to a degree rarely met with even in ornithology". Wilson's subsequent visit to the same rookery in 1910 has been described graphically in his own diary and in Mr. Apsley Cherry-Garrard's narrative *The Worst Journey in the World.* On this occasion, a short visit in the middle of winter, the observation period was necessarily limited. The birds were, however, seen to be incubating their eggs on the sea ice in July, and the visitors secured three partly incubated eggs, the object of their incredibly difficult journey.

It was obvious from Wilson's account that further rookeries would not readily be discovered. Coastal surveys by expedition ships are necessarily made during the summer months, after the dispersal of the birds. Whether the birds incubate on land or on ice, no nesting sites remain to mark the rookery area after the end of the breeding season. Alternatively, during the winter and spring months when the birds may be found in their rookeries, short hours of daylight and bad weather limit the amount of sledging which can be undertaken from a base hut. It is therefore hardly surprising that, until 1948, only three rookeries of Emperor Penguins were known on the whole of the Antarctic coastline.

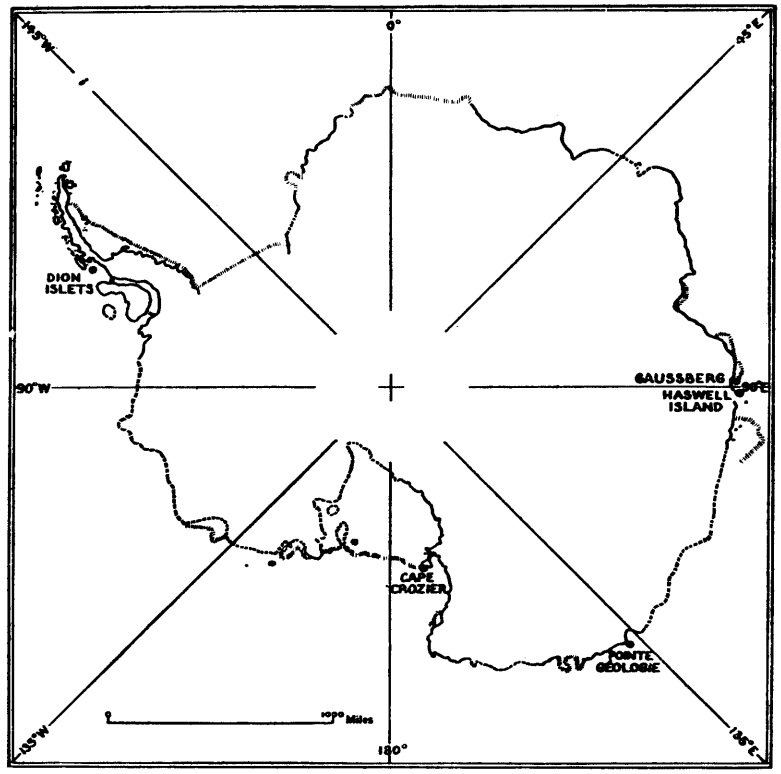

FIGURE 1

The presence of a second rookery, near Gaussberg in Kaiser Wilhelm II Land, was reported by the German South Polar Expedition of 1901–3; its existence was deduced from the number of juvenile penguins seen in the area (Vanhoffen, 1905). A third rookery was reported from Haswell Island by members of Sir Douglas Mawson's Expedition of 1911–3 (Mawson, 1915). Both the Cape Crozier and Haswell Island

rookeries are established on sea ice, and it seems that the Gaussberg rookery, which has never actually been visited, may be similarly placed. On the evidence of these rookeries various authors have been moved to repeat the statement, originally made by Wilson, that the Emperor Penguin never steps on land. It is a generalisation to which very little significance could be attached even if it were true; its falsity is shown in reports of visits by wandering birds to the South Orkney Islands, and in the establishment of the Dion Islets rookery itself on an island.

The existence of Emperor Penguin rookeries in the Falkland Islands Dependencies has long been suspected. Wandering and migrating birds have been encountered by the majority of the expeditions in this region, particularly near the northern tip of the Graham Land peninsula and among the off-lying islands. However, at least five major expeditions have operated in or near Marguerite Bay during the present century without meeting representatives of the species, and the discovery of a rookery actually in the mouth of the bay came as a complete surprise. Its convenience was immediately apparent. The rookery possessed the twin virtues of being easily accessible by sledging-journey from the Stonington Island Base during the winter, and being on an island which could be made the site of a semi-permanent camp. It provided facilities which had been denied to previous observers; for the first time continuous observation during the breeding season was possible with a fair margin of safety.

Advantage of this fact was taken at the earliest opportunity, and in June of the year following the discovery a party sledged out to the Dion Islets over newly formed sea ice. The camp was established on June 5th; a delayed start and difficult travelling conditions defeated the party's original object of arriving before the rookery assembled, and the first eggs were laid before observation commenced. However, birds were still arriving, and the activities of a few late pairs gave indications of what had been the general behaviour in the rookery immediately beforehand. Observations were continuous throughout the incubation and hatching periods, and the details of the birds' extraordinary life story gradually became apparent. When it became necessary to leave the islands in August, observations were continued on four captive adults and a chick. The birds responded well to hand-feeding and confinement, and the growth rate of the chick provided data which helped to link events on the Dion Islets with those recorded earlier on Cape Crozier. An account of the information gained from studies of the captive birds appear in Section 5 of this paper.

Since these observations were made in 1948 and 1949, two new sources of information have come to the notice of the author. A report has been received of the discovery of yet another breeding station, this time on the coast of Adélie Land. The position is marked on the accompanying map (Fig. 1), as Pointe Géologie and descriptions of this rookery have been published in *Notes Ornithologiques des Expéditions Antarctiques en Terre Adélie, 1949–1952*, by Dr. Sapin-Jaloustre and M. Jean Cendron. In addition, an interesting set of unpublished data has been made available to the author by the courtesy of Mr. J. M. Wordie; this includes day-to-day notes by Worsley and others of the movements of Emperor Penguins in the Weddell Sea area, as seen by members of the ill-fated *Endurance* Expedition during 1914–16. Some of these observations have been included in Section 6.

The author wishes to record his indebtedness to Surgeon-Lieutenant D. G. Dalgliesh, R.N., and Mr. H. D. Jones, who shared with him the uncomfortable but enjoyable winter months under canvas and assisted with the observations, and to Dr. David Lack, F.R.S., for his helpful suggestions and criticisms in the preparation of this paper.

Section 2. THE DION ISLETS ROOKERY

THE Dion Islets form a scattered group of low-lying volcanic rocks ten miles from the south end of Adelaide Island (Fig. 2). They are barren, snow covered, and windswept, with the largest island of the group rising to nearly 150 ft. Their position in the northern entrance to Marguerite Bay, and the distinctive shape of the main island, have led to the appearance of their name and description in the *Antarctic Pilot*; the absence of an ice cap distinguishes them from most of the other islands lying in the mouth of the bay. For about seven months of the year they are completely surrounded by a sheet of sea ice, which reaches a maximum thickness of from four to five feet. During the summer they lie either in open water or in extensive fields of pack ice. The fixed or "fast" sea ice of Marguerite Bay extends into the Bellingshausen Sea in May, June and July, but by August the outer edge of the sheet is visible from the Dion Islets, and

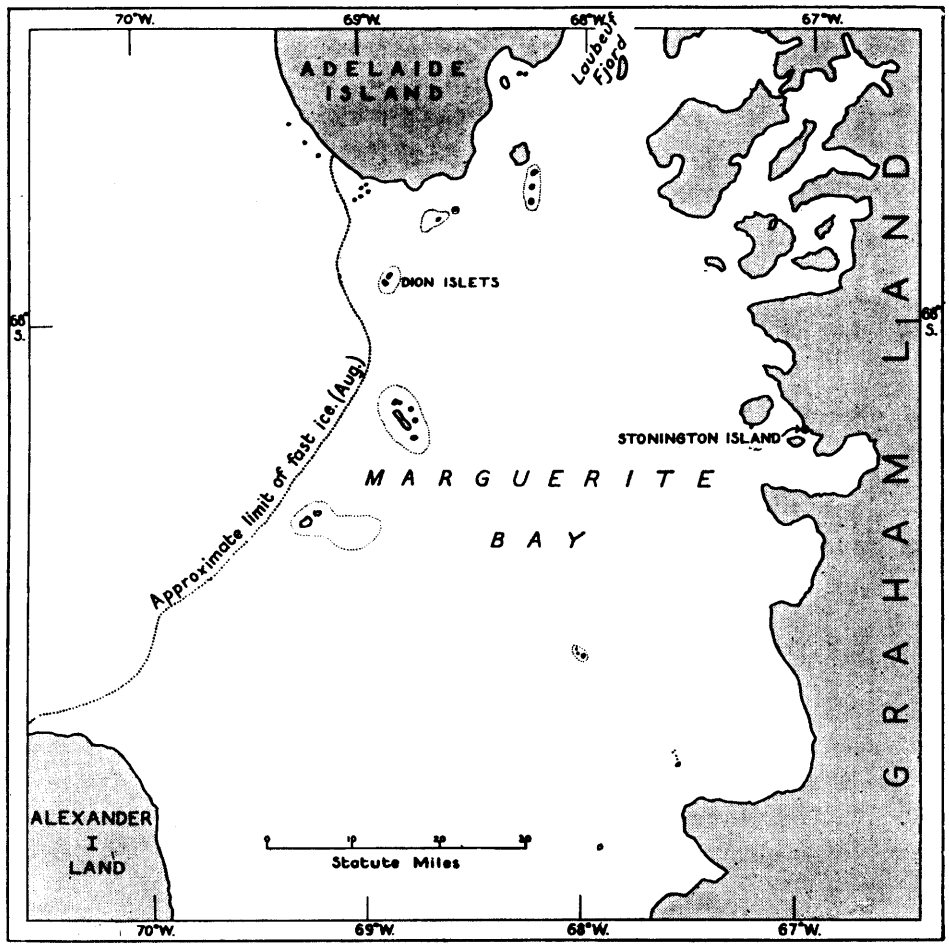

FIGURE 2

it seems likely that later in the year the group may normally be ice-free. The breaking-back of the ice edge is no doubt helped by the presence of reefs and strong currents in the area, which weaken the ice considerably in local patches and lead to the formation of open pools long before the fast ice sheet is actually dispersed. This is an important point in the selection of a breeding ground.

The part of the islands used by the birds as a breeding ground is limited to a small area on the south-east corner of the largest island. Here a narrow neck of low-lying shingle runs out to a promontory (see Fig. 3); the rookery area extends over most of the shingle and around the western side of the promontory. This rookery, unlike those previously described, is established on land. The birds spend most of their time on what is in effect a low-lying beach; the snow covering is firmly packed down to form a layer of ice about one foot thick over the stones of the beach, and there is little doubt that when the protecting sea ice has disappeared in summer the whole area may at times be awash. In the complete absence of any form of nest sites the rookery area is recognisable only by the presence of the birds, and they in their wanderings confine themselves to an irregular patch covering approximately 700 square yards. Their ground is limited to east and south by low rocky walls, but to north and west the only visible boundary is a wide expanse of flat snow which the birds seldom cross. Certain areas within the ground are used more frequently than others; the birds in huddling, for example, seem to prefer the "Saucer" or parts of the "Gallery" (Fig. 3) rather than open areas. The reasons for this are not obvious. With the strongest winds blowing always from a few degrees on either side of north, very little shelter is obtainable anywhere on the rookery, and neither the "Gallery" nor the "Saucer" offers more protection than any other part. During blizzards, the observer could escape from the direct blast of the wind by walking to the south side of the promontory or sheltering behind some of the smaller rocks in the area; the birds, on the other hand, preferred to remain in the rookery area all the time.

Figure 6 (see Appendix) summarises temperatures and winds experienced on the Dion Islets during the winter of 1948. Conditions were, on the whole, better than those which Wilson reported for the Cape Crozier area in 1910; a higher winter average temperature for the Dion Islets would be expected in view of the difference in latitude. From the table it will be seen that the coldest weather was usually associated with calm air or light winds, the stronger northerly winds invariably bringing higher temperatures. Most of the gales experienced were accompanied by temperatures of over + 10°F; these frequently followed heavy frontal snowstorms, resulting in blizzards of loose, drifting snow. In general terms the winter months brought the most extreme weather conditions of the year, and were certainly the least comfortable for prolonged periods of observation.

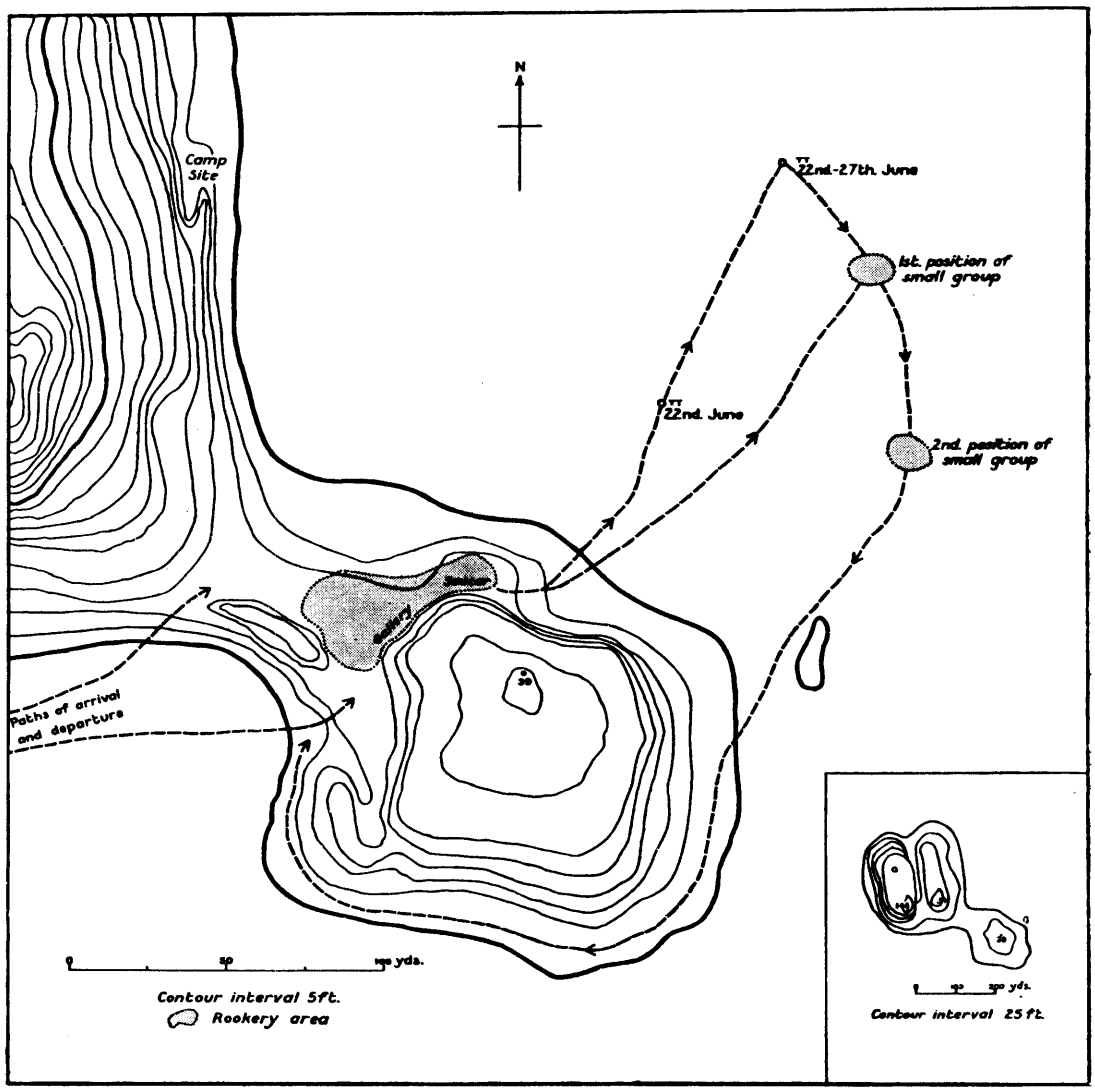

FIGURE 3

The number of adult birds which formed the Dion Islets rookery varied between 100 and 183 during the 1949 period of observation (see Appendix, Fig. 7). It seems probable from egg counts that a maximum of about 150 breeding pairs is accommodated on the rookery area. By comparison, Wilson estimated that one thousand birds were present at Cape Crozier in September, 1902, and Mawson's party reported three times that number at Haswell Island in November, 1912. Rookery size undoubtedly varies considerably throughout the season. On the Dion Islets the number of birds present during the incubation period approximated to the number of eggs which were being incubated; after hatching, birds flocked into the

rookery from all directions, sending the numbers up as shown in Fig. 7. In the previous year, 100 adults were recorded in October together with seventy chicks. The Cape Crozier rookery showed a very much wider variation, only one hundred birds (of which every fourth or fifth held an egg) being present in the winter of 1910. (Cherry-Garrard, 1922). However, this appears to have been an unusually late year for the formation of the sea ice in that area. Conditions at Haswell Island seem to have been more favourable, with a total estimated population of 7,500 birds, of which over half were chicks. This, a November observation, suggests a situation similar to that seen on the Dion Islets rookery in October, and shows clearly that the latter is a very small rookery by comparison. Its size can hardly be related to lack of ground space; so far as can be judged there is ample accommodation for considerably larger numbers. Nor does it seem possible that food supplies can be a limiting factor. There is no shortage of fish in the area during the winter, and later in the season when chick feeding is at a maximum, the same grounds provide food for the enormous numbers of fishing birds, and plentiful seals, which inhabit the Dions and neighbouring islands.

A striking feature of the area was the comparative absence of other forms of life during the winter, occasioned, no doubt, by the presence of the sea ice. A few Weddell seals (*Leptonychotes weddelli*) were seen from time to time on the ice associated always with open leads, or with holes in the ice which they themselves kept open. Snow petrels (*Pagodroma nivea*), giant petrels (*Macronectes giganteus*) and blue-eyed shags (*Phalacrocorax atriceps*) paid very infrequent visits. The Emperors were, in fact, entirely free from predators during that period of the breeding cycle; a similar immunity was observed during the previous October.

Section 3. METHODS OF OBSERVATION

THE birds were observed each day for periods of varying lengths depending on the weather and on the amount of activity within the rookery. On a cold and windy day it was seldom possible to watch continuously for more than thirty minutes at a time, but normally the birds were inactive in these conditions. During warmer periods, except during the strongest winds, the observation time could be extended for as long as daylight lasted. In the complete absence of the sun at that time of the year daylight at midday was equivalent to little more than summer twilight in England, and the observation period was limited to a maximum of about three hours. The birds showed little activity by night in the absence of a moon, but on one occasion of full moon and clear sky, when the rookery was illuminated more brightly than at any time during the preceding short day, the birds were seen to be particularly active in preening and wandering aimlessly about the rookery area.

For the first few days observations were taken from a distance through field glasses, and the rookery was disturbed as little as possible. It soon became apparent that the sight of the observer on the rookery had very little effect on the behaviour of the birds, and most of the later observations were made from a distance of about ten yards. The penguins showed no interest at all in the observer's activities, beyond slight reactions to changes of position, sounds, or sudden movements, all of which were naturally kept to a minimum. If the observer remained stationary for a long period the birds no longer seemed to recognise his presence at all. On one occasion they formed a huddle around him which he was reluctantly obliged to break up after half an hour. When the observer approached to within two or three yards of a group, and continued towards them, the birds would move slowly away without showing undue alarm or upsetting their neighbours; in this way it was usually possible to isolate birds from the main mass when it became necessary to handle them for marking, examination, or the removal of an egg. Handling was always resented, and could lead to panic in certain of the birds, particularly those without eggs. Eggless birds were generally more active and wary than were the lethargic incubating birds; they would seldom stay within six feet of the observer, and catching them for marking usually developed into a chase unless they could be cornered among the rocks or driven into a patch of very deep snow. Incubating birds tended to group together or shuffle slowly along well-trodden tracks in the snow; in most cases they could be marked without the slightest difficulty or excitement. Their preference for following tracks and moving when their neighbours moved was put to good use whenever it became necessary to count the birds; by starting two or three off along a track the whole rookery could be persuaded to migrate slowly to another part of the area. It was then easy to count them accurately as they passed a given point. The different gaits adopted by incubating and eggless birds made it easy to count the two categories separately.

A few of the birds showed a surprising variety of recognisable behaviour characteristics by which they could be identified with certainty, but for the rookery generally marking was a necessary preliminary to study. It would have been possible to mark every bird in the rookery, and this was in fact contemplated. However, there is little doubt that exciting a number of birds at once would have engendered panic in the rookery, with the possible loss of large numbers of eggs and a complete subsequent alteration in behaviour. Birds were therefore marked only when their behaviour was of particular interest, or when their position relative to their neighbours was being investigated. Grey enamel paint was used, the birds being marked with one or two Morse code symbols. Morse symbols of dots and dashes were found easier to apply than Roman letters, and could be dabbed on from a distance using a paint brush on the end of a light pole. The birds usually made some attempts to preen off their marks, but never in fact succeeded and seldom gave the matter further attention. The grey paint stood out remarkably well against the background of yellow breast feathers, and could easily be seen in the dullest light.

Any author who attempts to describe and interpret the activities of penguins is sooner or later faced with a problem; that of presenting the most anthropomorphic of birds in a manner which maintains their avian character and dignity. The solitary human being in the rookery of penguins is unusually liable to attribute personalities and human characters to his subjects, partly in a subconscious desire for companionship and partly in a bond of sympathy and admiration for animals which so successfully deal with their trying environmental conditions. A mechanical interpretation of their activities is as misleading as an interpretation in human terms, lacking as it does an acknowledgement of the resilience and vitality shown in every one of the birds' actions. In an attempt to avoid both pitfalls the author adopted the policy of observing in as objective a manner as possible, with conscious attempts to keep incidental interpretations to an absolute minimum. This policy resulted in the accumulation of a mass of notes from which recurring behaviour patterns have been extracted; interpretation has followed in the light of post-mortem examination results and other data which were not available at the time of observation. In this report, specific instances of "typical" behaviour are quoted in full whenever a subsequent interpretation is attempted; the author is well aware that far simpler patterns than those described can be interpreted in many different ways.

The comparative rarity of such a colony, its small size, and the peculiar personal charm of its inhabitants provided three sound reasons against the killing of large numbers of birds—eight were killed in all. (See Appendix). As the sexes could be distinguished only after dissection this imposed a limitation on the research. The removal of eggs for embryological studies was somewhat illogically felt to be less reprehensible, and a series of embryos was collected; these are the subject of a later report.

Section 4. BREEDING BEHAVIOUR

I. LAYING AND INCUBATION

Preliminary Observations

THE party arrived at the Dion Islets late in the evening of a short winter day, and the author visited the site where the birds had been seen in the previous year. The slope seemed deserted in the dim light, until a sudden sound from the nearby camp brought the whole scene to life. A large "boulder" in the middle of the area fell apart into a mass of shuffling penguins, and scattered "rocks" lying in the snow stood up and moved away. The birds were strangely silent, walking stiffly or hobbling unsteadily away from the observer. Eventually they settled again into small groups or pairs. Three abandoned eggs showed that breeding had started, and it seemed that once again the Emperor Penguin had forestalled those who came to inquire into its breeding habits.

However, during the first few days it became apparent that laying could only just have begun, and the behaviour of a number of eggless birds provided the clues necessary for an assessment of the situation. The whole matter would have been simplified considerably if marking and observation had started earlier; by June 5th the behaviour of late arrivals, superimposed on the pattern set by the earlier birds, complicated the picture considerably. At this stage the problem of identification was particularly acute. The identity of a bird could not be related to a known point on the ground, as is the case with the territorial penguins, and

continuous movement within the rookery made it almost impossible to follow the activities of a particular subject for any length of time. Random marking would certainly have upset the rookery considerably at that early stage of incubation. Observations during the first few days were therefore limited rather to the collecting of general impressions.

It was obvious from the outset that the behaviour of Emperor Penguins was markedly different from that of other penguins at similar stages in the breeding cycle. The most striking contrast was in the complete absence of belligerence between the Emperors; for most of the time the birds stood quietly together in groups, displaying occasionally, wandering slowly from one point to another, or sleeping. The absence of nest sites has already been mentioned; associated with this was a complete absence of any form of territorial behaviour. No behaviour which could be related either to nesting or to the defence of territory was seen on any occasion. No mating was seen, and only the faintest traces of epigamic display could be found. Apart from the complex and universally employed "exhibition" ritual described below, the behaviour patterns were all markedly simpler than those of the more familiar territorial penguins.

The absence of copulation at this period is worthy of comment. Copulations could have occurred either on the rookery site before the arrival of the observers, or elsewhere before the rookery assembled. The numbers of birds in the rookery increased rapidly in the first few days of observation, suggesting that the rookery was still in the process of assembling when observation started. It therefore seems that copulation occurred earlier and elsewhere, a conclusion which is not wholly inconsistent with other remarkable features of the birds' breeding habits.

Grouping and Huddling

Although during the first few days of observation discrete pairs could be recognised, and many birds with or without eggs were seen in isolation, a tendency towards group formation characteristic only of Emperor Penguins could clearly be distinguished from the outset. In the rookery the birds showed a marked preference for standing together in irregular lines or masses, so that on no occasion were birds found in more than about one third of the available space. The most highly developed manifestation of this tendency was seen in the "huddle", a formation which occurred only during the incubation period and depended for its existence on extreme lethargy in the birds themselves (see Fig. 6).

During the first days of observation the birds were generally scattered across the rookery area in three or four loosely formed groups. These were composed mainly of incubating birds, with eggless individuals and a few ill-defined pairs keeping to the outskirts and extending onto the sea ice. Within the groups the customary attitude was a shoulder to shoulder stance, forming lines and circles of sleeping birds. Eggless birds wandered restlessly, pushing their way through the silent incubating groups. Some left the rookery, moving across the sea ice to the west where more could be seen travelling in both directions. After a week it became apparent that the number of pairs and individuals was decreasing, while the groups were enlarging and consolidating. Fewer birds left the rookery, and those on the sea ice either joined the groups or disappeared from the area altogether. The numbers of birds in the rookery increased from 100 on June 5th to 153 on the 10th, gradually stabilising to 143 as eggless birds left and the flow of traffic ceased (see Fig. 7). The number of eggs increased rapidly at first, then more slowly to June 22nd; the last eggs were laid one week later (see Case 2 below). The incubating birds gradually settled into more compact groups, in which they were joined from time to time by the few remaining eggless birds. Small huddles were seen on many occasions, but the first complete huddle in which all were involved was found on the morning of June 20th. (Plate 1, Fig. a). The group covered a circular area about 15 feet in diameter, with the birds packed together as tightly as possible in the customary standing position. All faced towards the centre, leaning slightly inwards with beaks resting on the shoulders of the birds in front. This was a response to a particularly cold and unpleasant day, with temperatures slightly above 0°F. and a strong wind. The birds on the windward side of the group were seen to lose no opportunities of forcing their way into the middle; occasionally one would leave the windward side altogether and walk around to rejoin in the shelter provided by the rest of the birds.

Huddles tended to form overnight in particularly cold weather. When investigated, the birds were usually found to be asleep, but easily disturbed. An unusual sound—the howl of a dog from the nearby camp or the rustle of the observer's windproofs—was sufficient to alarm them; birds on the perimeter, usually eggless, would break away and approach the observer, and inquiring heads would shoot up from the

mass, lunge at each other, and subside. After a few alarms of this kind the huddle would break up into smaller groups, re-forming only when darkness fell once again. Rather less than half of the incubation period was spent in huddling by most of the birds; a few of the eggless ones preferred occasionally to lie in the snow on the leeward side of the group, or stand preening in front of the observer until a sudden urge drove them back to dig their way into the periphery of the huddle.

As observations continued it was seen that, during the incubation period, huddles formed whenever the weather approached certain recognisable degree of discomfort. Later, after the eggs were hatched, the birds remained apart during extremely bad weather conditions, showing far more activity generally and less tolerance of each others' company. The necessity for such a method of heat conservation among inactive birds was suggested by an experiment with a single marked bird, TT, which was isolated from the main rookery in a spell of cold weather. At a temperature of –24°F. with a slight wind blowing, when the main mass of birds had formed a tight huddle, TT was seen to be shivering, at first slightly and later more violently. Birds on the outside of the huddle occasionally shivered after short periods in that situation—their reaction was to press forward into the centre of the group as soon as shivering commenced. Ten more birds placed near to TT in the course of a separate experiment formed a small huddle on their own, which TT joined overnight. Shivering in these circumstances indicated that heat losses from the solitary or exposed birds were sufficient to invoke special measures in order to maintain body temperature. TT's heat losses were obviously considerably greater than those of the huddled birds, and may, in fact, have been greater than the bird could afford over a long period. Assuming the rate of loss of heat in these circumstances to be proportional to the area of surface exposed, comparison of the surface areas of the huddle and of a single bird suggests, at a conservative estimate, that losses per bird from the former are about one sixth of the losses from the latter. The inadequacy of TT's defences against cold is apparent; it seems probable that no isolated bird would be able to survive the winter in the inactive state required for incubation.

A second formation, adopted by the birds in milder conditions, is an effective but less extreme form of mutual protection. The birds stand in what may be termed "open conclave", in a solid group or in a series of lines and crescents (Plate 1, Fig. b), with backs to the wind and in the lee of each other as much as possible. This formation occurs particularly during strong winds with temperatures above 25°F., conditions which can be tolerated for long periods by an inactive observer suitably dressed. In calm weather with a comfortable temperature range the birds stand in unorganised groups, preening, sleeping, or merely incubating quietly.

Aggressive Behaviour

Huddling, and group formation generally, are characteristic of the Emperor Penguin; they require degrees of proximity between individuals which would not for one moment be tolerated by any of the territorial penguins. They have a distinct value to the species in its extraordinary environment, and must depend on the maintenance of peace between individual birds. It was of interest therefore to see how very few of its neighbours' movements hold any aggressive significance to an Emperor Penguin, and how its own responses to surprise, interference, or open attack are directed towards escape rather than defence.

Animosity among Emperors is engendered by small, apparently innocuous movements. A bird pushing into a huddle from the outside, or stumbling forward while shuffling in line invariably evokes an aggressive response in its neighbours. A more striking response is seen when a huddle is disturbed; birds in the middle of the group, on raising their heads to investigate an unusual sound, are immediately attacked by their neighbours. The common element in all the evocative movements is a forward and upward movement of the head and beak. The movement is also found in the response, which takes the form of a series of lunges towards the offending bird. These lunges, delivered with head and beak only, are always peculiarly ineffectual, seldom striking home and with very little force behind them. They release aggressive movements in other bystanders which retaliate in kind; in the case of the huddle the responding neighbours are in turn attacked by their neighbours, most of which were probably unaffected by the original stimulus. A similar lunge appears at the conclusion of the "exhibition" ritual, when both birds involved dart their heads in all directions; this is described in detail later. In all cases the lunges are accompanied by short, low pitched, gutteral croaks or growls.

Other sudden movements not involving head or beak were generally ignored by other birds. On many occasions a bird would be seen standing in the middle of a sleeping group, stretching, gaping, and fanning

its flippers violently after a period of sleep. In the process it might be beating its neighbours soundly about the head and chest, an error of judgement which would be found unpardonable in most communities, but which caused not the slightest disturbance among the Emperors. Flipper beating is not generally used as an aggressive movement, and is not apparently recognised as such by other Emperors.

If threatened, the Emperor's first consideration is retreat. If compelled to defend itself, weak lunges or pecks are the only means at its disposal. A bird captured and held for marking, if agitated, occasionally grasps the captor with its beak, in a grip which for the size of beak seems ludicrously inadequate. Meanwhile, it beats the air slowly and powerfully with its flippers, showing little ability to use them adequately in defence. If placed in the prone position on the snow (a position which it attempts in its struggles to adopt), the flippers propel the bird forward in an escape movement similar to that of most other penguins. This is essentially the movement which the birds use while swimming slowly on the surface of the water; the feet are used to provide extra power and steerage. The strength of the strokes may be judged from the fact that on one occasion the author was dragged twenty yards across the sea ice while attempting to mark a particularly lively and active bird; the effortless ease with which the penguin accomplished the feat was indicative of the enormous reserves of power lying in the pectoral muscles. It seems, however, that the Emperor Penguin uses this power only for movement, whether in the water or on land, and has never developed it for aggressive or defensive purposes.

With no predators on land, its supreme ability in the water, and no territorial ambitions or responsibilities, there can be few occasions in the life of an Emperor Penguin when an ability to fight is of any advantage. There is, unfortunately, no positive evidence for the absence of aggressive behaviour during mating; none was seen among the late arrivals at the rookery, and no relics of aggressive behaviour were detected. It seems likely, in view of the small importance which pairs of breeding birds seemed to attach to each others' company, that mating behaviour would cause as little excitement and bother as the remainder of the birds' activities.

The "Exhibition" Display

The "exhibition" ritual or display referred to earlier in the text is a remarkably constant feature of the birds' behaviour. It seems in fact to be a mode of expression used, with little variety, in all conceivable circumstances. When first seen as a performance between two birds one of which held an egg, it was assumed that a mutually stimulating display involving the egg, possibly as a preliminary to a change of guardian, was being demonstrated. The ritual was later seen performed between two eggless birds, and then between two, both of which held eggs. Eggless and incubating birds gave solo performances in front of the observer or entirely on their own on the opposite side of the rookery. Finally, the captive birds, which were eventually hand fed and to a limited extent responsive to their keepers, gave the display in reply to calls from the author or any other member of the expedition Base. This was, in fact, the only display of its kind shown by the birds involving a sequence of actions which could be evoked by stimulus. The display may be described as follows:

(i). The displaying bird (if two or more are involved, the originator) drops its beak suddenly onto its chest (Plate 2, Fig. a). This may be preceded by a short period of posing with the beak slightly elevated above the normal position.

(ii). Simultaneously, the bird raises the feathered fold of abdominal skin, exposing the egg, chick, or empty space. (Plate 2, Fig. b).

(iii). Leaning forward slightly, and apparently emptying lungs and air sacs, with head pressed low on the chest and neck curved in a graceful loop, the bird gives vent to a very distinctive cadence of sound, with a definite and complex rhythm and melody. The beak is almost vertical at this stage, and the head may be turned slightly so that the vivid auricular patches are visible to a bird standing in front of the exhibiting bird. (Plate 2, Figs. b, c and d).

(iv). The fold is lowered after a slight pause, the bird raises its head, and then sweeps its beak backwards rapidly over its shoulder with an irritated low pitched growl. (Plate 2, Fig. e). This often leads to an exchange of lunges with its neighbours.

When a responding bird faces the displaying bird, the responder performs the ceremony in exactly the same way, starting and finishing two or three seconds later than the originator. The cadences of the

responder are delivered usually about one tone lower than those of the originator; this is a function of the office rather than of the individual.

The cadence described is almost certainly the "interrupted musical cry" of Wilson (op. cit. p. 18). It is probably also the call of "greeting" given by birds encountered by various parties among the pack ice or at expedition bases. Its significance is discussed later.

Rookery Organisation

To understand the organisation of the rookery it was necessary to find out as early as possible the relationships existing between incubating birds, and to explain the significance of the departures seen during the first few days. It was at first assumed, by analogy with the known life-histories of other penguins, that the rookery, as seen on June 5th, contained a number of breeding pairs, that half the birds present would eventually hold eggs, and that the remainder would periodically take over the duty of incubation. It soon became apparent that this was not the case; the number of eggs increased until most of the birds present were incubating. Furthermore, the incubating birds, which tended to stand together in groups and small huddles, showed no signs of being paired. A few recognisable pairs, eggless or with one egg between them, remained on the outskirts of the groups; their behaviour was quite distinct from that of the grouped birds. In an attempt to discover whether or not pairs could be distinguished within the groups, a small compact assembly of a dozen birds was spotted with marking paint from a distance, without disturbing the birds. A few hours later, after the rookery had shifted its position slightly, the spotted birds were seen to be distributed completely at random among the rest of the rookery. The experiment was repeated later with similar results, the conclusion being that no affinities suggestive of pairing could be detected among the incubating birds.

Meanwhile, the existence of pairs outside the groups could be demonstrated more clearly. The scattered birds tended to sit or lie together, exhibiting to each other frequently, and following each other in pairs about the rookery. This was the limit of their epigamic display at this stage. The pairs seemed to be loosely bound, with no elaborate rituals serving to stimulate the members mutually; their behaviour contrasted sharply with that of the territorial penguins at an equivalent stage in the breeding cycle. On occasions when two or three pairs were sitting near to each other it was sometimes difficult to tell which birds belonged to the respective pairs. As the number of pairs decreased, the behaviour of the remaining birds was thrown into sharper focus, and it became possible to follow the sequence of events through which each pair was passing. Two cases are quoted in detail as showing behaviour typical of the period; the second case relates to a pair which actually produced their egg very much later than the rest of the birds, a fact which did not appear to affect details of their behaviour in any marked manner.

CASE 1. June 10th. Birds "X" and Y were seen standing together outside the groups over a period long enough to suggest they formed a breeding pair. "X", although not marked by the observer, was distinguishable by bloodstains arising from a grazed flipper. Both were eggless. On the morning of the 11th both were standing in the main body of the rookery; they were together and Y held an egg. The egg was removed by the observer and placed before "X", who had been displaying; "X" showed no interest and would not pick it up. Later in the day "X" was seen exhibiting, with Y responding. On June 14th "X" was missing from the rookery.

CASE 2. June 16th. Two eggless birds were seen lying on the snow away from the main groups. Dalgliesh and Jones reported "unusual behaviour", involving rolling in the snow, the stretching of neck and flippers (probably comfort movements after sleep) and the copious eating of snow. The prone resting position was in itself an unusual sight at the time. The two were marked E and G respectively, G being considerably fatter and stronger than E. They were seen in each others' company frequently during the ensuing days, always slightly withdrawn from the rest of the rookery, and remaining on the outskirts of any huddles which formed. On June 29th, long after the main body of the rookery had settled down to incubation, the two were again seen standing together, bowing and posturing in a marked manner. E was then seen to be holding an egg. A ceremony was witnessed which had not previously been observed. The birds stood facing each other, a few inches apart. G touched the tip of its beak on the snow between E's feet. E moved slightly forward, pressing G's head between their breast-feathers. G raised its head and in turn shuffled forward, pushing E gently back. At this point two eggless birds approached to within three feet; both E and G lunged slightly at them without altering their position, then gave the "exhibition" cadence and reply. After standing perfectly motionless for ten minutes G again touched the snow with its beak and pushed gently forward. E suddenly stepped back, and relinquished the egg. Both "pointed" to it with their beaks, and G picked it up after some

hesitation. The exhibition ceremony was again completed, initiated by both birds in turn; E then turned sharply, walked down the snow incline to the sea ice, crossed the tide crack, and made off towards the south. This was remarkable in being the first departure recorded for thirteen days. On the following day nine more birds followed E's track.

In both cases eggless birds behaving as pairs subsequently produced an egg between them. The possibility that the eggs had been taken from other birds was not overlooked; in the light of Wilson's report such behaviour was in fact expected. However, all observations before and after the events of Cases 1 and 2 combined to show that eggs were very seldom relinquished by incubating birds, and then only if the other member of the breeding pair (describable as such on independent evidence) were present to pick it up.

A third case, rather more complex in detail but with a similar underlying pattern, was seen at a time when only three pairs of birds remained in the rookery.

CASE 3. June 17th. Two birds, previously noted as a possible pair although unmarked, were standing as usual slightly apart from the main rookery, one holding an egg. The incubating bird suddenly walked away, leaving the egg lying in the snow. Its behaviour was completely unexpected and without visible warning. The second bird, noticeably thinner than its mate, picked up the egg without hesitation. This bird was marked AA. The egg was removed from AA and placed between the two birds. The first, later marked BB, ignored it, but AA once again picked it up. AA then leant over and lunged at a number of bystanders, including BB. On the following day the two were again seen together, both eggless, and an abandoned egg was seen in the snow. This was presented in turn to AA and BB. Both approached with interest; AA straddled the egg, lunged at BB, and appeared to be trying to take up the incubating position. AA then walked away a few paces, and BB went through exactly the same performance. A third eggless bird, BS, then approached and showed interest, pecking the egg gently with the tip of its beak. All three stood around the egg, excited, and lunging frequently at each other. After half an hour AA and BS fell asleep, and BB sat watching from a distance of a few feet. One week later AA was missing from the rookery.

The behaviour described in Cases 1 to 3 was by no means confined to the pairs mentioned; similar behaviour in fragmentary form was seen throughout the rookery during the first few days of observation. Its significance, however, was not apparent until the marked birds had been followed through their sequence. The actual relinquishing of the egg was rarely seen, but this is hardly surprising in view of the activity in the rookery at the time. The pattern underlying the three, when applied to the group as a whole, clearly shows how the rookery came to be composed almost entirely of incubating birds; in each case one of the original pair, after holding or showing interest in an egg, left the rookery. The interference of the observer in Cases 1 and 3 altered the subsequent behaviour of the other member of each pair.

In Cases 1 and 2, the birds which later left the rookery were the ones which held the eggs when the behaviour was first noticed. This was not so in Case 3, and very little significance can be attached to it; during the early stages of observation a number of exchanges could have occurred without the knowledge of the observer. It is perhaps more significant that, in Cases 2 and 3, it was the smaller bird of the pairs which left. A fact which was not apparent at the time, but which emerged later (see Section 6), was that incubation was undertaken throughout by the male birds; the females were therefore leaving the rookery at this stage. The question of a "dimorphism" arising from widely different feeding habits at different times of the year is discussed later.

The three cases showed that, for at least a short time after laying, transference of the egg from one bird to the other of a pair was a normal procedure. A few abandoned eggs, found mainly in patches of soft snow which incubating birds negotiated only with difficulty, were mainly newly laid. This suggested a laxity in the matter of early incubation which disappeared as the incubation period progressed; Wilson's report mentions the discovery of eggs at a similar stage of development; it is possible that they too were dropped by birds in which incubation behaviour was not fully developed (op. cit. p. 6). At the time when this conclusion was reached the birds had passed the stage at which tests could be made, but the observer's notes contain references to birds which, on the first and fourth days of observation respectively, had failed to retrieve their eggs after being deprived of them. The behaviour of AA and BB, in marked contrast to that of E and G, had suggested that both were on the threshold of being prepared to incubate, with BB losing interest and AA in an indeterminate state.

It was by this time known that most of the incubating birds were unwilling to part with their eggs. The behaviour of birds in relation to abandoned eggs was therefore a matter of considerable interest. Cases 1, 2 and 3 had suggested the existence of an incubating "urge" which varied in intensity from time to time,

and evidence for such an urge was seen every day in the rookery. Various tests were therefore devised in an attempt to find out why some of the birds incubated all the time while others remained eggless, and what happened to incubating birds when their eggs were removed. In most of the experiments frozen eggs or ice filled shells were presented; the real eggs were removed for embryological studies. None of the birds seemed in the least aware of the difference. Particular attention was paid to the question of whether or not eggless birds were willing to incubate if given the opportunity, as previous writers had suggested; observations showed that in fact most of the eggless birds present preferred to remain eggless.

CASE 4. June 9th. Two birds were sitting together preening away from the main group. One held an egg, which the observer removed without undue disturbance and placed on the ground. Both continued to preen their neck feathers, showing no interest in the egg. After five minutes the bird which had originally held the egg suddenly stepped forward and replaced it under the fold. The other remained unmoved.

CASE 5. June 9th. An egg was rolled toward two birds which were sitting together away from the main rookery. One already held an egg; neither showed interest. The egg was then rolled toward a group of four eggless birds. All showed great interest, examining it closely from all angles but not attempting to touch it. The previously mentioned pair "pointed" at the egg (i.e., stared fixedly with lowered beaks) but did not move towards it.

CASE 6. June 12th. A bird was selected, marked N, and its egg was removed. A few minutes later it was seen standing near to the place where the egg was removed, staring about the ground in all directions. A frozen egg was rolled to within eight feet of it. The bird continued to search, exhibiting frequently and showing agitation. After five minutes it appeared to notice the egg for the first time, walked straight over and picked it up. It incubated the frozen egg for the rest of the incubation period.

CASE 7. June 14th. An egg was rolled toward a suspected pair, one of which was incubating. The eggless one showed interest, leaning forward and pecking the egg gently, then approaching as though to pick it up. After a few moments it returned to its partner. The experiment was repeated ten minutes later, with the same result. The egg was then rolled actually between the feet of the bird; after initial slight alarm had subsided the bird stepped over the egg, pecked it gently, and then ignored it completely. A passing bird, eggless, "pointed" at the egg and walked on.

These examples are selected from many as showing behaviour typical of the various categories of eggless and incubating birds. Eventually it became possible to predict the response when the history of the bird was known, allowing a small amount of latitude for expression of individuality. The following categories could be defined:

(a). Incubating birds. These generally showed no interest in abandoned eggs. Some would "point", a pose in which the bird leaned forward slightly craning its neck forward to stare fixedly at the egg. None ever attempted to take up a second egg if a complete egg was already in position. It is interesting in this connection to see that King Penguins (*Aptenodytes patagonica*) with similar methods of incubation are recorded as attempting to take up a second egg and place it above the one already in position (Murphy, op. cit. p. 348, and Rankin, 1951, p. 127). Birds incubating unsatisfactory material, an egg shell or snowball, as a result of having recently been deprived of their own egg, readily exchanged such material for a complete egg, and those with only a small bulk of material under the fold frequently continued to rake in other shell fragments, etc., until a satisfactory bulk was attained.

(b). Eggless birds. These showed reactions which varied with the history of the individual.

1. Birds recently deprived of their eggs by the observer usually showed particularly strong responses to abandoned eggs, or to objects reminiscent of their lost eggs. When any alarm due to handling had passed off, interest was at a maximum. Interest then fell rapidly, but at a rate which varied considerably between individuals. In general terms, a bird deprived of its egg would search the surrounding snow for a time ranging from ten to twenty minutes, exhibiting freely and showing agitation (Case 6). In some cases an egg near by or alongside the bird would be missed completely, while one twenty feet away would be seen immediately. Frequent lunges and aggressive passes would be made at nearby birds, but in no case was a bird seen to remove an egg from another bird. An egg found would be picked up with every sign of satisfaction, the bird using its beak to roll the egg directly onto its feet. Replacement of the egg would invariably be followed by a series of aggressive lunges in all directions, whether or not other birds were present in the immediate vicinity. A bird in the condition of searching for its egg would readily take up an extraordinary variety of substitute objects, ranging from a brown leather camera case to dead fish—so long as

the object was of a suitable size, and portable, the shape and colour seemed immaterial. The incubation urge was usually lost after a bird had spent two or three hours without an egg, although in one remarkable case a bird left a loose huddle shortly after midnight and picked up an egg lying five yards away, to replace its own which had been removed eight hours previously. The bird's tracks in the snow showed clearly that the egg was picked up as the object of a direct journey, and not in the course of casual wanderings about the rookery.

2. Birds from which eggs had been removed some time previously, and birds which, so far as was known, had never incubated during the current season, often showed a certain amount of passing interest in abandoned eggs (Case 5). BS, an eggless male which remained in the rookery for the whole of the incubation period until killed as a specimen, was outstanding in this respect, occasionally straddling an egg as though to pick it up, only to abandon the attempt a few moments later. Others, particularly when strolling in groups of two or three, would generally pause and "point", often pecking the egg gently and examining it closely (Plate 4, Fig. a). With the exceptions cited in Cases 1 to 3, no birds in this category were ever known to pick up abandoned eggs. Many of the eggless birds left the rookery before the end of the incubation period. They usually departed in groups, after a prolonged period of huddling (see below).

On the few occasions when an egg was dropped accidentally, it was always picked up immediately by the same bird. Exceptions to this were seen at the beginning of the incubation period, and have already been mentioned. After this initial period eggs were dropped only when the birds were hurried unduly or when they walked through soft snow; in either case a lengthening of the bird's hobbling steps was necessitated, splitting in halves the cradle formed by the tarso-metatarsal bones. In response to these dangers, the birds hardly ever moved voluntarily from established paths through the snow, and never hurried. After a heavy snowfall the first paths were always cut by the eggless birds; often the soft snow would remain untrodden for days, while the birds spent all their time congregated along the Gallery, or huddled in the Saucer. The birds show remarkable tenacity while holding their eggs, and are capable of extraordinary acrobatic feats. Scratching the back of the head with the claws of one foot while balancing and holding the egg firmly on the other was seen on a number of occasions. Again, a bird holding an egg was seen to cross a nine inch wide crack in the ice by falling bodily across and dragging itself forward with beak and flippers. Similarly, birds have been known to fall over small precipices, roll down snowy slopes, trip over rocks, tumble heavily on slippery bare ice, or navigate their way among very rough sastrugi without releasing their grip on the eggs. A bird held off the ground will continue to hold its egg while struggling to free itself, releasing the egg only when completely overtaken by panic.

The Significance of the Rookery Area

Aspects of the behaviour of bird TT have already been described. The case is of interest also in showing the behaviour of certain birds when separated from the main rookery and removed from the rookery area. TT was marked originally on June 22nd, as an incubating bird which seemed to be associated closely with another incubating bird EM. After marking, TT moved slowly down the northern side of the promontory onto the sea ice under the guidance of the observer, until it was out of sight of the other birds and about 100 yards from them. It was incubating quietly, seemed very lethargic, and was quite unperturbed by its unusual surroundings or the attentions of the observer. During this period it was seen to be shivering and showing signs of excessive heat losses. Although its track over the hard, windblown snow was clearly visible, it made no attempts to return to the rookery. On June 26th ten more birds were moved slowly down to a position fifty yeards southeast of TT. Of these, three were incubating birds and the remainder were eggless. On the following morning TT had joined their group. During subsequent bad weather the small group huddled whenever the main rookery huddled; in general their behaviour mirrored that of the birds in the rookery itself. On July 17th, a particularly cold and windy day, they moved fifty yards to the south, finding shelter among brash ice. On July 19th one of the group, BS, was killed for specimen purposes. On the following day D_1, a very timid bird from the small group, eggless, suddenly showed agitation, left the group, walked around the outside of the promontory, joined the main rookery from the south side, left again almost immediately and headed out toward the open sea. On July 25th two more eggless birds D_2 and D_3 left the group and followed D_1's tracks to the main rookery. On July 31st, the day when hatching commenced, all the remaining birds in the small group moved slowly along the same path to rejoin the

main rookery. This coincided with increased activity in the rookery itself and also with an influx of birds from the sea.

It was originally supposed that some form of barrier would be required to separate one bird from the main rookery. TT, however, showed no inclination to return, although within earshot of the remainder of the birds and with a clear return track over hard snow. The other ten similarly remained in isolation until, apparently, stirred by the onset of hatching. Both eggless and incubating birds were included in the small group; their reluctance to move could not, therefore, be ascribed merely to the lethargy of incubation. It is significant that their return to the rookery coincided with the return of the main mass of birds from the sea.

Summary

As a result of the observations made during the incubation period it was possible to form a picture of the rookery organisation, and speculate on the significance of the behaviour seen. It is convenient to summarise the points already dealt with before proceeding to a description of activities on the rookery after incubation:

1. The Dion Islets rookery, on June 5th, 1949, was composed of incubating birds, eggless pairs and possibly a number of unmated individuals. In the absence of territories the pairs were sometimes difficult to define; distinctive epigamic display was extremely limited, and members of pairs paid little attention to each other in this post-copulation period. Egglaying extended from about June 1st (on the evidence of some of the earliest embryos) to June 29th. Most of the eggs were laid in the first week. Between 145 and 150 eggs were laid, and it is therefore supposed that about 150 breeding pairs are accommodated on the rookery. There was no evidence to suggest that pairs laid more than one egg each, or that replacement eggs were laid when the originals were lost.

2. The eggs, when laid, were passed possibly more than once between the members of the pairs. Each egg was eventually held firmly by one member, the male, while the partner left the rookery. The partners did not return during the remainder of the incubation period; incubating birds therefore held their eggs for periods of up to two months without respite. Some of the birds deprived of their eggs for experimental purposes left the rookery also, usually in small groups after long periods of huddling. No birds entered the rookery, after the initial period of flux until the first of the returning birds arrived on July 19th, preceding the return of the main mass by twelve days.

3. After the initial period the eggs were not generally transferred from one bird to another. Incubating birds showed a strong urge to continue incubating, eggless birds showed "interest" in eggs but no inclination to incubate. Incubating birds were generally lethargic and disinterested, eggless birds were active, responsive, and more individualistic in behaviour. Birds deprived of their eggs lost their incubation urge within a few hours and took on the characteristics of eggless birds.

4. The Emperor Penguins showed a degree of communal behaviour unique among the penguins in their lack of animosity, propensity for huddling, and absence of territorial behaviour.

5. The rookery area was seen to occupy a position of varying importance in the lives of the birds, an importance which could not simply be related to the territorial attraction. Birds moved while incubating showed no inclination to return to the rookery until the onset of hatching. This point is discussed later.

II. HATCHING AND FEEDING

Onset of Hatching

THE month of July passed slowly and on the whole uneventfully, with incubation progressing steadily and few departures from the rookery. Biting winds with low temperatures caused the birds to huddle for days on end. The re-appearance of the sun after a two-months absence seemed to pass unnoticed in the rookery; the birds in the small group turned towards the bright light at midday on the 18th, when the sun appeared for a few moments above the horizon, but the main mass slept undisturbed in their huddle. The first indication of renewed activities and the end of the incubation period came on July 19th, with the sudden arrival of an Emperor Penguin from the north-east.

Its repeated call note, a single short interrogative cry, was heard for some time before the bird was actually seen; the cry was repeated by more than one bird on the rookery area, and the huddle, which had lasted continuously for four days, dispersed immediately. The direction of approach was somewhat unexpected, as all departure had been to west and south. However, open water was known to exist at that time of the year between Adelaide Island and the mainland and is it possible that the bird had travelled over the sea ice from that direction. The bird appeared, tobogganing at high speed over the wind-packed snow, and apparently in a state of great excitement. It stopped and gave the "exhibition" display in front of the author, who was standing directly in its path to the rookery, and then moved on, displaying again before climbing over the tidecrack onto the island. This bird was marked FS later in the day; its identity from the first was never in any doubt as it was considerably larger and more substantial than any of the other birds. FS had an appearance of prosperity and grooming which contrasted sharply with the faded and emaciated condition of the rest of the birds; their steadily decreasing weight and progressive shabbiness had been overlooked by the observer in the absence of a standard.

FS joined the nearest group of penguins in the rookery and exhibited before an incubating bird, which responded. This was repeated four times within as many minutes, after which FS pushed forward, causing the incubating bird to step aside. It was immediately obvious that FS was attempting to secure either egg or chick to hold, in an action which was to be seen many times within the next few weeks. The exhibition was repeated before a number of other birds in the group, each time followed by a gentle push from FS, which in no case resulted in the dropping of an egg. The bird was excited and extremely active during its first day on the rookery; by the following day its behaviour had altered considerably and was indistinguishable from that of the other eggless birds. Its excretory products were yellow, the normal colour for a feeding bird, in contrast with the green bile-stained products of the fasting birds.

The arrival of FS was apparently premature by twelve days. During the following week the level of activity within the rookery rose considerably, but no more birds entered the rookery. The incubating birds wandered restlessly and displayed more frequently than had been their practice, until a gale, starting on July 27th, drove them into a tight huddle. The weather became particularly unpleasant, with low temperature and drifting snow; the birds in their huddle remained watchful and more alert than usual, raising their heads at the slightest sound and grunting angrily when their neighbours moved.

On the morning of July 31st a spectacular change had occurred. The weather was still bad, with clouds of drifting snow periodically obscuring everything. But the birds were lined out across the rookery area, displaying and calling almost continuously. Above the roar of the wind a new sound could be heard—the shrill voices of chicks. The small group, which had spent so long on the sea ice, was moving slowly around the outside of the promontory, and a group of three new arrivals appeared suddenly from the north. It was obvious that hatching had commenced and was causing considerable excitement; so far as could be judged about thirty chicks had hatched out overnight; one was picked up dead from the site of the previous evening's huddle. Few fragments of shell were seen, but any large pieces would undoubtedly have been swept away by the wind.

In the course of the day five new arrivals were recorded. In each case their behaviour followed the pattern set by FS, and by late afternoon three of the five had secured chicks. The process was simple; after displaying, the new arrival pushed steadily on the chest of the responding bird. The latter either turned away maintaining its hold on the chick or stepped backwards leaving the chick lying on the snow. In the latter event the new arrival would scoop the chick up and hold it firmly on its feet, while the other bird stood by exhibiting, apparently reluctant to leave the chick and its new guardian. In one case the new arrival experienced difficulty in holding the chick securely; the other bird appeared to make strenuous efforts to take the chick whenever a part of it appeared, but the new arrival finally held it securely and the other wandered away. Incubating birds, if pressed by a new arrival, turned away without releasing their eggs. In one case a new arrival marked TD secured a chick on the morning of July 31st, held it throughout that day and on the following morning, but had relinquished it, possibly to another new arrival, by the late afternoon of August 1st. The bird D_6, from which the chick was taken, was seen in the rookery on August 1st without egg or chick; it had not made a dash for the open sea and supplies of food as might have been expected in the circumstances. It was particularly noticeable that TD and D_6 did not associate together at all after the transfer of the chick. They did not, in fact, appear to form a breeding pair. As more and more new arrivals crowded into the rookery it became increasingly obvious that securing a chick was a random process. The birds did not return to specific partners with the object of securing

specific chicks, but passed rather from one to another until they found a bird willing to surrender its burden.

The birds which were still incubating after the first few days of August showed considerable resolution in holding their eggs. In no case was a returning bird successful in securing an egg, and an egg taken experimentally from an incubating bird would be picked up again without hesitation. Hatching eggs on the other hand seemed to be regarded with some suspicion; on more than one occasion a hatching egg, with the chick's head protruding, was seen lying on the snow, with two or three eggless birds standing about it listening intently and with obvious interest to the sounds which issued from it. Occasionally the birds would touch the egg gently with the tips of their beaks, but no efforts to assist the chick in its struggles were ever seen. Usually, such an egg would be taken up, and the relinquishing of hatching eggs by birds which had previously held them with determination might well have been in many cases the opportunities required by returning birds. One egg was, however, the object of interest for three eggless birds for over half an hour. The struggles of the chick ceased after ten minutes, and the egg was eventually abandoned completely by all the birds.

Struggles between Adults.

Actual competition between the returned birds was first seen a few days after the onset of hatching. On August 6th a total of 109 birds was seen to be holding either eggs or chicks, and over 140 birds were on the rookery area. Of the unoccupied birds, many were undoubtedly anxious to hold chicks. They moved from one bird to another, exhibiting and pushing in the manner described. Eggs passed to them experimentally by the observer would be held for a few moments and then dropped, often to be picked up by other eggless birds. If presented with a living chick, their response was immediate; the chick would be swept firmly onto the feet and held there. On a number of occasions the frozen chick was used in experiments with these birds, Case 8 describing a typical example of their behaviour at this period.

> CASE 8. August 6th. A large bird, Q, was holding the dead chick, somewhat awkwardly as a result of the chick's shape and rigidity. A second bird, unoccupied, exhibiting before Q, pushed forward and succeeded in dislodging the chick. Q recovered the chick while the other was attempting to place it in position. Q then moved away, but dropped the unresponsive chick in the process; a third bird, Z, picked it up. All three birds struggled together, each trying to sweep the chick to safety, digging their beaks into the snow and pushing hard against each other. A curious feature of the struggle was that no animosity seemed to be engendered; each bird treated the other two as obstacles rather than rivals. After a few minutes a second object, a small frozen fish about six inches in length, was introduced into the struggle by the observer. This was immediately taken by one bird, and then stolen by another. Three more unoccupied birds joined in the struggle, and the six pushed their way back and forth across the rookery area, often leaving both chick and fish apparently forgotten. Eventually the six stood upright, and the one nearest to the two objects placed both on its feet. In moving away, it dropped the fish, which was then picked up by another of the six. The game continued.

This was undoubtedly the sort of struggle which Wilson and others have described. Wilson (op. cit. p. 12) compares the struggle to a football "scrimmage" with some accuracy. It must, however, be stressed that these struggles took place only after the period of incubation—nothing resembling them was seen at any time previously.

Later observations showed that the unoccupied birds responded only to the movement of an abandoned object, or to the struggles of other birds over abandoned objects. With few exceptions, a dead chick lying in the snow would be ignored completely (Plate 4, Fig. A). If the chick were moved by the observer, or accidentally kicked by a passing bird, all the unoccupied birds in the area would converge upon it. Interest was maintained so long as the object was kept moving; if it passed out of the "scrimmage" it would frequently be ignored. The sight of a struggle, with a chick or object somewhere beneath it, would often bring unoccupied birds in from the opposite side of the rookery area.

NB, NH and FS, three unoccupied birds, together with three other unmarked and unoccupied birds, spent most of one day in a series of struggles of this nature. Their object was a piece of eggshell about two inches square. While it remained on the ground, all were disinterested. As soon as the wind or a passing bird disturbed the shell slightly, all piled onto it vigorously. Then the fragment would again be abandoned, until one of the contestants showed more interest than the others, perhaps leaning over to touch it with the tip of its beak. Immediately the remainder would throw themselves at it. If one succeeded in pushing

the shell onto its feet, the others would retire until that bird shuffled off. The shell would invariably fall out, precipitating another violent but quite impersonal struggle. The dead chick, the frozen fish, a bar of chocolate in a red and white wrapper, and a heavy Contax camera were all introduced into the game at different times. All produced exactly the same effect on the birds, irrespective of colour, shape and size. However, a living chick introduced while the birds were preoccupied with the chocolate bar produced an immediate effect; the chick was taken in preference to all other objects. Later in the day, when the six birds had dispersed to different parts of the rookery, NB, NH, and FS were introduced individually to the objects which throughout the day had caused so much excitement. In each case the response had altered completely; the birds showed no more than a passing interest, and finally ignored the objects completely.

The interest which the unoccupied birds displayed in moving objects on the snow was simple enough to demonstrate at any time when the birds were assembled. The value to the species is clear; a chick abandoned for a few seconds has only to wave its head in a characteristic movement to be descended on by a horde of anxious adults (Plate 4, Fig. b). It was, however, noticeable that although NB, NH and FS, to quote only three examples, always featured prominently in the struggles, they were never in the course of the experiments prepared to hold the chicks for any length of time. FS, the early arrival of which has already been noted, never held egg or chick for longer than an hour; its method of holding was distinctly unprofessional and inadequate, usually resulting in almost immediate loss. Similarly, NB and NH, two birds which returned from the sea soon after the hatching began, never held a chick for more than ten minutes at a time. Experiments with living chicks were rarely attempted, involving as they did considerable personal danger to the chicks themselves; the few which were tried, and the occasions when chicks were accidentally dropped, showed results very similar to those obtained with the use of dead chicks or inanimate objects. It was apparent that not all the unoccupied birds were prepared to hold and feed the chicks, although all were stimulated by the sight of one.

By marking certain of the new arrivals it was possible to follow their movements in sequence, and find out which of the returning birds were in fact prepared to undertake guardianship. To this end eleven were marked on August 4th; two days later four were holding chicks, four were unoccupied, and three had disappeared. At this time many birds were scattered on the sea ice, particularly to the south and west, and it seems likely that the missing birds would have been found among them. On August 9th the four which had held chicks previously were still holding chicks, and all the remainder of the original eleven had disappeared. It was therefore apparent, if the behaviour of these could be taken as typical, that birds which were unsuccessful in securing a chick soon after their arrival in the rookery remained unsuccessful for the remainder of their stay. All appeared to show the same degree of interest on arrival, and the question of whether or not they were successful in obtaining the custody of a chick was probably decided by the reactions of the first few birds visited. Those birds which managed to secure chicks started almost immediately to feed them, and in this rests a possible explanation of the birds' behaviour. Murphy's suggestion (op. cit. p. 361) that the interest of feeding birds might decline as their stock of food decreased by digestion within the crop, allowing others with full crops to assume guardianship, can be extended. Birds which did not secure chicks immediately, and therefore lost the opportunity of feeding chicks, retained sufficient interest in the chicks (i.e., were sufficiently stimulated by the sight of abandoned chicks) to participate in struggles and take up the chicks for short periods. This casual interest, a relic of a much stronger predecessor, ensured that the chicks, if dropped, were never abandoned completely to the mercy of the weather; in addition the struggles drew the attention of other unoccupied birds to the existence of an abandoned chick, ensuring that sooner or later a suitable guardian would be found.

As was the case with the eggs, the chicks which found security on the feet of an adult were safe from the attentions of all others. They sat as a rule with their own feet squarely placed on those of their guardian, facing forward under the canopy provided by the adult's fold of feathered abdominal skin. For the first few days it was impossible for the observer to tell with any certainty whether a particular bird held an egg or a chick; frequently the chick's head could be seen as it waved up and down in almost incessant supplication. The newly hatched chicks were for all practical purposes naked, with the finest of grey down merging into the black and white head pattern which Wilson has so beautifully and accurately depicted in his report. Their lack of adequate covering is probably of considerable advantage to them, in that they may absorb heat more readily from a bare patch of skin which appears under the abdominal fold of every breeding bird; as D'Arcy Thompson (1942, p. 35) has pointed out, there may be additional advantages in a thin covering for small animals.

Chick Feeding

The chicks were fed by the regurgitation of material from the guardian birds' crops. Feeding was first seen on July 31st, when a bird which had spent the previous two months in the rookery regurgitated food material to its newly hatched chick. This was later seen in many other cases, and there is little doubt that it is the normal practice. The food was seen in one case to consist of strips of epithelium or similar tissue invested with fat globules. Green flecks suggested the presence of bile, and a number of stones and fragments of cephalopod beak were included; the whole was no doubt a secretion of the crop wall together with hard material from the crop itself. Most of the three-day-old chicks examined contained pebbles sufficiently large to be felt through the abdominal wall.

Later, feeding was undertaken by the new arrivals. Post-mortem examinations on some of these showed that each returned to the rookery with about seven pounds of triturated food material, consisting almost entirely of fish. The food was transferred in a way which seemed to involve considerable discomfort for the guardian. A bolus of food material was passed upward to the back of the throat, often with some difficulty, and this was nibbled by the chick which reached upward into the gaping beak of the adult. The remainder of the bolus was then swallowed, to be regurgitated again a few seconds later. In a crowd of birds bystanders would often show considerable interest in the process, watching the feeding closely and exhibiting frequently. On no occasion did a bystander assist in the feeding of a chick.

Although feeding was normally accompanied by the almost continuous whistles of the chicks, on more than one occasion circumstances suggested that the feeding response was evoked in other ways. In one case, a chick was removed while being fed, and a large fragment of eggshell was substituted rapidly. Five minutes later the bird had recovered composure and resumed its feeding activities, regurgitating and gaping over the unresponsive shell. Later, on August 10th, a bird was seen holding a hatching egg. The chick had managed to extricate its head and one flipper, and was obviously far too preoccupied with its struggles to consider the question of feeding. The adult, however, was calmly regurgitating over it in an attempt to feed it, dropping the egg occasionally to examine it closely, and continuing with the feeding when satisfied. A third case, of a bird attempting to feed an egg, was reported by H. D. Jones, and at least one case was seen of a bird presenting food to a chick which was either asleep or dead. The act of regurgitation was clearly shown to be a function of the physical condition of the guardian, with the presence of an object on the feet acting as the trigger mechanism required to initiate the activity. It is possible that the whistle may have assumed importance as a means of ensuring that feeding continued after the adult bird's initial impulse to feed was spent.

Huddling and Group Behaviour

Only one huddle formed after the beginning of the hatching period. This occurred on the third day, August 2nd, when winds of over ninety miles per hour swept over the rookery, accompanied by temperatures of about 0°F. Equally strong winds were experienced two weeks later, with slightly higher temperatures; the birds on this occasion grouped closely together along the Gallery, but made no attempt to huddle. In these conditions the birds crouched in the normal upright position, with backs to the wind and eyes closed—if disturbed their nictitating membranes were used to protect their eyes from the stinging drift snow. In calmer weather the birds remained in open groups spread well across the rookery area—the few remaining eggs were incubated quietly, the chicks demands for food were attended to, and the calm, busy atmosphere of the rookery was disturbed only by the occasional rushes of the unoccupied birds. New arrivals could always be identified by their air of eagerness and vitality, and the appearance of the rookery changed as the drab, weary incubating birds were replaced by the newcomers. With the increased activity of all the birds, huddling was no longer necessary; it was particularly noticeable that the remaining incubating birds always adopted the closest formation, in a steadily diminishing group which retained its identity to the end of the observation period. By contrast, many of the unoccupied birds wandered in groups of twenty or thirty about the sea ice, returning to the rookery area periodically, but not in these journeys attempting to secure chicks.

End of Continuous Observations

The last observations of the period were taken on August 15th. By this time the numbers in the rookery had increased to 183, while many more birds could be seen travelling to and from the sea across the sea ice

to south and west. Open water was visible a few miles away, and local wet patches and leads made the ice about the islands uncertain. Many birds which had been marked while incubating, and had subsequently disappeared from the rookery, were by this time returning to feed the chicks. The scene was gradually assuming the form seen by the observer in his visit during the previous year. Four captive adults and a chick were taken with the returning party to the Base, and observations on these birds helped considerably in bridging the gap between the two years' observations.

An observation made during the previous year may be mentioned at this point. The chicks in October, 1948, were seen to be massed together in a *crêche*; observations made on the captive chick in 1949 suggested that the *crêche* would form in September, allowing a greater number of birds to leave the rookery on feeding journeys. No evidence was seen for the adoption of any particular chick by returning birds. *Crêche* formation was similarly reported from Cape Crozier and Haswell Island. It was interesting to see that, when disturbed, the chicks crowded together in the centre of the rookery, with a ring of adults forming a barrier about them.

The mortality rate among eggs and chicks in the Dion Islets rookery was considerably less than the 77% recorded at Cape Crozier; by the end of the period of continuous observation six chicks had died through natural causes (careless parental handling or hatching difficulties) and six eggs were either abandoned or found to be addled at the end of incubation. Interference by the observer may have caused some of these fatalities, but this is unlikely. Twelve deaths in a total of about 150 eggs gives a mortality rate of 8%. Taking into account possible potential fatalities among the eggs which were removed for embryological work, the natural mortality rate for the year up to August 15th would not have been higher than 10%. Only seventy chicks were present in October, 1948. If these were the remnants of a brood similar in size to that of 1949, a 50% mortality rate is indicated, although it is difficult to imagine the reasons for so high a death rate between August and October in any year. No dead chicks were seen in 1948, and no predators were in evidence.

Section 5. OBSERVATIONS ON CAPTIVE BIRDS

Return from the Rookery

BY the middle of August the sea ice was undergoing rapid deterioration locally, and the edge was breaking back towards the Dion Islets. For various reasons connected with the scientific plans of the expedition both men and dog teams were required for other work, and the party returned to Base after an absence of exactly three months. In order that observations might be continued into the summer it had previously been decided that a small number of birds should be transported to the Base, and preparations had been made for their reception. Accordingly, four adult penguins were selected shortly before the party left the rookery, and these were placed in a specially constructed plywood case built on the front of the author's sledge. Of the birds taken two held chicks and were in fact engaged in feeding them when apprehended; the other two were unoccupied birds. Local names were, of course, applied as the birds became domesticated, but they bore little relation to sex and eventually became confusing; for the sake of simplicity the birds are described in this report as A, B, C and D respectively.

They travelled quite calmly over the fifty miles of sea ice, wedging themselves firmly into the corners of their partitioned sections during rough passages, and sleeping in the normal standing position while the sledge travelled smoothly. Stout wire netting protected them from the attentions of the dogs at night. Unfortunately one of the chicks was killed shortly after the birds were captured, and B, its guardian, was seen occasionally to pick up the dead chick and attempt to feed it. On the last day of the journey the sledge overturned, and in the ensuing mêlée the remaining chick, which had previously been in the custody of A, transferred its attentions to B. Shortly after their arrival at the base, however, the chick was again seen to be in A's care.

The birds were transferred to a large pen and were left undisturbed for twenty-four hours. On the following day feeding began. The four adults were fed on locally caught fish (mainly *Trematomus pennellii*) of length between six and eight inches. For the first three weeks forced feeding was necessary; the birds showed no recognition of fish as food in the circumstances and the violent struggles which accompanied each feeding time were not conducive to rapid learning. Bird A started to take food from the author's hand

long before the others could be persuaded to do so. A was responsible for the feeding and protection of the chick and was therefore fed more frequently than B, C and D.

Behaviour in Captivity

The group soon settled down after the journey, and within a few days were showing as little fear of observers as had been shown by all the birds in the rookery. C and D were on the whole uninstructive. Most of their time was spent in the northwest corner of the pen, the side nearest to the Dion Islets and the open sea. C on one occasion held the chick for a few moments, but neither showed any interest in the rearing at all. Later, when the chick left its shelter on the feet of A and wandered about the pen, C and D showed definite signs of antagonism, lunging when the chick pestered them for food. They finally escaped from their pen on October 25th during a blizzard, when a large snowdrift built up inside and allowed them to walk out over the top of the wire netting. Their tracks were followed for about half a mile in a west northwesterly direction, but were soon lost on the iron hard surface of the sea ice. They had been receiving a ration of rather less than one pound of fish per day, and this was apparently sufficient to keep them in good condition during the short period in which they were observed.

A, B and the chick were more responsive and their progress and activities became a focus of interest for all the members of the Base. B, which had originally held and fed a chick, and had shown interest in the chick at the Base during the first few days, lost all interest and took no part at all in the rearing. A took control from the outset, and acted as permanent guardian for over four months. The chick was fed entirely by A until early January, when the condition of the adult made direct feeding necessary. The actual amount fed to the birds daily varied with the supplies available and the apparent needs of the birds. B received on the whole the same weight of food as was supplied to C and D; A, on the other hand, frequently received more than the other three rations combined. During the first month of captivity A was given about 1¼ lb. per day. This was increased during October to 3½ lb. daily, in response to the incessant demands of the growing chick. Finally, in November and December, A was receiving over 6 lb. of fresh fish daily. This necessitated the catching of about fifty fish every day, and fishing became a spare time occupation in all weathers for everyone at the Base.

Growth and Development of the Chick

The growth of the chick was observed closely, its weight and certain measurements being recorded two or three times each week. The chick showed every indication of good health and steady progress towards maturity; in October its growth had reached a stage closely similar to that seen in chicks during the visit of the previous year, and the steady food supply allowed by its guardian ensured that no undue strains were placed upon its digestive system by unsuitable foods. Its growth curves are therefore considered to give a fair indication of the course of development which would be seen in the rookery itself.

The weight of the chick at hatching was unknown. Two newly hatched chicks weighed on the rookery (although on a balance which had been damaged and was not reliable to within two ounces) were found to weigh fourteen and fifteen ounces respectively. Six eggs weighed on the same balance averaged fifteen-and-a-half ounces, a figure which compares closely with that given by Wilson (op. cit. p. 26). The hatching weight is therefore estimated at about fourteen ounces. The date of hatching was similarly doubtful, although by comparisons at the time of departure the date was estimated as August 6th. On August 27th the chick weighed thirty-six ounces, and from that date onwards a series of weighings is available. These appear in the Appendix in tabular form and as a growth curve (Fig. 4).

During the first week in September the chick spent progressively lengthening periods away from its guardian, returning to shelter during bad weather or when danger threatened. Its gait at this time was unsteady, and the head and neck seemed enormous in comparison with the minute body and flippers. An increasing sturdiness and steadiness of posture was noted, and by the end of the month the chick was able to control its movements far more satisfactorily. The growth curve at this period shows a slight deviation from the related exponential curve, suggesting a period of consolidation before the onset of rapid linear growth and weight increase.

The weights taken during September showed considerable variations and daily fluctuations, due to the fact that the daily food intake approached one fifth of the body weight. Later, a similar relation between body weight and food intake was seen, the intake being estimated as a very high proportion of the total

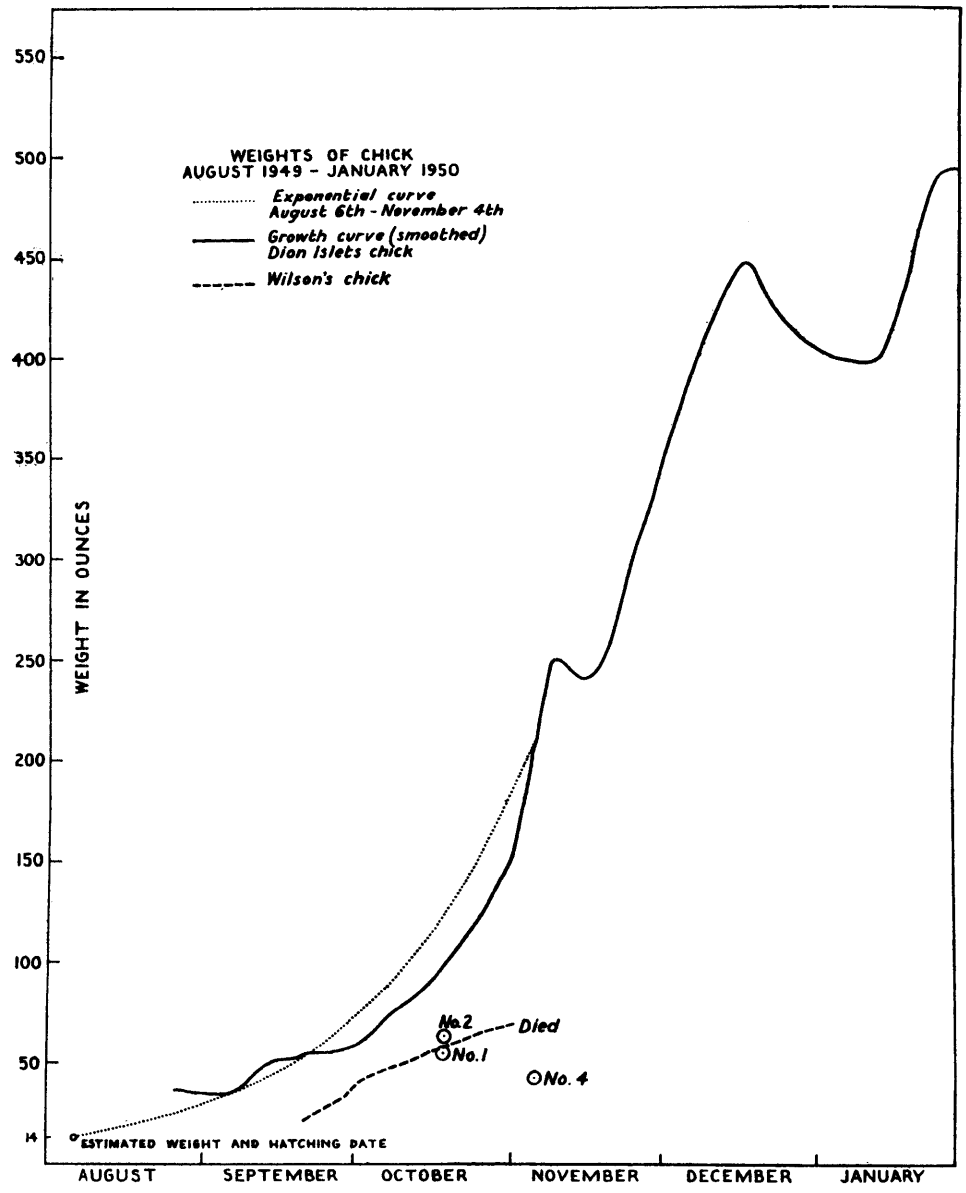

FIGURE 4

food supplied to the guardian bird. During October the chick's weight increased from sixty ounces to 110 ounces and growth at this rate continued until the second week in November. Here the chick experienced a slight setback; the adult avoidad feeding it for some days, possibly as a direct result of bad weather, and its weight fluctuated around 240 ounces for nearly two weeks before proceeding in the rapid climb which had started after the consolidation period.

The transition from neossoptyle to mesoptyle down had occurred during August, and throughout September and October the chick was covered in a dense grey furry growth; the first signs of the adolescent plumage appeared during the third week in November. Down was lost from the inner surface of flippers, which remained bare for a week before the first white feathers became visible. Simultaneously, black feathers appeared under the down of the outer surface. On December 6th blue tipped contour feathers appeared under the down of the tail and legs; three days later contour feathers were just visible on chest and back. The head and neck were the last to produce their feathers, which were first seen on December 16th. By this time large patches of down were missing from flippers, chest, and back, while the legs and tail were completely feathered; the chick had the somewhat undignified appearance of wearing a very ragged

and particularly dirty grey smock over a respectable and well-tailored suit. During this period the weight fluctuated considerably from day to day and did not increase; feeding was continuous throughout the moult, and it was apparent that all the available energy was being devoted to the production of feathers rather than to the process of growth. On December 25th the top of the chick's head was free of down, leaving grey patches about the eyes and neck as the last remnants of the mesoptyle covering. The auricular patches were the last to clear, and the moult was completed by the end of the first week in January.

The condition of bird A was by this time giving cause for concern; it was obvious that in spite of increased food allowances the bird was losing condition. The strain of feeding the chick was apparently very considerable. Early in January its condition suddenly deteriorated rapidly and the bird died on January 6th. Post-mortem examination showed that the normal reserves of subcutaneous and visceral fat were completely and startlingly absent; although the direct cause of death was probably due to an inflamed and doubtless infected intestinal tract the bird was obviously suffering from malnutrition. During the previous two months it had received six pounds of fresh fish daily, but its condition suggested that none of the food had been used by the bird itself in its own metabolism; all had been fed to the chick. The bird was, in

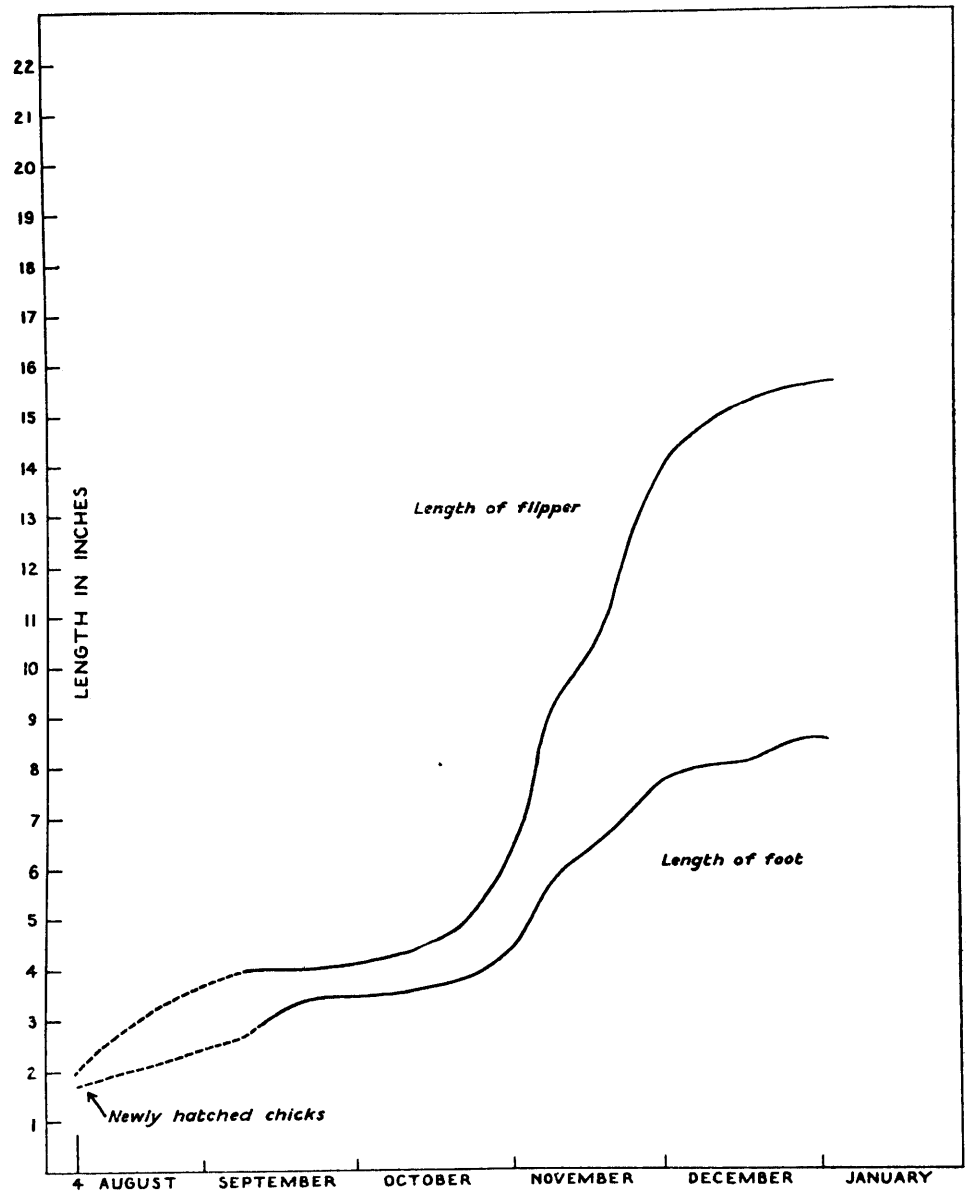

FIGURE 5

fact unable to feed the chick and itself simultaneously, and would in normal circumstances probably have taken periods of a few days in which to replenish its own stores between bouts of chick-feeding. The examination also showed that this bird was a male.

The chick was fed directly on fish; it was by this time sturdy and well proportioned, and was making unsteady attempts at the "exhibition" cadence. B seemed extremely healthy and calm, displaying and calling vigorously whenever a member of the Base approached the pen. Its weight on January 10th was 50 lb., marking the loss of 8 lb. during captivity. Fish was in very short supply during January, and it was not possible to feed B more substantially in preparation for its moult; it was in fact necessary to feed both birds occasionally on canned fish, apparently without ill effects.

The birds were, on the whole, left to their own devices as much as possible; apart from their daily feeds and an occasional spraying down with sea water in warmer weather they saw little of their captors. The story of their subsequent transfer to the Regent's Park Zoological Gardens is written elsewhere (Stonehouse, 1951); observations on the birds in Antarctic conditions ceased later in January, and the only other information gained from them appeared at their post-mortem examinations—both were shown to be female.

Data collected from the growing chick included periodic measurement of flipper and foot lengths (see Fig. 5). All were subject to greater personal errors than were the weights, and their curves are presented mainly for comparative purposes. Slow growth during the consolidation period is indicated in all the curves, followed by an acceleration in late September and October corresponding to the rapid weight increase of this period. The sudden and rapid lengthening of the flipper is particularly marked. The mid-November setback shows clearly in foot and flipper growth curves, and both respond to the onset of the moulting period. Lengths of beak (gape to tip) were also taken periodically. At five months the length of beak agreed to within 0.1 in. with the figure quoted by Wilson (op. cit. p. 21) for chicks of that age.

Comparisons with Cape Crozier Data

Interesting comparisons can be made between the growth curves of the Dion Islets chick and the weights and measurements taken by Wilson from a number of Cape Crozier chicks. Assuming that growth rates in the early stages are fairly constant it is possible to estimate the dates of hatching of the chicks concerned. A set of figures given by Wilson (op. cit. p. 26) relating to a hand-reared chick appears in the Appendix, and these figures have been plotted alongside the weight curve of the Dion Islets chick for comparison. Growth is seen to be slightly slower in Wilson's chick, probably as a result of unsuitable feeding, and the rate of increase in weight falls considerably before death. Wilson's estimated hatching date of September 3rd is shown to be reasonably accurate by comparison, and the chick is seen to be about one month behind the Dion Islets chick throughout its development. The weights of three more of Wilson's chicks, those which were taken alive and were therefore known to have reached certain weights by certain dates, have also been plotted. Of these, Nos. 1 and 2 compare closely with the curve, but No. 4 is obviously a much later bird.

There is, therefore, evidence that three Cape Crozier chicks were hatched at least within the first week in September. If these may be taken as representing the main mass of chicks to be hatched in that year, and if this in turn may be taken as a normal year, it will be seen that events in the Cape Crozier rookery were later by about three weeks or a month relative to corresponding events on the Dion Islets. Wilson states in his report (op. cit. p. 8) that chicks of successive years were as nearly as possible identical in size on corresponding dates, an observation which suggests normal conditions, but the question of whether or not the three chicks hatched during the peak period cannot be settled on available evidence. In the Dion Islets rookery, most of the eggs were laid during the first and second weeks of observation; if similar rates of egg laying existed at Cape Crozier the peak laying period might have been anywhere between mid-August and mid-September. It is clear that a difference of timing does exist between the two rookeries, but the exact discrepancy cannot be determined accurately. Such a discrepancy would, of course, be expected in view of the 9° difference in latitude between the two rookeries (Baker, 1938).

It may be of value at this point to introduce Murphy's observation (op. cit. p. 356) that no significant morphological distinctions could be detected between adult birds taken in the Ross Sea area and those taken in the Weddell Sea. Such isolated colonies might possibly be expected to give rise to races or subspecies, but no trace of such differentiation can be found at present.

Section 6. DISCUSSION

THE work so far attempted in the Dion Islets rookery has been concerned mainly with breeding behaviour. A few points have emerged incidentally in the course of the investigations which throw light on other aspects of the life history of Emperor Penguins; in addition the unpublished records of the *Endurance* Expedition have been found to contain certain observations on migrating birds which add detail to the story told by Wilson and others. The activities of the birds can now be traced throughout the year, and can be related more directly to those factors in the environment which control them. There can be little doubt that an environment so rigorous as that found on the shores of the Antarctic must exert a very considerable influence on animals which attempt to colonise the region. In this discussion the effects are considered firstly in relation to the annual cycle as a whole, and then in relation to details of the breeding behaviour.

The Environment

The discomforts of the Antarctic have unfortunately been exaggerated to the point of absurdity. This does not in itself become important until the effects of the discomfort on species living within the area are considered. Some of the spectacular aspects have been stressed at the expense of the more commonplace features; one hears more of the effects of cold and darkness than of the effects of a semi-permanent layer of ice over the sea or of prolonged spells of continuous light in the summer. Extreme temperatures are more widely known than average temperatures, and the effects of Polar weather on men from temperate zones are considered rather than the effects on animals which are clearly and obviously well adapted to such conditions. Emperor Penguins have been presented as a race of giants in the twilight of their existence, struggling valiantly but quite hopelessly in an almost Wagnerian setting of darkness and cold. This is not an accurate picture, and it is not the picture which Wilson drew in his clear and factual account.

Animals do not live in environments to which they are unsuited; the inhospitable shores of Antarctica would long ago have disposed of unsuitably equipped forms of life however "valiant" their struggles. As more and more colonies of Emperor Penguins are found at widely scattered points along the coast it becomes increasingly obvious that the birds are numerous and successful. However rigorous and exacting their environmental conditions may be it is quite clear that the species has discovered ways of living which enable it to deal successfully with those conditions.

Climatic data are available for short periods in both Cape Crozier and the Dion Islets rookeries; the effects of weather on birds and men cannot, however, always be judged from temperature and wind speed figures. The personal discomfort experienced by the penguins in varying weather conditions is a matter which cannot accurately be assessed by human standards. So far as could be judged, however, from their behaviour, their own sensitivity to cold was similar to that of the observers who were watching them. Discomfort experienced in cold climates is related to combinations of factors rather than to extremes of any single element; the activity, state of health, and degree of acclimatisation of the subject must also be taken into account. In general terms an active person suitably clad has little difficulty in keeping warm in air temperatures as low as $-40°F$ or $-50°F$, so long as there is no wind. Extreme discomfort can, however, be experienced in temperatures forty or fifty degrees higher in light or moderate winds. At still higher temperatures below freezing point the "warmth" of the wind may be appreciated by an acclimatised person even though the air temperature is actually so low. In the case of an inactive person, when the temperature gradient across the clothing is not maintained, cold is felt more readily and higher temperatures in calm air or light winds can produce acute discomfort. It was noticeable that during incubation the huddle formed whenever sub-zero temperatures were experienced accompanied by light winds, or whenever stronger winds with temperatures up to 15°F were recorded. These were exactly the conditions which the inactive observer found most uncomfortable. The huddles usually dispersed during the warmer gales, suggesting that the birds also found these more tolerable. It was noticeable that the birds became progressively more inclined to huddle as the weeks of incubation passed; they were living during this period entirely on their reserves of fat, and the increased lethargy and tendency to huddle was no doubt associated with a slowing down of metabolism.

If, then, it may be assumed that the birds were no more affected by cold than were the men who watched them, and that huddling formed for them a reasonable answer to very cold weather, it will be seen that cold in itself could hardly be a controlling influence of outstanding importance in the birds' lives. The fact that they spend the coldest part of the winter in their rookeries suggests that other controlling forces

are stronger. Their comparatively large size, low surface-volume ratio, and relatively small extremities are, as Murphy pointed out (op. cit. p. 358) all consistent with the minimising of heat losses, and there is little doubt that they are unsurpassed in their ability to withstand low temperatures over long periods.

A factor in their environment which is of paramount importance, but which has received very little attention so far, is the sea ice. Its importance as a site for rookeries has, of course, been mentioned, and Wilson's account of the migration of the Cape Crozier rookery onto the off-shore ice immediately prior to its dispersal suggests that the birds make use of floes and large ice pans in the initial stages of their annual journey to the north. But it is now clear that the presence or absence of the sea ice cannot fail to be a controlling influence throughout the year, and in fact the whole of the annual cycle can be related to its formation and dispersal. In the summary which follows particular attention is paid to the state of the sea ice in each month, and it will be seen that the activities of the birds are rigidly determined by what the sea ice will permit them to do.

The Breeding Cycle

March and April. The onset of the breeding season causes a southward migration of adult birds only; immature birds remain in the pack ice to the north. In comparison with other vertebrates it may be assumed that maturation of the gonads takes place in response to a steady alteration in day length; in this case, the length of day is decreasing, completely reversing the stimulus which brings other penguins into breeding condition. No particular problem is presented in such a reversal; work by Hoover and Hubbard (1937) on fish, and Yeats (1947) and others on mammals has shown that autumn-breeding animals respond to decreasing day lengths in a way which may be compared directly with the more familiar situation in spring breeders. The birds are feeding after their moult in their southward migration. Worsley in the *Endurance*, recorded a single moulting bird, an unusually late example, early in March in the Weddell Sea, and mentions the presence of many more in full plumage. Wilson (op. cit. p. 15) recorded a party of twenty-eight on March 30th, wandering offshore along newly frozen cracks in the sea ice endeavouring to find a place where they could enter the water. Nine days later a party of between thirty and forty was recorded, one of which tipped the scales at 90 lb. A few others appeared during the following weeks, the last on May 6th.

May. The southward migration continues into the belt of rapidly forming fast ice. The time at which this ice actually becomes established varies considerably with season and latitude; ice formed in April may be blown out or shattered by winds and swell in May, and earlier formation may be expected at Cape Crozier than at the Dion Islets. In both areas the sea ice has formed substantially by the end of May in normal years. This is of importance in the Dion Islets, where the ice affords protection from wave action for the incoming birds. At Cape Crozier ice is, of course, required for the rookery to assemble at all. Worsley reported seeing many birds in the Weddell Sea in May, all in outstandingly good condition and with one at least weighing 85 lb. He also makes the interesting observation that, of twenty-four immature birds killed in the pack in May, all but two were female.

June. In the Dion Islets rookery, egg laying is in progress. Birds arrived during the first few days, pairing and copulation occurred earlier and elsewhere. All the birds arrived from the west, and must have passed over twenty miles of solid sea ice. Feeding had ceased for many of the birds for a period of two or three months. The sea ice which protected their rookery necessitated their fasting; in this is seen the advantage shown by the birds in being able to carry with them enormous stores of fat, a capacity in which they cannot be equalled by other penguins. It is equally likely that fasting would be necessary at Cape Crozier; there the rookery would assemble on solid sea ice at the end of June. Many birds left the Dion Islets in early and mid-June to return to the sea, and similarly the departures from the Cape Crozier rookery would presumably be made early in July. It is noteworthy that Worsley's log recorded the presence of Emperor Penguins by the ship on only three occasions in June; other evidence in the same documents points to the existence of a rookery on the Caird Coast in Lat. 74° 07′ S., and it seems likely that the birds in this rookery would be engaged in their breeding activities at this time.

July. Incubation is in progress during June and July on the Dion Islets, late June, July and August at Cape Crozier. Few birds would be travelling across the miles of sea ice separating the rookery from open water.

August. Birds return to the Dion Islets to feed the chicks. In 1948 the return was well timed, with the

notable exception of FS, who arrived too early. The return is made over a rapidly diminishing stretch of ice; chick feeding involves many journeys to and from the rookery, and a good rookery site is therefore one which at this critical time is still safe from the direct action of the sea but is within easy reach of it. Feeding started at Cape Crozier in September, when the birds appeared to be fishing through leads in the ice. Worsley encountered birds with empty stomachs and average weight of 55 lb. in August; these were clearly birds which had incubated their eggs and were on their way to open water.

September onwards. These months would be characterised by rapid increase in the tempo of feeding, and many changes would be occurring in the ice of both rookeries. By Cape Crozier the ice splits under the action of lateral pressure from the active face of the Ross Barrier, allowing the birds to fish within easy reach of the rookery. By the Dion Islets the ice weakens under the action of strong currents forcing over reefs and shallow water patches. In both cases the rookeries are still protected from the open sea. Enormous quantities of food are required by the growing chicks, and by the birds themselves in proceeding from incubating condition to premoult condition. Weights of adult birds taken in November show considerable increases over the weights of some of those recorded earlier in the season; in the Bay of Whales, 1940, the weights of twenty-two ranged from 52 to 68 lb. (Friedmann, 1945) and eighteen specimens taken by the second Byrd Expedition ranged from 60 to 84 lb., averaging 70.1 lb. (Siple and Lindsey, 1937). Wilson records a similar average figure from the west side of the Ross Sea.

The chick reared in captivity was ready for the sea in early January. By this time it was quite probable that the Dion Islets rookery as a whole had broken up after a migration onto the sea ice. Further south in Marguerite Bay, an immature bird had been encountered by a sledging party on January 12th, 1949, testifying to the dispersal of the rookery by that date. At Cape Crozier and Haswell Island the birds were moving out to the ice edge in November and December, when the chicks were in full down. Worsley reported the presence of chicks in the last stages of moult floating on ice floes past the ship on January 12th, and this seems to be the normal method of migration, at least for rookeries which form actually on the sea ice. During the last few days of the moult the chicks are apparently left to their own devices, to dive into the sea when the fancy takes them and the condition of their plumage permits. The migration of the adults seems to occur independently; during the first few months of the year they may be seen in various stages of the moult, travelling well to the north of their breeding grounds among the pack ice of the sub-Antarctic.

The fate of the chicks is not known; they have been encountered on the breaking ice in mid-January, as self sufficient, small replicas of their parents in distinctive plumage. The duration of their adolescence, and their destination when sexually mature, are also doubtful. Detailed observations over many years, with adequate ringing schemes, would be necessary before information of this nature could be collected, and it does not seem that opportunities for such studies are likely to present themselves in the near future.

The sea ice therefore controls the activities of the birds in two ways. Primarily, it limits the choice of site on which a rookery may be established; a rookery must be protected from the sea in winter, and accessible to but not exposed to the sea in summer. The second effect is more direct in that it alters the whole of the breeding behaviour of the birds from the normal pattern seen in other penguins. The presence of many miles of solid ice between rookery and open sea during the incubation period prevents the birds from relieving each other in incubation duties. Long journeys over the ice at that time of the year would be fraught with danger; with the weather at its worst and both pack and fast ice impenetrable, a great deal of irreplaceable energy would be spent by the partners' travelling to and from the rookeries. The birds therefore adopt the more economical method in which half the birds incubate for the whole period, while the others feed, preparing themselves for the later work of feeding the chicks. Incubating birds live as quietly as possible, huddling together to minimise heat losses. This necessitates the elaboration of a type of behaviour totally distinct from that seen in any other species of penguin.

Breeding Behaviour

To an observer familiar with the activities of small penguins, the most striking difference between their rookeries and an Emperor Penguin rookery is the complete lack of aggressive behaviour in the latter. The Emperors do not acquire territory, and do not, therefore, defend it. A remnant of territorial behaviour may perhaps be seen in the spaced pairs of birds found in the rookery during the first few days of the breeding season, but all trace of this disappears after the eggs have been laid. Among the smaller penguins, on

the other hand, mutual antagonism arising from the necessity for defending territory have reached an extreme pitch. The behaviour of Adélie Penguins (*Pygoscelis adeliae*) may be cited as typical of the territorial birds; among the nests of a rookery the approach of an intruder of any kind is greeted by a crooned warning, and followed by a sharp attack. Birds passing a nest site are attacked on principle, and actual trespassers are dealt with in a most ferocious and effective manner. Away from the nests the birds tend to travel in parties, but each bird remains isolated from its companions; quarrels and exchanges of pecks or blows are frequent whenever neighbours approach too closely. The lack of such antagonisms among Emperors has already been mentioned; it permits the development of closer relations between individuals, the true value of which becomes apparent in the depth of winter. Group formation does not appear to be a marked characteristic of travelling birds, although the author has seen a group of migrating Emperors huddling in very closely formed groups some miles from the rookery in particularly bad weather. The mid-winter "huddle" marks the height of the grouping tendency. As the experiments with TT suggested, it is necessary for the birds to huddle in order that their body heat may be conserved; birds which are sufficiently tolerant of each others' close proximity to stand together in groups, and sufficiently sensitive to cold to appreciate the shelter provided by neighbours, will take up the formation automatically under the influence of weather which causes them discomfort. This seems to be the case with Emperor Penguins.

The suppression of aggressive tendencies, and the adoption of huddling propensities, are therefore necessary qualities in birds which spend the winter months in these particular circumstances. The reason why incubation must take place in mid-winter can easily be seen—the chicks take five months to develop into independent although immature birds, and their independence must be achieved at a time when the sea ice is open. The five months' growth period is surprisingly short in comparison with the year required by the nearly related King Penguin (*Aptenodytes patagonica*) chicks; this point is dealt with more fully later. But mid-winter incubation involves the acquisition of a number of other characters, as has already been seen in the description of the breeding behaviour. Periodic relief for the incubating bird by its partner is impracticable, and the presence of both birds on the rookery throughout the incubation period would be wasteful; one member of each pair therefore undertakes the duties for the full period of two months. This in turn requires the ability to amass enormous food reserves, as is clearly shown by the difference in average weights between birds which have incubated for two months and those which have fed continuously over a long period.

The question of which bird from each pair stays behind to incubate can be answered with some certainty, although few incubating or wandering birds were killed for sex-determination purposes. Simultaneously, the significance of the somewhat puzzling observations recorded in Cases 1–6 (Section 4) may be explained. The whole question is one of economy of effort. In any pair of eggless birds standing outside the expanding huddle early in the season, the female, on laying the egg, presumably has an urge to incubate. If a period of recuperation after laying is necessary, as it appears to be in most other species of penguin, her incubation urge must decrease and that of her partner must increase correspondingly. For a short period after egg laying, therefore, both birds show only spasmodic interest in holding onto the egg. This is a critical period in the life of the eggs as the number of abandoned newly-laid eggs showed. During this period the eggs may be passed back and forth; it is, however, significant that eggs in these circumstances are acceptable only directly from the partner—an egg abandoned on the ground is ignored. In this way birds are saved from incubating frozen eggs and protected from the dangers of losing physical condition over a period of two months to no purpose. As the incubation urge in the male increases, the female finds herself free to leave the rookery, and commences her journey over the fast ice to the sea. If now the male drops the egg accidentally, his incubation urge is sufficiently well established to cause him to pick it up immediately. If deprived of his egg, he too leaves the rookery in most cases. The varying, but usually slight, interest shown by eggless birds is, in these terms, a remnant of the incubation urge; those eggless birds which most often showed interest (e.g., BS) remained in the rookery throughout the incubation period. Evidence that the incubating birds were in fact male was not secured until the end of the observation period; it was, however, shown to be true in the birds killed (see Appendix). The mechanism providing the incubation urge is presumably hormonal, acting on the direct stimulus of the presence of the egg.

The rather slender evidence on which it was concluded that the males were incubating (Stonehouse, 1952) has happily been backed by observations from the rookery at Pointe Géologie (Cendron, 1952). In a population of 5,000 Emperors found in June, 1951, about 88% held eggs. Of nine birds taken, six held eggs; all of the nine were males. During the return journey of the French party to its base, a group

of Emperors was found by open water under an iceberg about 60 kilom. from the rookery. Two taken at random proved subsequently to be females.

There was no indication in the rookery that any female returned to a specific male, or took charge of any particular chick; there is no family life. A most interesting point is the fact that the females returned to the rookery, after absences of up to two months, in time to feed the newly hatched chicks—the mechanism underlying this accurate timing cannot profitably be discussed until further data have been obtained. However, as a precaution against mistiming, and in order that the chicks may be fed during the period of indetermination when females have returned but males are still responsive to the sight of an abandoned chick, the males are provided with the means of feeding the newly hatched chicks. Examination of the crop of a male bird which was killed in the act of feeding a chick showed the presence of a large area of secretory tissue and about four ounces of semi-solid material in the lumen of the crop. This material, when fresh, was of the colour and consistency of scrambled egg; its secretion and analysis will be made the subject of a separate publication.

The importance of parental relations and pair bonds in this species is a matter of some interest. In the past an impression has been gained that in most species of penguins individual recognition between birds followed only as a result of epigamic displays, and that chicks were fed indiscriminately by adults. More recent work by Richdale (1951) on Yellow-eyed Penguins (*Megadyptes antipodes*) gives clear evidence of recognition between members of pairs in successive seasons. The author has investigated this matter in Adélie Penguins, in a small rookery in Marguerite Bay, and found that of ten pairs of birds ringed on marked nest sites in early January, 1948, five pairs returned intact to the same nest sites in the following season. Four other nests each contained one of its original pair mated to an unmarked bird, and the remaining nest was occupied by two birds from an adjacent area. Very similar results were obtained independently by other observers in the same season (Andrew and Roberts, 1951). Although these results show that individual birds form alliances which can be renewed annually, the importance of the nest site in providing ground on which recognition can take place must not be overlooked. Similarly, recognition of chicks in a small localised *crêche* may be at least facilitated by the position of the chick, a point which requires further investigation by carefully designed experiments. In the case of the Emperor Penguins all the evidence suggests that pair bonds were relatively loose, and that parents did not necessarily feed their own chicks. This may well be related to lack of territory, and of the recognition displays which are associated with territory.

The "exhibition" display is an aspect of behaviour which although clearly adapted to the birds' simple requirements, cannot be explained solely in terms of those requirements. Its performance can be evoked by a number of differing stimuli (see Section 4); its complexity and universal application suggest that it may be a relic behaviour pattern, combining the remains of a number of diverse patterns which were of use to the birds during a territorial period in their phylogeny. The display is generally released on the sight of a moving object; another bird, a dog or a man have been known to evoke the same reaction. Involving, as it does, the exposure of the brilliantly coloured neck feathers, the display may have in it an element of identification or epigamic significance. Movements of the abdominal muscles, with the resulting exposure of egg, chick, or unoccupied cavity, suggest that offspring have at some time been more significant in the display than they are at present. The aggressive terminating lunges may simply be relics of a time when crowding was not tolerated, when in fact the birds were territorially inclined. The combination of these elements, possibly with more which can no longer be isolated, has resulted in a single display which has no precise significance at all; it may be used for recognition, identification, mutual stimulation, or to express consciousness of the presence or absence of offspring. As the birds passed from territorial to non-territorial behaviour, the need for elaborate and specific display patterns was lost; degeneration of these patterns followed, and the curious "exhibition" display has resulted.

Its complexity makes this display particularly difficult to classify in terms of the relatively clear-cut behaviour "types" shown by other penguins and listed by Richdale (op. cit. p. 9). Although both "bowing" and "trumpeting" are involved, the display is clearly the direct equivalent of neither in function.

Evolutionary Considerations

In the light of newly acquired information it has been possible to suggest interpretations of some of the "eccentric" habits of Emperor Penguins which so puzzled Wilson during his studies. Their life history is

seen as a successful attempt to fit into a rigid environmental framework, and ways in which their evolution may have progressed have been indicated. In conclusion, these points are discussed relative to other aspects of penguin evolution.

The penguins form a well defined and easily recognisable group of birds; their precise taxonomic status is of no immediate importance to this study, and the question of their descent from flying or non-flying ancestors need not be discussed at the moment. Both controversies have been profitably pursued for many years, and the reader is referred to a recent paper by Simpson (1946) for information and bibliography. The geographical origin of the group is, however, of some immediate importance; the author is inclined to take the view, advanced by Simpson, that penguins are primarily birds of temperate latitudes, adapted for life in cold water. They originated in all probability in the zone of cool latitudes encircling the southern hemisphere rather than from the Antarctic continent itself. From this locus of origin groups have spread north and south, following cold currents to the Equator, to Africa, and to southern Australia. Fossil penguins from Miocene deposits are contained within a similar range; none has been found outside the southern hemisphere.

Of those penguins which penetrated southward into the sub-Antarctic and finally to the shores of the Antarctic continent, two size groups may be distinguished. The smaller birds are included in the genus *Pygoscelis*, *P. papua*, the Gentoo, *P. antarctica*, the Ringed or "Chinstrap" Penguin, and *P. adeliae*, the Adélie Penguin. Of these three species, the Adélies range furthest south of all. Their incubation periods approximate to thirty-five days, and development of the chicks to a state of fitness for the sea is similarly short, occupying from five to eight weeks. An important result is that the birds are able to complete their breeding cycle within the short space of time afforded by the Antarctic summer, a consideration which must be extremely critical in the case of the Adélie Penguins. The author's own observations on these birds have supported this point. In the summer of 1949 the sea ice remained firm in Marguerite Bay instead of dispersing in the normal way. During the following spring investigations on an Adélie Penguin rookery at Lagotellerie Island a few miles from the expedition base disclosed an unusual situation. Many penguin chicks were found dead on the rookery site, without doubt chicks of the previous year. They were in moult, almost fully grown in stature, but emaciated and with empty stomachs. It was apparent that their growth had been delayed, and that they were finally abandoned by their parents as a result of the acute food shortage engendered by the persistence of the fast ice. The Adélie Penguins in their life histories show many features which appear to be related to the sea ice formation and dispersal, features which have, no doubt, contributed to their success in colonising the actual coastline of the continent.

The second of the two groups contains only the genus *Aptenodytes*, with the two species *A. forsteri*, the Emperor Penguin, and *A. patagonica*, the King Penguin. The Kings, which are the slightly smaller species, are sub-Antarctic in range, being found in South Georgia, Kerguelen Island, etc. Their incubation period is of about fifty days, but their period of adolescence in down extends for over a year. The adults hold the single eggs on their feet throughout incubation, a necessary precaution in view of the quagmire which invariably forms about them. There seems to be little doubt that they are closely related to the Emperor Penguins; the marked differences in behaviour seen between the two species are therefore of considerable interest. Unfortunately, accurate descriptions of the behaviour of King Penguins are not readily available; it is a curious fact that, although the birds have been accessible to man for over 150 years, no major study of their natural history has so far been attempted.

Environmental pressure, the sum of those forces which tend to alter the structure and behaviour of a species to conform with existing conditions, is undoubtedly more marked in its effects on Emperor Penguins than upon the Kings. Birds of the more northerly ranging species are not, for instance, required to produce their eggs within a closely defined and rigidly circumscribed time limit; their laying season is extended over half the year (Murphy, op. cit. p. 347). They are, moreover, able to feed their young throughout the year and are under no obligation to curtail the development period. Their lives are less rigidly controlled by their environment, and it may be inferred that their behaviour and form is therefore closer to that of the stock from which both species evolved. Emperor Penguins may reasonably be supposed to have passed through a form of life history similar to that followed by the Kings; it is possible that they were territorial at one stage in their phylogeny. Evidence for this may be seen in the isolation of pairs early in the breeding season, and in the "exhibition" display, which may be interpreted as a curiously telescoped summary of the many separate displays required in a territorial life.

Geological records have so far yielded no information at all which would help to fix the time when the

two species diverged. It is clear, however, that the southward movement of the Emperors was accompanied by their gradual adaption to colder conditions. The birds may have increased their size slightly. They must have reached a compromise over the question of the length of time which could be allowed for development and the time of the year at which breeding could reasonably commence; the long incubation and development periods of so large a bird would clearly be an embarrassment when the species attempted to colonise the coastline of Antarctica. By reducing the period of development to five months, during which a small but self-sufficient juvenile could form, and by setting back the incubation period to a time of the year when little other than purely static incubation could be accomplished, the species could reach a state of finely balanced equilibrium with its environment, making use of the protection afforded by the sea ice and conforming in every other respect to its phases. It is significant in this respect that the incubation period itself has not markedly been shortened; there would be no advantage in reducing the incubation period at a time when no other activities are possible.

There would, however, be considerable advantages in the reduction of territorial behaviour and in the adoption of the distinctive way of life which Emperors have adopted. It is difficult to imagine any other way in which they could have resolved their basic problems of long growth period, and short season in which chick feeding is possible.

SUMMARY

THE discovery of a rookery of Emperor Penguins in Marguerite Bay, Graham Land, near to a base of the Falkland Islands Dependencies Survey, has made possible further studies of the birds. This paper is chiefly a survey of work undertaken in 1949, on the Dion Islets rookery.

A permanent camp was established by the rookery and breeding behaviour, with the exceptions of courtship behaviour and mating, was studied. The birds were seen to be non-territorial; pairs divided shortly after the laying of the single egg. The males incubated the eggs for the full period of two months in group formations which depended on the state of the weather. The females spent the whole of the incubation period away from the rookery, returning as the chicks hatched. The males fed the chicks at first from a secretion of the crop wall; later both parents carried fish from the sea in their crops, feeding by regurgitation. No family life was seen, the chicks entering a *crêche* at the age of five weeks. The mortality rate was considerably lower than that recorded at Cape Crozier. The growth of a captive chick is discussed.

An attempt is made to relate the unusual features of the birds' breeding cycle with certain factors in the environment; a close correlation is shown between annual changes in the sea ice and details in the annual life cycle of the birds. The mode of life is described as a compromise achieved by the birds between a long growth period necessitated by their size, and a short season in which chicks can be fed intensively. Details of the birds' behaviour patterns are shown to be necessities imposed by the sea ice, or adapted remnants of previous behaviour lost as the birds adjusted themselves to living in the Antarctic.

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APPENDIX

BIRDS KILLED

Date	Specimen No.	Sex	Weight (lb.)	Remarks
19.7.49	E 547	♂	54	Bird BS. Prolonged stay on rookery
23.7.49	E 548	♂	59	Bird D4. Had incubated
12.8.49	E 551	♂	56	Bird which had incubated and was feeding newly hatched chick. Crop contained secreted food material
15.8.49	E 549	♀	69	Newly arrived bird. Crop full
13.8.49	E 550	♀	69	Newly arrived bird. Crop full
15.8.49	E 552	♀	65	Bird which arrived three days previously. Crop empty after feeding chicks
5.8.49	E 553	♀	72	Newly arrived bird. Crop full
15.8.49	E 554	♀	62	Newly arrived bird. Crop empty after feeding chicks

GROWTH RATES OF FLIPPER AND FOOT

August 1949–January 1950. *See* Fig. 5

Date	Length in inches	
	Flipper	Foot
Sept. 13	4.0	3.0
21	4.0	3.5
Oct. 5	4.25	3.5
20	4.75	3.75
Nov. 1	6.5	4.5
8	9.0	5.75
18	10.5	6.5
Dec. 1	14.0	7.75
16	15.0	8.0
Jan. 6	15.5	8.5
11	15.5	8.5

NEWLY HATCHED CHICKS FOUND ON ROOKERY AREA, FOR COMPARISON

Date	Length in inches	
	Flipper	Foot
July 31–Aug. 2	2.0	1.75

(Average of three specimens)

WEIGHTS OF CHICKS

DION CHICK

August 1949–January 1950. *See* Fig. 4. Estimated date of hatching—August 6th. Weight approximately 14 ounces.

Date	Wt. in ozs.	Date	Wt. in. ozs.	Date	Wt. in. ozs.
Aug. 27	36	Oct. 17	92	Dec. 3	384
29	38	20	108	6	400
		23	120	9	424
Sept. 7	34	29	136	12	408
8	38			16	456
9	37	Nov. 1	176	18	432
10	46	5	212	22	432
11	48	6	240	23	416
13	49	8	256	27	408
14	51	10	248	30	408
15	53	14	240		
17	50	18	248	Jan. 6	400
21	55	21	276	10	400
24	57	24	306	11	416
28	55	27	324	15	448
		29	344	17	432
Oct. 5	70	30	352	22	496
9	80	Dec. 1	368	27	496

An exponential curve, plotted between August 6th and November 4th, has been superimposed on the curve relating to the above figures. The weight curve of Wilson's chick (op. cit. p. 26) is also shown. Weights of Wilson's chicks numbered 1, 2 and 4 are plotted alongside.

WILSON'S CHICKS

WILSON'S CAPTIVE CHICK (1903)	
Date	Wt. in ozs.
Sept. 3	14–16 (Estimated)
20	22
27	32
Oct. 4	45
11	51
18	58
25	66
Nov. 1	70

CHICK No. 1. October 18th, 1903. 56 ozs.
CHICK No. 2. October 18th, 1903. 64 ozs.
CHICK No. 4. November 5th, 1903. 44 ozs.

Printed in England by Jarrold and Sons Ltd, Norwich

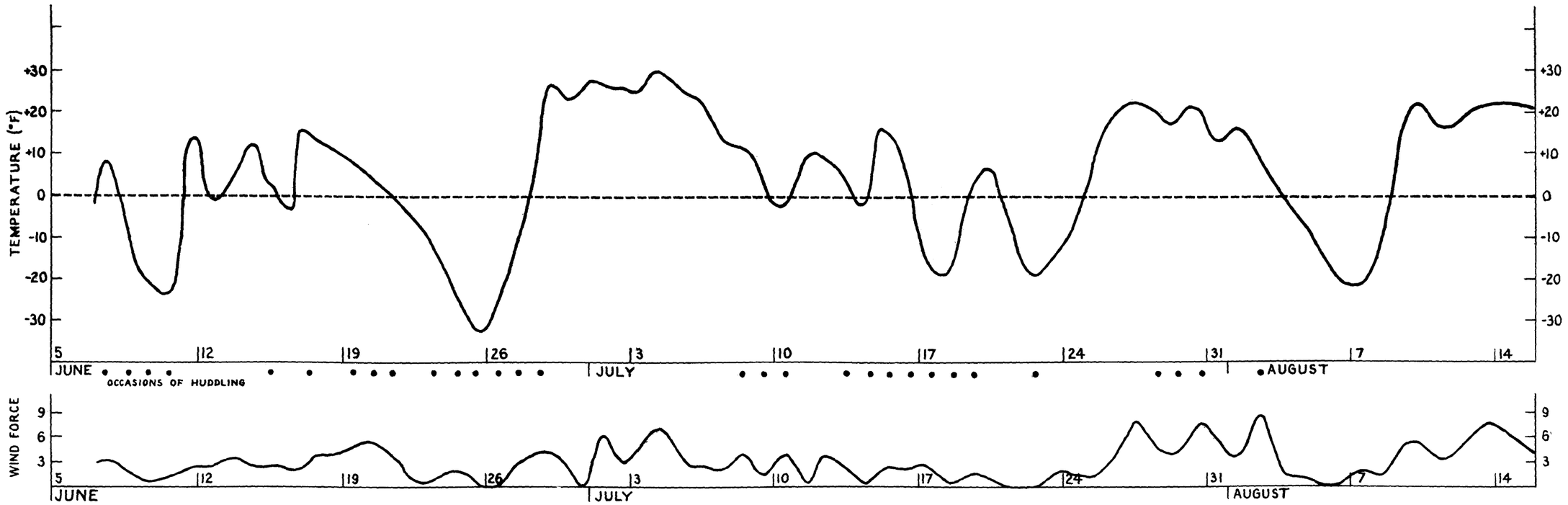

Fig. 6
TEMPERATURE, WIND FORCE, AND OCCASIONS OF HUDDLING

Temperature is expressed in degrees Fahrenheit. The temperature curve has been smoothed to reduce diurnal fluctuations. The wind force is expressed in accordance with the Beaufort Scale. Direction of the wind has been ignored; of the thirty-six occasions when a wind of force 5 or over was recorded, thirty-three occurred with warm winds from the NW–N–NE sector. Frequency of huddling is indicated by dots, each dot representing a day part or all of which was spent in one or more close huddles by the majority of the birds. By cross-reference to Fig. 7 it will be seen that departures from the rookery during the incubation period always followed prolonged periods of huddling.

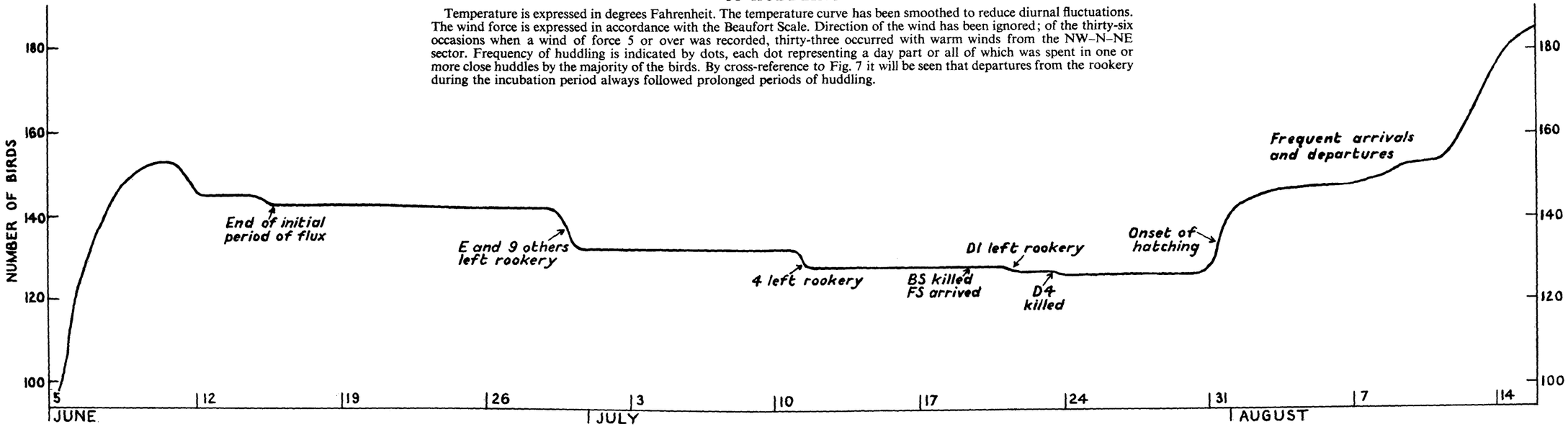

Fig. 7
VARIATIONS IN THE SIZE OF THE DION ISLETS ROOKERY, JUNE–AUGUST, 1949

During the observation period the number of adult birds present in the rookery varied between 100 on June 5th and 183 on August 15th. After the initial period of flux associated with laying, the numbers decreased slowly as unoccupied birds left the area. The first of the returning birds appeared on July 19th, and the main influx commenced on the first day of hatching.

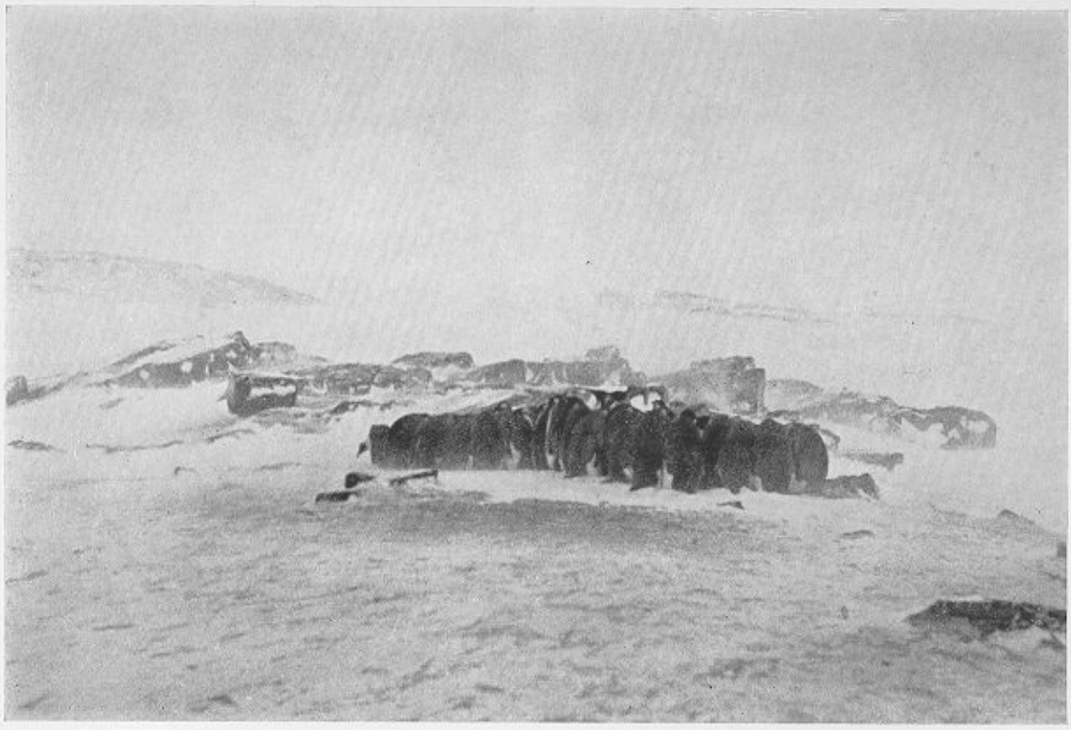

Fig. a. The Huddle, a bad weather formation.

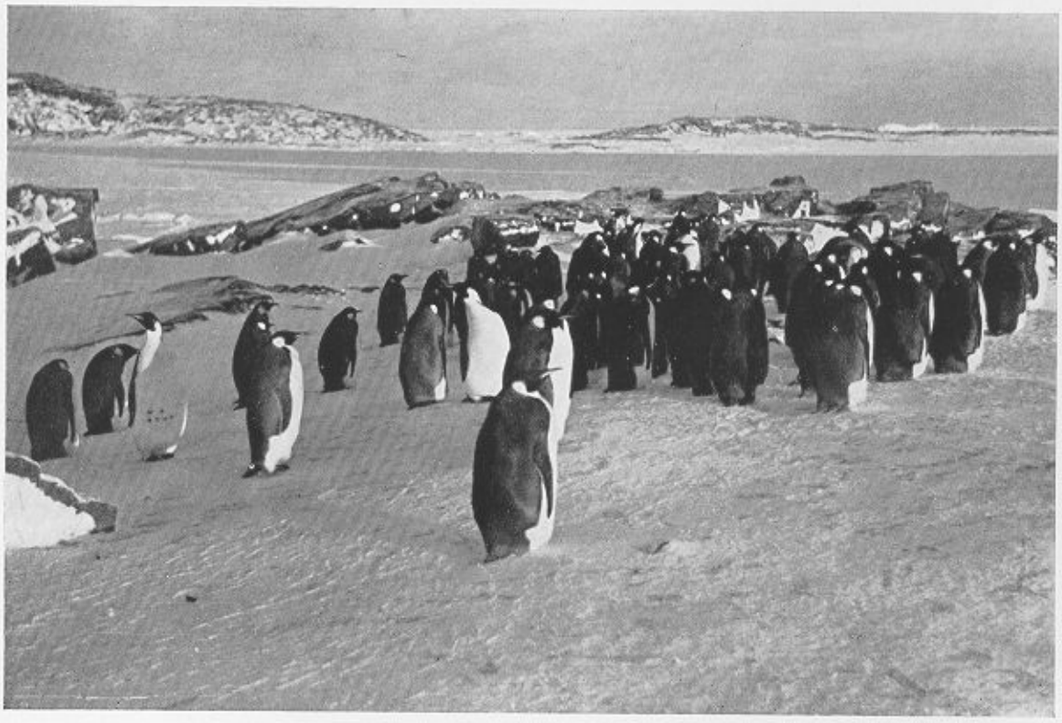

Fig. b. Open formation in calm weather.

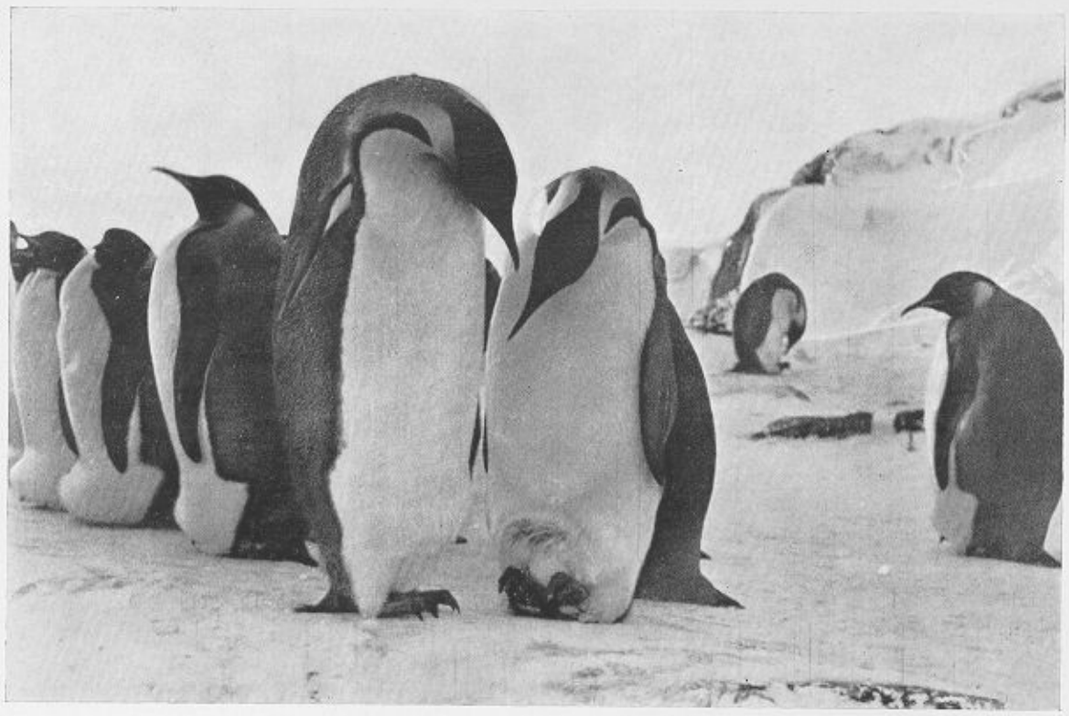

Fig. a. Display ceremony with an egg.

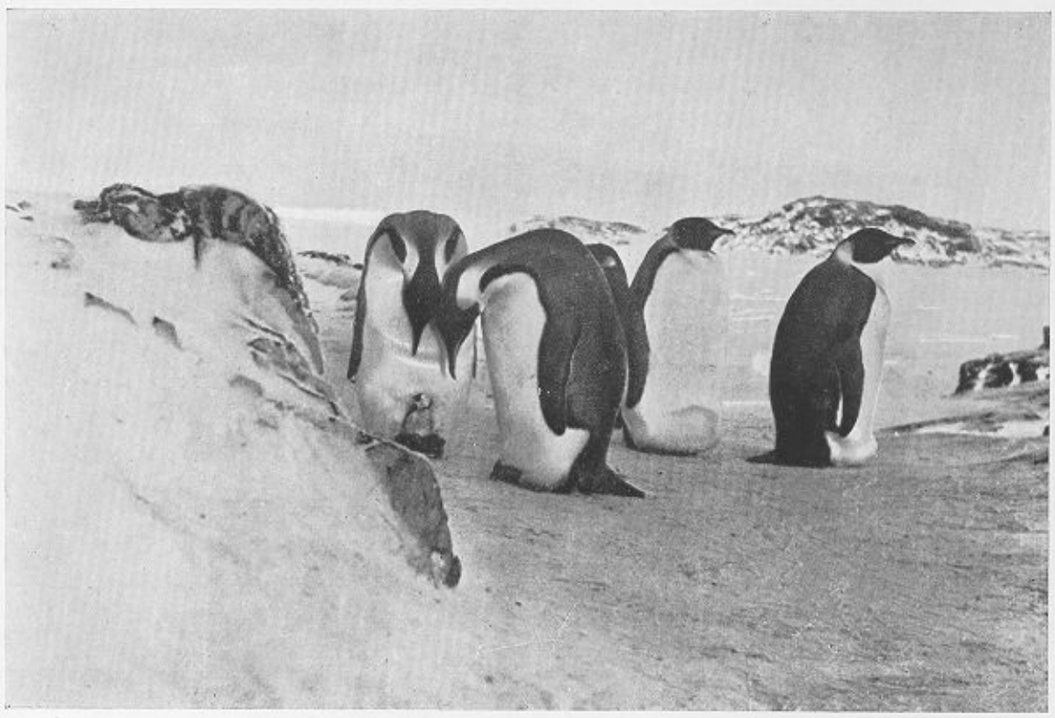

Fig. b. Display ceremony with a chick.

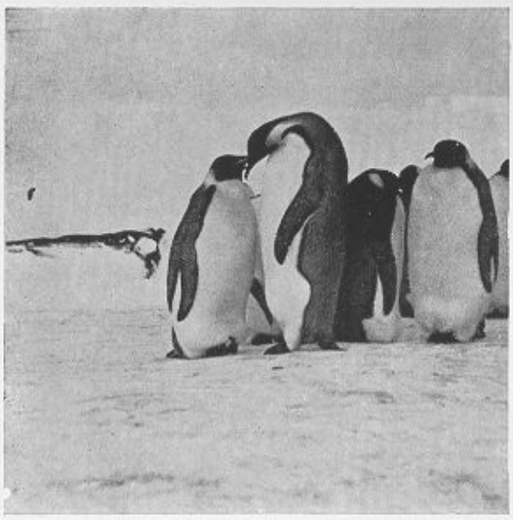

Fig. a

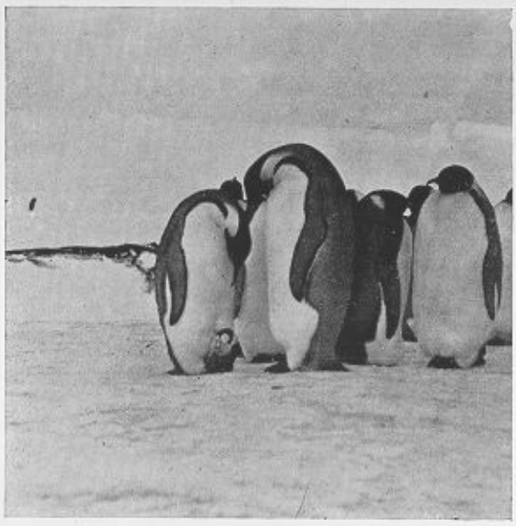

Fig. b

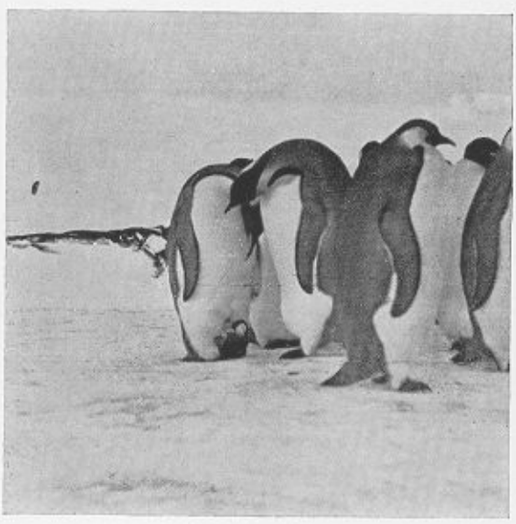

Fig. c

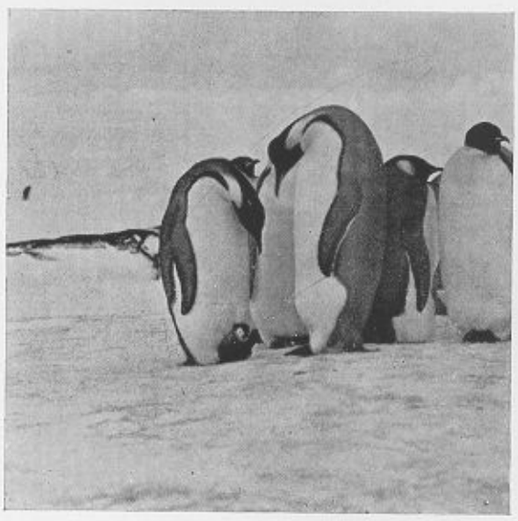

Fig. d

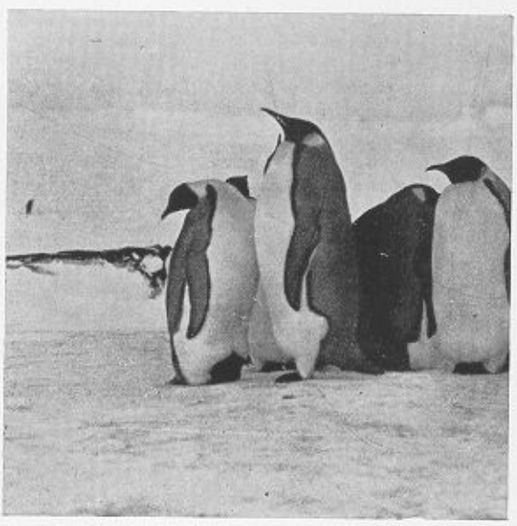

Fig. e

Five stages in the display ceremony. Bird A, on the left, holds a chick. Bird B initiates the display (Fig. a) by dropping its head sharply on to its chest. Bird A responds with a similar movement, drawing up the covering fold and exposing the chick (Fig. b). Both inflate their airsacs and crow (Fig. c), draw themselves up, (Fig. d) and finally lunge in all directions (Bird A in Fig. e).

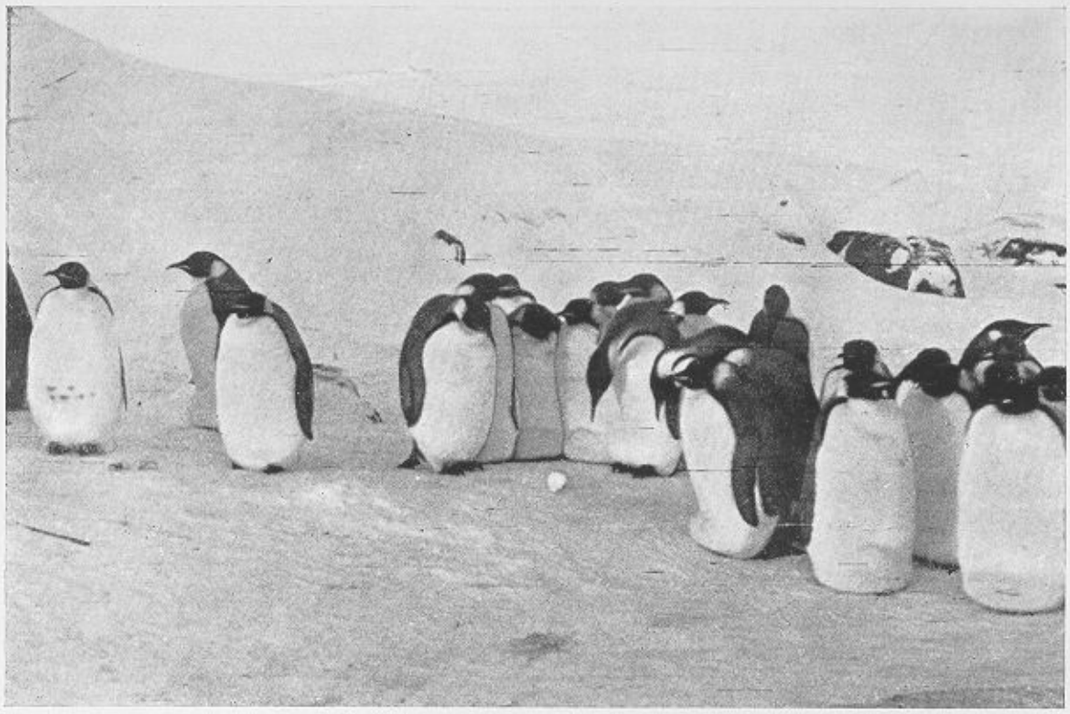

Fig. a. "Pointing" at abandoned egg. Dead chick ignored on left.

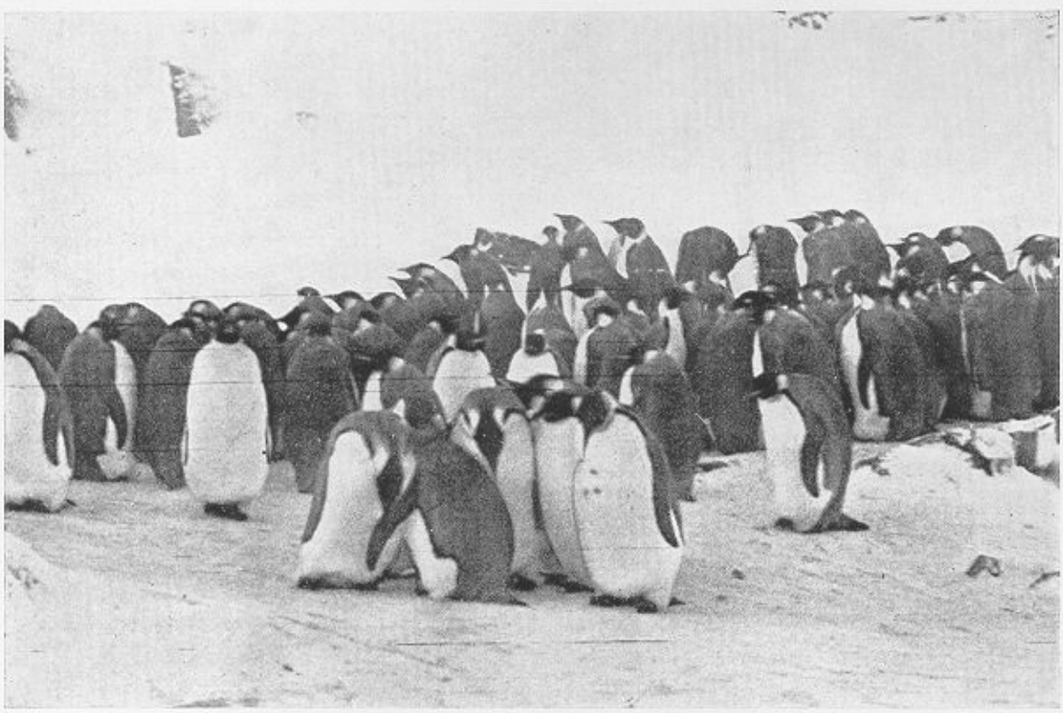

Fig. b. Struggle over abandoned chick.