

FALKLAND ISLANDS DEPENDENCIES SURVEY

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THE KING PENGUIN

Aptenodytes patagonica

OF SOUTH GEORGIA

I. BREEDING BEHAVIOUR AND DEVELOPMENT

By

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*Edward Grey Institute of Field Ornithology, Oxford
and Falkland Islands Dependencies Survey, London*



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(Manuscript received September 1957)

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INTRODUCTION: THE GENUS *APTENODYTES*

NOMENCLATURE

THE genus *Aptenodytes* includes two distinct but similar species, *A. forsteri*, the Emperor Penguin, and *A. patagonica*, the King Penguin. Both inhabit the southern oceans, possibly overlapping slightly in their range among the pack ice but breeding separately and far apart. Distinguished from all other species of penguins by their size and colouring, similarities between Kings and Emperors led to some confusion of the two in early accounts. The first to be recorded was the King Penguin; Pennant (1768) gave an illustrated description of an unusual bird:

“. . . brought by Capt. MacBride, from the Falkland Isles, off the Straits of Magellan; we believe this species to have been undescribed; for the birds that bear the same name are mentioned by every writer, who treat them as far inferior in size to this; some compare their bulk to that of a duck; but none make it larger than a goose; the colours also of this species are too striking not to have been taken notice of, had it been before discovered.

“Capt. MacBride was so obliging as to inform us that this was a very scarce species, though he saw in the same place multitudes of a lesser kind with which it agreed in the manner of its life.”

This bird was given the name “Patagonian Penguin”:

“not only because it is found on that coast but because it as much exceeds in bulk the common kinds, as the natives are said to do the common race of men.”

At the time only two other penguin species were listed by Linnaeus (1758), *Diomedea demersa* and *Phaethon demersus* (pp. 132 and 135). Of these the latter, since renamed *Eudyptes chrysolophus*, was probably the smaller species mentioned by MacBride. The illustration (Plate Ia) accompanying Pennant's account is clearly drawn from an ill-shaped skin; in spite of the dramatic pose and elongation, it is recognisably a King Penguin.

In 1776, the French naturalist Pierre Sonnerat published an account of an expedition to the islands of the East Indies, under the title “Voyage à la Nouvelle-Guinée, etc.”. In his descriptions of plants and animals Sonnerat included accounts of three penguins which he claimed to have observed in the course of the voyage. Although the expedition did not actually visit New Guinea, the largest of the three penguins was given the name “Manchot de la Nouvelle-Guinée”; from descriptions and illustrations (pp. 179–80, Pl. 113) this species may be identified with Pennant's Patagonian Penguin. The two smaller species (“Manchot a collier de la Nouvelle-Guinée” and “Manchot Papou”) were almost certainly Magellanic (*Spheniscus magellanicus*) and Gentoo (*Pygoscelis papua*) penguins respectively. A possible explanation of how three sub-Antarctic species came to be included in a collection of animals from the East Indies has been suggested by Lysaght (1952). Sonnerat was for a time trained under the guidance of Commerson, the naturalist and artist who sailed with Bougainville on his voyage round the world between 1766 and 1769; it is believed that Sonnerat included designs from Commerson's original sketches in his own publication, and added for good measure descriptions of penguins which Commerson observed at Tierra del Fuego. I am informed by Dr. Lysaght that Commerson's sketches (now in Paris) are better representations than those of Sonnerat; it would certainly be difficult to believe that Sonnerat's “Manchot de la Nouvelle-Guinée” was drawn from a skin or living specimen (Plate Ib).

From 1776 to 1785 a series of plates by J. F. Miller appeared under the title “Icones Animalium” or “Various Subjects of Natural History, etc.”. The work was published in ten parts, each consisting of one page of text accompanied by six plates (Sherborn and Iredale, 1921, p. 302). Part IV, published in 1777 or 1778, contained a drawing of a King Penguin bearing the name *Aptenodytes patagonica*. There is some doubt as to whether the name was coined by Miller himself, or by G. Shaw, who later co-operated with him in producing “Cimelia Physica” and may have supplied the text for “Icones Animalium”. *Aptenodytes patagonica* was apparently the first specific name to be applied to the King Penguin (Plate Ic).

In 1781 J.-R. Forster, one of the two German naturalists who sailed with Captain James Cook on his second voyage round the world (1772–75), published a note on Penguins under the title “Historia Aptenodytae”. Forster listed nine species under the generic name *Aptenodytes* and provided illustrations of five; he made reference to Miller's plates, mentioning that the plate of the King Penguin was drawn from a specimen in the collection of the Duke of Brunswick, but applied the trivial name *patachonica* to his own description of the same species. However, his plate (Plate Id) carries Miller's name of *patagonica*.

Forster explains the derivation of *patachonica* in a long footnote (1781, p. 127):

“Gens ab Hispanis in extremitate australi Americae primum visa, nomen gerit Chonos, et quod pedes haberent pellibus involutos pedibus bestiarum ideo simillimos quos Hispanica lingua appellare solent Pata; has gentes proceras dixere Pata Chonos, unde reliqua Europae nationes esculpserunt suos Patagonas.”

(“This race was first seen by the Spaniards in the extreme south of America and bears the name ‘Chonos’; because their feet are wrapped in skins, very like the feet of those beasts which in Spanish are called ‘Pata’, those tall races are called ‘Pata Chonos’, which other Europeans have changed into ‘Patagonas’.”)

and ends with a plea for the use of the technically correct form. Forster’s version of the name has frequently been used in preference to Miller’s, on the grounds that Miller’s “Icones” was not published until 1785, the date of the final issue. However, Forster’s own reference to Miller’s plate would alone suggest that parts I-IV of the “Icones” were already in print in 1781. Forster’s name is therefore invalidated on grounds of priority.

The Emperor Penguin was first described and named by G. R. Gray, from specimens brought home by Sir James Clark Ross of the *Erebus* and *Terror* expedition. Gray’s note (1844, p. 315) attempted to distinguish between two species which he felt had been confused in the past; he suggested that Miller’s plate was in fact of an Emperor Penguin, that it had been copied from drawings of the Forsters, that the same figure was in turn copied by Pennant for the illustrated second edition of his “Genera of Birds” (1781), and that Forster again made use of his original figures for his own (Gottingen) paper of 1781. In view of the confusion and in view of the fact that the names *patagonica* and *patachonica* were by this time both being used indiscriminately, Gray suggested a fresh start, suppressing both trivial names and naming King and Emperor Penguins *A. pennantii* and *A. forsteri* respectively after the two naturalists who, in his opinion, had first described them.

In listing differences between skins of the two species, Gray was in fact the first to distinguish the King Penguin from the Emperor; his name *Aptenodytes forsteri* for the Emperor Penguin may therefore be accepted. However, his argument on the nomenclature of King Penguins is untenable; there can be little doubt that the Forsters’, Miller’s and Pennant’s plates were drawn independently and that all represented King Penguins. The Forsters, with Cook, sailed to the edge of the pack ice on several occasions but did not penetrate it; no mention is made in Cook’s account (1777) or in the accounts of the naturalists (Forster, G. 1777; Forster, J.-R. 1778) of the capture of large penguins (i.e. Emperor Penguins) in the far south. However, the expedition spent some days in the region of South Georgia, where the naturalists were struck by the abundance of large penguins. Unless the last century-and-a-half has seen a radical change in the fauna of Antarctica and sub-Antarctica, these can only have been King Penguins. They are described and illustrated by the Forsters who appear, however, to have copied the pose from Miller’s work. It seems unlikely that Miller’s plate was based on unpublished material from Cook’s expedition, particularly in view of J.-R. Forster’s statement that it was based on a specimen in the collection of the Duke of Brunswick. In fact, more accuracy is shown by Miller than by Forster (e.g. in representing the vestigial fourth toe), suggesting that Miller drew from a skin rather than from another drawing; both make the mistake of continuing the post-auricular bar across the throat. Pennant’s plate (Plate IIa) of 1781 shows a different pose and improves slightly on Miller’s; like Miller’s, it cannot have been copied without reference to a specimen. All the plates are fair representations of King Penguins, showing clearly the dilated and unfeathered lower mandible and the slightly curved beak distinguishing this species from the Emperor (Plate IIb). Although Gray’s trivial name *pennantii* is frequently found in the literature, it is clear that the grounds on which it was submitted were inadequate. The trivial name *patagonica* must stand for the King Penguin.

The seven additional species originally listed by Forster in the genus *Aptenodytes* were gradually dispersed among other genera (Mathews, 1910, p. 496), leaving only the King and Emperor under Miller’s cognomen. A full list of synonyms for both species appears in Ogilvie-Grant (1898, pp. 626–7).

The question of sub-species has been raised by Mathews (1911, Vol. 1, p. 274) who records three for the King Penguin; of these, Peters (1931, Vol. 1, p. 29) accepts two, *A.p. patagonica* and *A.p. halli*. Observations in the field have not supported Mathews’ statement that “in the typical sub-species the feathers of the tarsus are blue all round, forming a collar.” Mathews’ additional suggestion, that *A.p. halli*, *A.p. patagonica* and *A.p. longirostris* form a series showing slight but significant variation in the amount of blue feathering on their flippers, is dismissed by Murphy (1936, p. 354) as inapplicable to the many specimens examined by him. This character varies widely in a single colony, and little importance can be attached to it in diagnosing sub-species. No sub-species have so far been postulated for the Emperor Penguin.

DISTRIBUTION

BOTH species of the genus inhabit Antarctic waters. King Penguins are found, or have in historical times been found, on most of the islands and shores between latitudes 45° and 58° South (Murphy, 1936, p. 344). During the nineteenth century, they suffered depredations on many of their breeding grounds, both plumage and oil being valued commercially. It seems probable that stocks remaining in protected areas are now increasing; reports of single pairs breeding among other species of penguins in the Falkland Islands (Hamilton, *in litt.*), and of small colonies establishing themselves on other islands where concentrations were known to have existed in the past, suggest that the species may at last be recovering. Emperor Penguins, by contrast, are associated with the Antarctic coastline and the pack ice. Five* breeding colonies are now known; of these four form on the sea ice, making the birds completely independent of land, while the fifth is established on a low islet. The colonies form in winter, at the time when they are least likely to be discovered by exploration. As Emperor Penguins are seldom found in large groups away from their breeding grounds, their commercial possibilities have never been exploited. The ranges of the two species overlap only slightly; wandering juvenile Emperors are occasionally reported from South Georgia, the South Shetland Islands and the Falkland Islands but Kings are seldom found in waters south of the breeding range.

I. THE KING PENGUIN SURVEY, SOUTH GEORGIA

1. HABITAT AND METHODS OF STUDY

a. The Habitat

THE island of South Georgia lies between latitudes 54° and 55° South, and across longitude 37° West (Fig. 1). Mountainous, ice-capped and rugged, its interior offers little hospitality to animal life; only the coastal valleys, raised beaches and sea cliffs provide accommodation for the island's twenty-six species (Harrison Matthews, 1929) of breeding birds. South Georgia's position relative to the Cape Horn current has been described by Hardy (1928, p. 220); Antarctic water rich in phosphates rises against the island shelf and is carried eastward with the current in a wide surface eddy, supporting immensely rich shoals of plankton which, directly or indirectly, are responsible for maintaining most of the bird life of South Georgia. Accounts of the island's history, natural history and character may be found in Harrison Matthews (1931), Murphy (1936, 1947) and Rankin (1951).

Four species of penguins are known to breed on South Georgia. The Antarctic or Chinstrap Penguin (*Pygoscelis antarctica*) is found only in two or three small colonies; the Macaroni (*Eudyptes chrysolophus*) and Gentoo (*P. papua*) Penguins are by far the most numerous species, occupying many large rookeries about the island. King Penguins are plentiful, but in spite of their size and brilliance are generally less in evidence than either the Macaronis or the Gentoos. Seven† King Penguin colonies are listed (Fig. 2); small additional groups are reported from time to time by the sealers and whalers, who do not, however, always distinguish clearly between breeding colonies and assemblies of moulting or resting birds.

It was originally intended that these studies should be undertaken on the Salisbury Plain rookery, which both Rankin and Murphy had previously described and visited. However, lack of shelter and fresh water made the Plain unsuitable as the site for a permanent base, and an alternative rookery on Paul Beach, west of Grace Glacier, was selected instead. Later the Paul Beach rookery was found to offer many advantages which had not previously been considered; overhanging cliffs provided good vantage points, the colony was small enough to be studied as a whole yet not so large as to be overwhelming, the sheltered site made observing more comfortable and handling easier.

*Excluding one of doubtful existence in the Gaussberg area. Since going to press the Australian National Antarctic Research Expeditions have reported the discovery of six more colonies in the Australian Sector, five of them on sea ice. The largest included about 12,000 breeding pairs. A colony has also been found on the Filchner Ice Shelf (Willing, 1958).

†I am indebted to W. N. Bonner for recent information (1958, *in litt.*) on this point. Colonies previously reported in King Haakon Bay and Right Whale Bay no longer exist. The colony at Fortuna Bay included only three chicks and seven adults in October 1957.

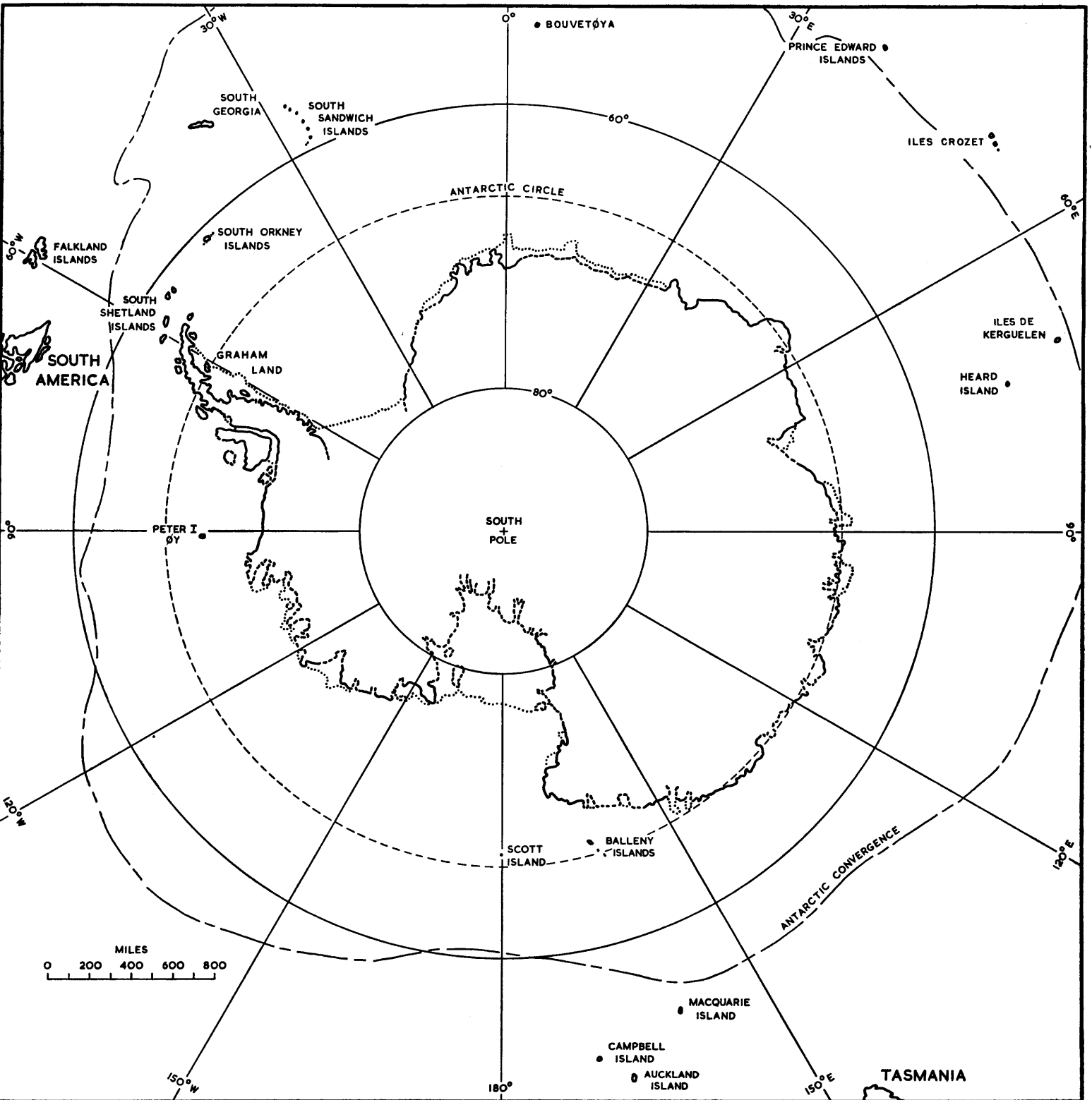


FIGURE 1. Antarctica and the Southern Ocean.

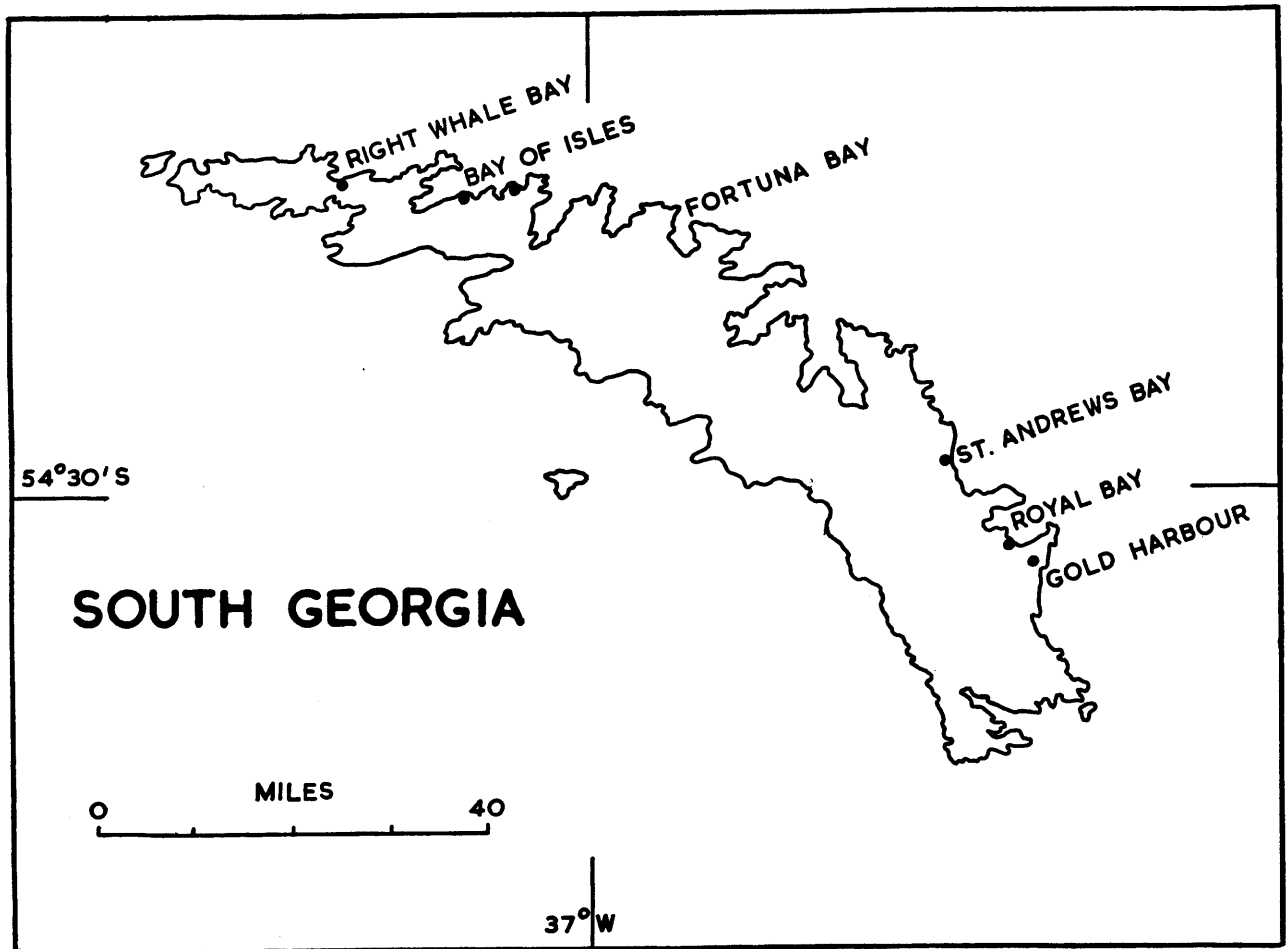


FIGURE 2. The King Penguin colonies of South Georgia. The position of the Fortuna Bay colony is uncertain.

Paul Beach extends along the southern shore of the Bay of Isles, between Grace Glacier and Markham Point (Fig. 3). With a height of about four metres above mean sea level, it forms part of the raised beach system which can be traced around most of the coast line of South Georgia; sloping gently up from the storm beaches it terminates abruptly at the foot of an old sea cliff now up to 200 metres inland from the sea. The landward half of the beach is covered by a belt of dense tussock grass (*Poa flabellata*) through which winding paths have been trodden by the penguins; seal wallows and shallow pools persist throughout summer and autumn, swelling under occasional heavy rains to morasses and lakes which the birds can cross only with difficulty. Two headlands of the old cliff enclose an embayment half-way along the beach, and in the shelter afforded by cliffs on three sides the King Penguin colony is found (Fig. 4 and Plate IIb). Within the embayment a higher raised beach is represented, forming a cobbled, sloping and comparatively well-drained floor to the rookery. Through spring and summer, snow melt water from the rolling grassland above the cliffs crosses the rookery in two shallow streams and drains into a large, muddy pool. From April to October the pool is frozen, the streams dry out, and extensive snow-drifts form below the cliffs. These gradually encroach upon the rookery floor, which itself disappears below a metre or more of well trodden and impacted snow.

The rookery area is limited on the north side by the pool and tussock belt; as the colony slowly increased in numbers during the 1953-4 breeding season, many incubating birds were compelled to settle among the fringes of the tussock. Relics of old tussock heads and recently trampled tussock patches indicated that, over a number of years, the colony had increased in size and was expanding steadily into the belt of grass. This question is discussed more fully in a later section.

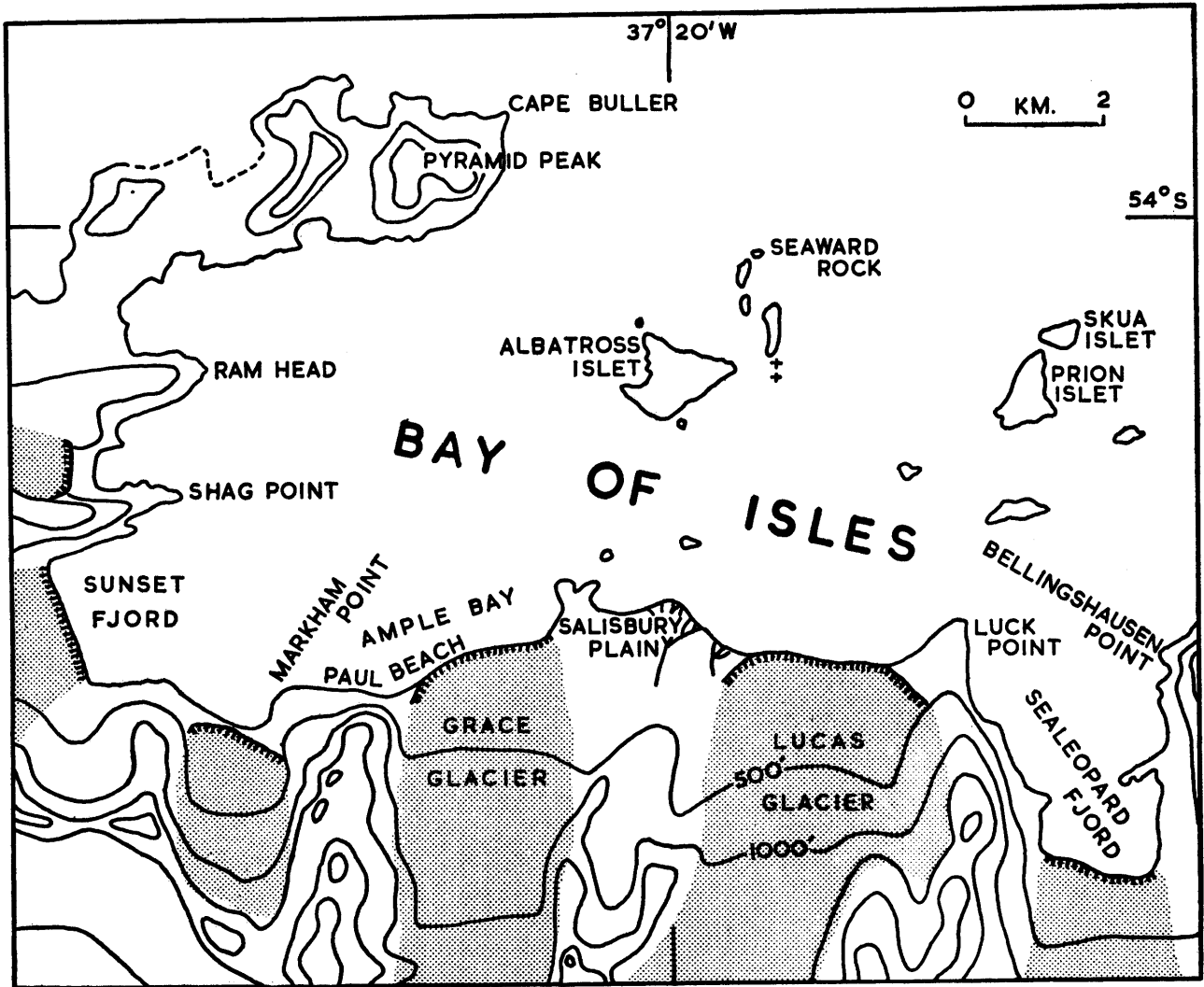


FIGURE 3. The Bay of Isles, South Georgia.

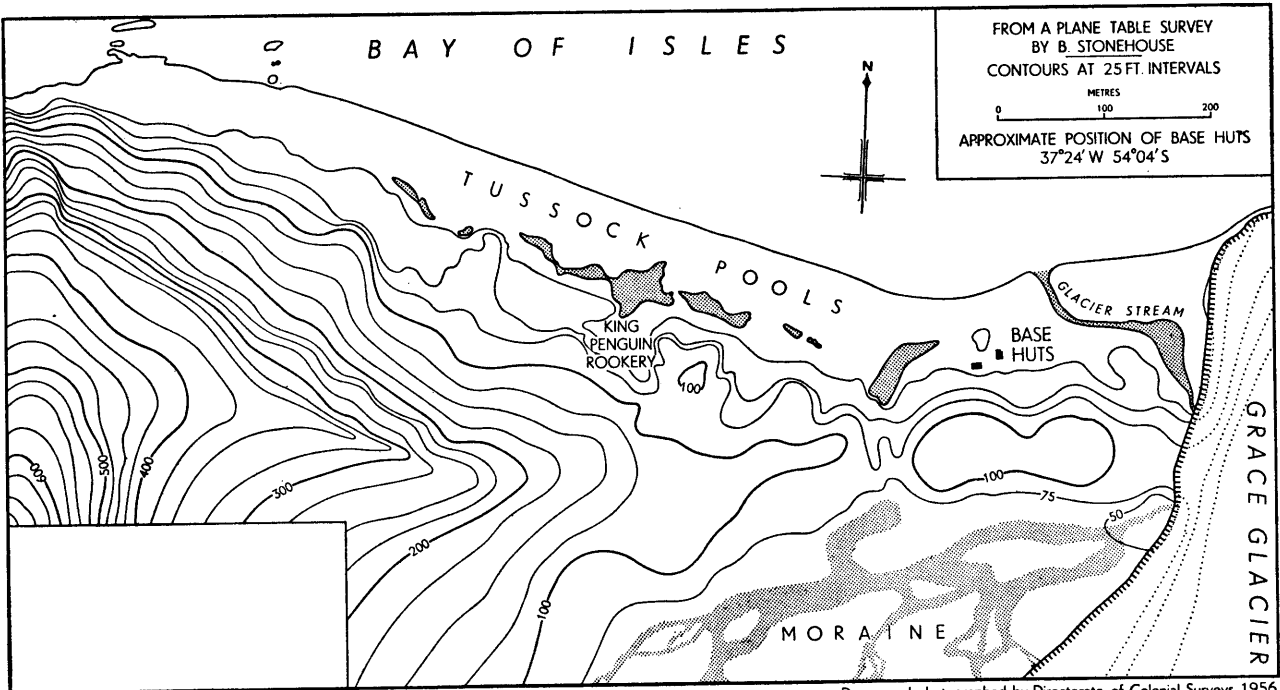


FIGURE 4. Paul Beach, showing the position of the King Penguin rookery.

The situation of the Paul Beach colony is generally representative of South Georgia's King Penguin rookeries. Sloping ground within a few hundred metres of the water, some degree of shelter and the assurance of a large snow-drift from the which birds drink in summer, seem to be important considerations in the choice of a satisfactory site.

South Georgia lies south of the Antarctic Convergence and is therefore surrounded by Antarctic water throughout the year (Fig. 1). Although loose pack ice is frequently seen near the island there are no records of the formation of fast ice, other than temporary and localised patches in the more sheltered harbours. The island also lies in the belt of westerly winds; its steepness and rough topography give rise to a variety of local weather conditions, sometimes to startlingly violent changes within a few minutes. On the whole, the climate may be summarised as damp, overcast, cold and windy. Weather observations were taken twice daily by the author at a fully equipped Normal Climatological Station established near the rookery, and the results are summarised in Table I. Table II is a summary of information collected over a number of years at the Government Meteorological Station, Grytviken, 65 kilometres from Paul Beach.

The behaviour of the birds suggested that they were most affected in their daily lives by combinations of low temperatures and strong winds; their response to these conditions was to sleep in sheltered spots, usually grouped closely together. Chicks in crèches packed tightly together to form huddles similar to those seen among incubating adult Emperor Penguins (Stonehouse, 1953, p. 8 and Plate Ia; Cendron, 1953, Plate IX) in the same circumstances. Drifting snow, carried by winds at higher temperatures, elicited a similar response. Other climatic conditions seemed to have little direct effect on the birds' lives; they swam in the surf, preened, walked to and from the rookery or tended their chicks alike in heavy rain, in clear, sharp frost, in damp warm weather or brilliant sunshine. Although weather conditions in Marguerite Bay were generally more severe than in South Georgia, the responses of Emperor and King Penguins to the same kinds of adverse conditions were remarkably similar.

b. Methods of Study

A small base hut was established at the eastern end of Paul Beach in October 1953, about 300 metres from the King Penguin colony. Daily observations on the birds began late in October and ended with the relief of the base on December 19th, 1954. An additional visit was paid late in January 1955, when the activities of every marked bird present were once again recorded. Thus, one full breeding season was witnessed, overlapped by the first few weeks of a second. The birds were watched for periods ranging from one to eight hours daily, except on a few occasions of particularly foul weather. Early morning watches were occasionally kept, but most of the routine observations were taken during the late mornings and afternoons. Activities were recorded in pencil on the sand-papered surface of a transparent plastic map-case, containing a list of marked birds with spaces for notes; thus the business of a marked bird (e.g. wandering, pairing, incubating) could be recorded by a symbol against its number, together with more extensive notes if necessary. This method was developed as wind and rain made the use of notebooks almost impossible.

Notes were also recorded directly onto a tape-recorder. From the shelter of a tent, and using a recorder equipped with battery, vibrator unit and small, portable generator, direct running commentaries could be made on the simultaneous activities of a number of birds. The method eliminated the tedium of constantly exchanging binoculars for pencil, with the accompanying danger of losing a watched but unmarked bird in the crowds. Activities could be recorded verbally in more detail than would have been allowed by the observer's normal speed of writing; the recordings could be transcribed at leisure or played over repeatedly to gain their full import. The machine was also used to record the call notes of King Penguins and other local birds.

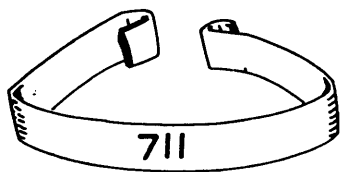


FIGURE 5. Aluminium alloy flipper-ring; two-thirds natural size.

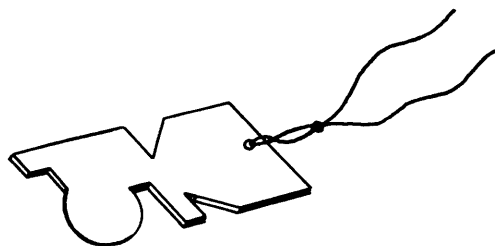


FIGURE 6. Aluminium alloy marking tag for identifying chicks; two-thirds natural size.

A programme of marking was necessary for studies of individual behaviour; birds were marked temporarily with paint, and later those whose activities were to be followed were banded with soft aluminium flipper-rings bearing stamped three-figure numbers (Fig. 5).^{*} The numbers, 7 mm. high, could be read in reasonable light conditions from a distance of 25 metres, using a pair of 8 x 30 binoculars with coated lenses. In winter, some advantage was gained by filling in the numbers with black paint. In most cases, the last two figures of the number were, in addition, painted on the bird's white front using a black bituminous ship's paint. Figures 10–15 cm. high could be read from a distance of 200 metres, and birds in the rookery could be identified without disturbance from the cliff top. Repainting became necessary after each prolonged absence at sea.

Only 149 birds were fitted with permanent bands (Stonehouse, 1956, p. 137); the majority were breeding birds, the remainder being second and third year juveniles. It was felt that most information could be obtained from the detailed study of small numbers, and each marked bird was, if possible, identified whenever it was seen. With larger numbers of marked birds, the difficulties of making a positive identification each time would have increased enormously. Birds breeding early in the 1953 season were banded on the left flipper, others were banded on the right; thus at a glance the observer could determine a bird's category and decide, in particular circumstances, whether it would be profitable to continue watching behaviour before approaching (and possibly disturbing) the bird for positive identification.

Chicks were marked with temporary indicators of various kinds. Newly hatched chicks could usually be identified as being in the care of marked adults; where only one partner of a pair was banded, the chick was daubed with red paint on the fine down of rump and head. This frequently resulted in the discovery and banding of the unmarked partner. It was necessary to renew the paint marks daily; painting became more difficult as the down grew, but in older chicks which spent more time in the open it became possible to daub the sparsely covered flippers too. Later still, when the flippers grew more sturdy, aluminium tags were tied onto them with thick string (Fig. 6). Tags cut in the shapes of the numbers which they represented could easily be identified from a distance except on the rare occasions when they slipped into the axilla. Both flippers were tagged so that the chicks could be identified from either side. Care was necessary to see that the loops securing the tags were loosened periodically, to accommodate the growing bones.

In no case did any of the methods of marking appear to inconvenience or even interest the marked birds in any way. No attempts were made to preen off paint marks and neither rings nor tags affected the behaviour of marked birds or the behaviour of other birds toward them.

The penguins were generally found easy to study; in most circumstances they were indifferent to the presence of an observer, and only after handling were individual birds inclined to be timid. A group standing on the beach could, with care, be approached closely enough for any banded birds to be identified; single birds were generally easier to approach than large groups. Sudden movements from the observer were liable to cause panic, however, and the alarm of one bird would usually be sufficient to scatter a group. Birds which were handled regularly for weighing tended to be slightly more timid than others when encountered away from the rookery. Incubating birds and those carrying small chicks would generally stand their ground and could, in many cases, be weighed in a rope sling without losing their grip on egg or chick. Catching a marked penguin away from the rookery usually involved a chase, but with good fortune the bird could be cornered by a steep bank or snow-drift and weighed, measured and marked with little difficulty or alarm. Long chases were avoided; over thick snow the penguins could easily outstrip their pursuer, and over rocks or cobbles they were likely to abrade their flippers and exhaust themselves.

Certain of the marked birds were weighed periodically throughout the year, using a spring balance graduated to 20 kg. in 0.2 kg. stages. A rope sling long enough to pass around the chest and lower abdomen was used to support the bird in a slightly inclined position during weighing. Weights were recorded to the nearest 0.1 kg. For incubating birds a standard amount (0.3 kg.) was subtracted to allow for the weight of the egg. Small chicks were weighed on a spring balance graduated in 10 g. stages to 1 kg., the chicks being held in a small canvas bucket. Older chicks were weighed in a larger bucket on the 20 kg. balance. The balances were checked frequently and adjusted when necessary.

Variation in size was noted among the adult penguins; it was observed that members of pairs might differ by as much as 3 cm. in length of flipper, a difference which could easily be detected before measurement when the two were standing side by side. Live and belligerent penguins are difficult to measure accurately; after some experiment three dimensions were selected as being comparatively easy to measure,

^{*}For a discussion of penguin-marking methods see Sladen (1952).

constant throughout the annual cycle, and representative of the general size of the bird from which they were taken. These are shown in Figure 7 and are referred to as beak, foot and flipper measurements respectively. All were measured to the nearest millimetre, but errors of up to 2 mm. in beak and foot lengths and up to 5 mm. in flipper lengths are likely. The clear sexual dimorphism shown by these measurements is discussed in the next sub-section.

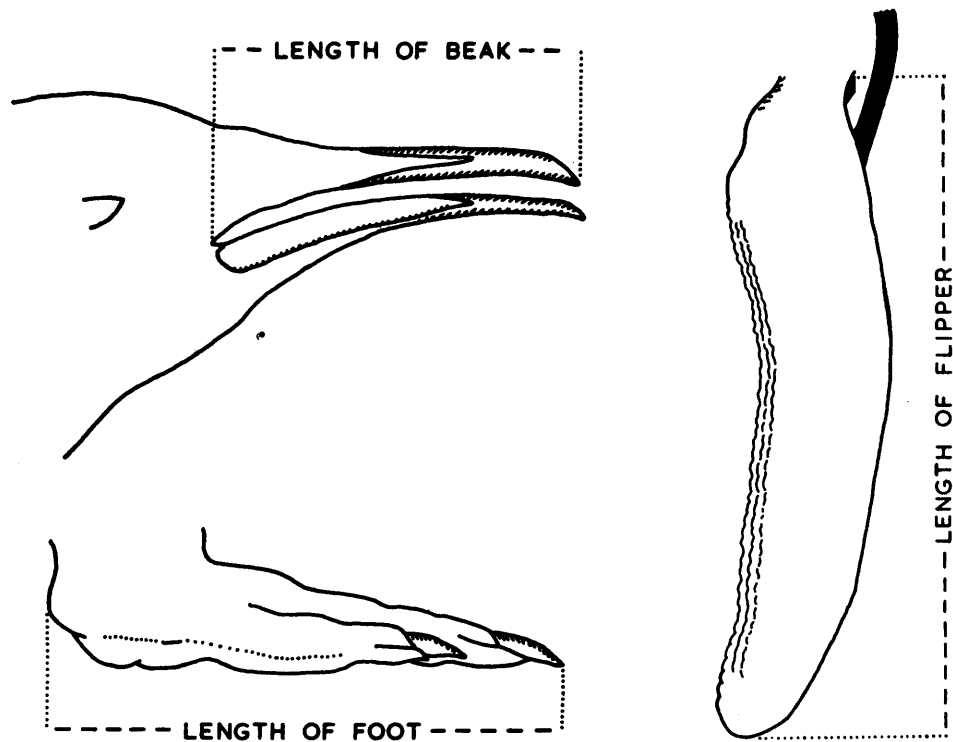


FIGURE 7. Methods of measuring the lengths of beak, foot and flipper.

Marked chicks of known ages were measured periodically throughout their growth. Measurements taken from normally reared chicks were found to agree closely, and standard curves for beak, foot and flipper lengths in relation to age were produced; from these the age of any measured chick could be determined with some accuracy during the first six weeks of its life. However, growth was found to be retarded in chicks which received food irregularly or from one parent only, and all chicks hatched after February grew more slowly than those hatched earlier.

A 35 mm. Pontiac camera was used for still photography; high speed films (e.g. Kodak Super-XX) gave reliable results in the dullest weather and filters were necessary on bright days. Light conditions were difficult to judge accurately without a meter. Kodachrome film was used with excellent results on clear days or bright, overcast days. A 16 mm. Kodachrome ciné film, taken with a Kodak Ciné-Special camera, was produced to show aspects of the breeding cycle throughout the year. All black-and-white film stock was processed at the base.

Little anatomical material was taken; four birds were killed, of which two were already suffering from injury or disease. The fullest use was made of their carcasses and of the few adults which died from natural causes. Many chicks died during the winter; whenever possible, the measurements and skeletons were taken. A series of over 100 embryos, in all stages from early blastoderm to hatching chick, was collected for embryological and growth studies.

c. *Differences between the Sexes*

The sex of a King Penguin cannot be diagnosed on sight, except in certain situations during the breeding season. No sexual dimorphism of plumage or beak colour has been observed, but many positive indications of sex appear during studies of banded birds. After a year's experience at Paul Beach, I felt confident to sex most of the marked breeding birds in the colony on the evidence of their appearance, behaviour and measurements. Similar evidence has been used by Richdale (1951, pp. 107–109) in sexing Yellow-eyed Penguins (*Megadyptes antipodes*) and by Sladen (1954, pp. 26–28) in his studies on Adélie Penguins (*Pygoscelis adeliae*).

The diagnoses were not confirmed by dissection; it was felt that more would be lost than gained by destroying any part of the marked population. Only two (males 671 and 690), both of which were crippled, were killed during the studies, and in both cases the sex had been ascertained correctly beforehand. The sex of one other marked bird was known with certainty: female 670 was seen to lay an egg. The behaviour of these three marked birds fitted into the patterns expected of males and females respectively.

Diagnosis of sex was based on the following criteria, which are arranged in order of practical value.

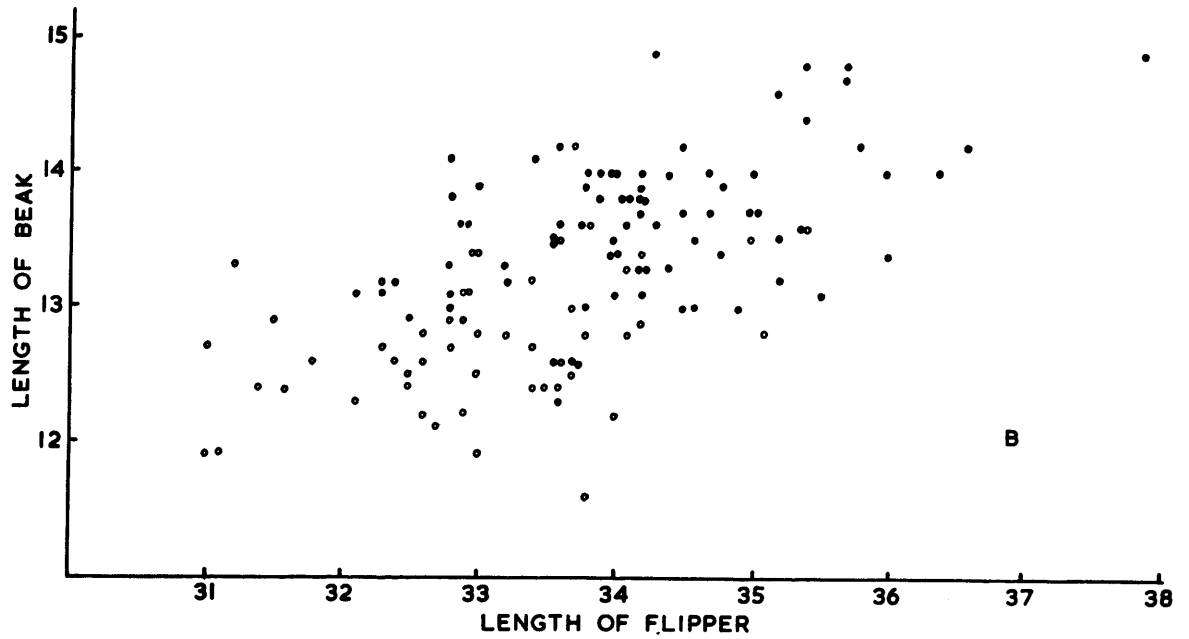
i. Order of incubation. Only one bird is present at a time during incubation; the other disappears altogether from the rookery and beach. The female usually holds the egg for the first few hours after laying, then allows the male to take it and leaves the rookery almost immediately. Occasionally the egg passes back and forth several times, but the male generally takes final possession within twelve to eighteen hours. He then incubates without relief for about a fortnight. In any pair, therefore, the bird which takes the first long incubation watch can be safely regarded as the male. Even if the egg is lost or destroyed the male tends to remain on the rookery for ten days or more, whereas females invariably leave within a few hours.

ii. Relative size. During courtship, when male and female stand closely together, one bird of each pair generally appears slightly larger than the other. During *high-pointing* displays (see Courtship and Pairing), the larger bird stretches higher than the other, and while at rest appears more bulky. The larger bird has, in my experience, always proved to be the male. Males are found to weigh more than females at the beginning of courtship (see Table XII), and tend to be larger in skeletal structure. Table III shows the beak, foot and flipper measurements of twenty-five mated pairs. Although not all the differences are statistically significant, it may be noted that in only five out of 75 paired measurements does the length of beak, foot or flipper in the female exceed that of her partner. The difference of mean length in each dimension is highly significant, exceeding the standard error of difference by 4.0, 4.2 and 4.8 times respectively for length of beak, foot and flipper.

iii. Behaviour in courtship. Males generally take the initiative in courtship displays and activities, which are described in later sections. No suspected female was seen to mount another bird (cf. Roberts, 1940, p. 208, and Sladen, 1954, p. 26). The positions in copulation gave rise to a useful indication of sex even when the act itself was not observed; females during the later stages of courtship often displayed a large patch of mud on their breast feathers, from lying on the rookery floor. Not all females showed it, for parts of the rookery were dry throughout courtship, while some males were marked in the same way from sleeping horizontally on damp ground. Other, less tangible, differences in behaviour and appearance were shown during courtship; males were generally more active, more frequently in display poses, more prominent in crowds due to their enhanced size. Females appeared sleeker, demonstrated less violently, but gave the impression of fighting more frequently than males.

iv. Absolute size. Although the relative sizes of two paired birds gave a reliable indication of sex, size measurements taken without reference to a partner were less informative. Table IV shows the beak, foot and flipper measurements of marked breeding birds, excluding those pairs listed in Table III. Figures 8a and b show beak and flipper, and foot and flipper measurements plotted against each other. It will be seen that the dimensions of males and females overlap considerably, although males are generally larger than females. Thus, a bird with long beak, foot and flipper measurements was likely to be a male and a bird with small measurements was likely to be a female, but nothing could be deduced with certainty from intermediate measurements. In Table IV the differences of mean length of beak, foot and flipper are statistically significant, exceeding the standard errors of difference by 6.2, 3.3 and 5.0 times respectively.

Combining the data of Tables III and IV, the following results are obtained from the measurements of 70 breeding males and 59 breeding females.



FIGURES 8a & b. Lengths of beak and foot (in cm.) plotted against length of flipper for seventy-one males and fifty-eight females.

	<i>Males</i>	<i>Females</i>
BEAK		
Mean length	13.7	12.9
Range	12.3–14.9	11.6–14.2
Difference of means		0.8
Standard error of difference		0.14
Factor of significance		5.7
FOOT		
Mean length	18.5	17.8
Range	17.0–20.0	16.0–20.2
Difference of means		0.7
Standard error of difference		0.17
Factor of significance		4.1
FLIPPER		
Mean length	34.3	33.1
Range	32.1–37.9	31.0–35.5
Difference of means		1.2
Standard error of difference		0.24
Factor of significance		5.0

2. THE BREEDING CYCLE

a. Introduction

Breeding behaviour in the King Penguin has previously been described only from casual observations in the field, and from records of captive birds in zoological gardens. The earliest field observations concerning breeding behaviour were those of the sealing captain, James Weddell (1825), who visited colonies on South Georgia and mentioned, among other points, the curious method of incubation, the absence of a nest and the fact that the chicks are tended for nearly a year. Moseley (quoted in Sclater, 1872, p. 123), Larsen and Sörling (Lönnerberg, 1906, pp. 88–90) and Wilson (1907, pp. 32–36) described breeding colonies on Marion Island, South Georgia and Macquarie Island respectively: Murphy (1915, pp. 103–113), and later Rankin (1951, pp. 113–141), paid a number of visits to South Georgia rookeries during the breeding season and described some aspects of breeding behaviour in detail. Neither was able to remain in the field long enough to record autumn or winter activities, and neither followed the behaviour of marked birds. In captivity King Penguins have bred with consistent success, particularly in the Edinburgh Zoological Park; for many years the records of Gillespie (1919, 1932) have provided the only information available on complete breeding cycles in this species. However, it is now clear that the behaviour of the captive birds was in many ways abnormal.

Many field observers have commented on the remarkable range of breeding activities which may be seen on a visit to a King Penguin rookery at any time during the long breeding season. In January and February, newly hatched chicks are found in company with those hatched a year earlier, and all stages of moulting, courtship, incubation and care of the young may be witnessed simultaneously. Figure 9 shows the annual duration of activities associated with breeding as seen in the Paul Beach colony. The figure was compiled and extrapolated from a single years' records; although other observations from South Georgia fit well into the framework none is sufficiently critical to show whether or not a typical year is represented.

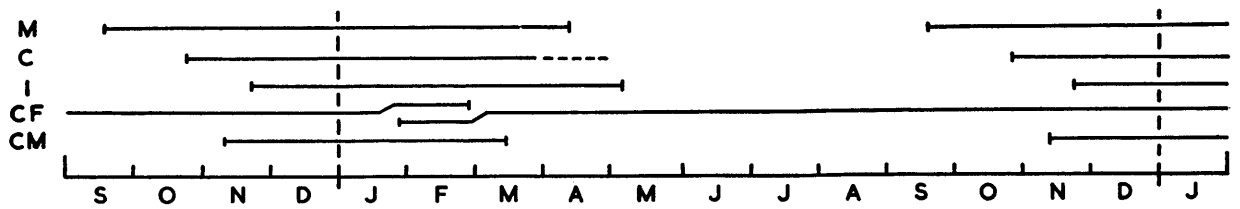


FIGURE 9. The annual duration of moulting (M), courtship (C), incubating (I), chick-feeding (CF) and chick-moulting (CM) in the King Penguins of Paul Beach.

Observations from other colonies suggest that breeding activities normally overlap in this way throughout the breeding range, and that the date on which breeding begins may vary with latitude. Thus, Loranchet (1916, p. 154) reported that eggs were discovered in October at Kerguelen, while on South Georgia (five degrees further south) the first eggs normally appear late in November. In his summary of reports by earlier observers, Murphy (1936, p. 347) noted that moulting birds had been recorded on various rookeries during every month between November and April; for South Georgia alone the limits may now be extended to include September and October, and it seems likely that all rookeries may, like those of South Georgia, contain moulting birds for at least half the year. It seems probable, too, that throughout the breeding range both courtship and incubation extend over at least five months of the year, while the chicks normally remain in the care of their parents from one breeding season to the next.

By contrast, in other species of Antarctic penguins all pairs in each colony begin and end the stages of their breeding cycles within a few days of each other, and the chicks achieve independence before their first winter has begun. Figure 10 shows the annual timetable of breeding activities seen in colonies of Emperor, Gentoo, Chinstrap and Adélie Penguins; comparable data for Macaroni Penguins are not available. It will be seen that, whereas the Pygoscelid penguins (in common, so far as is known, with those of

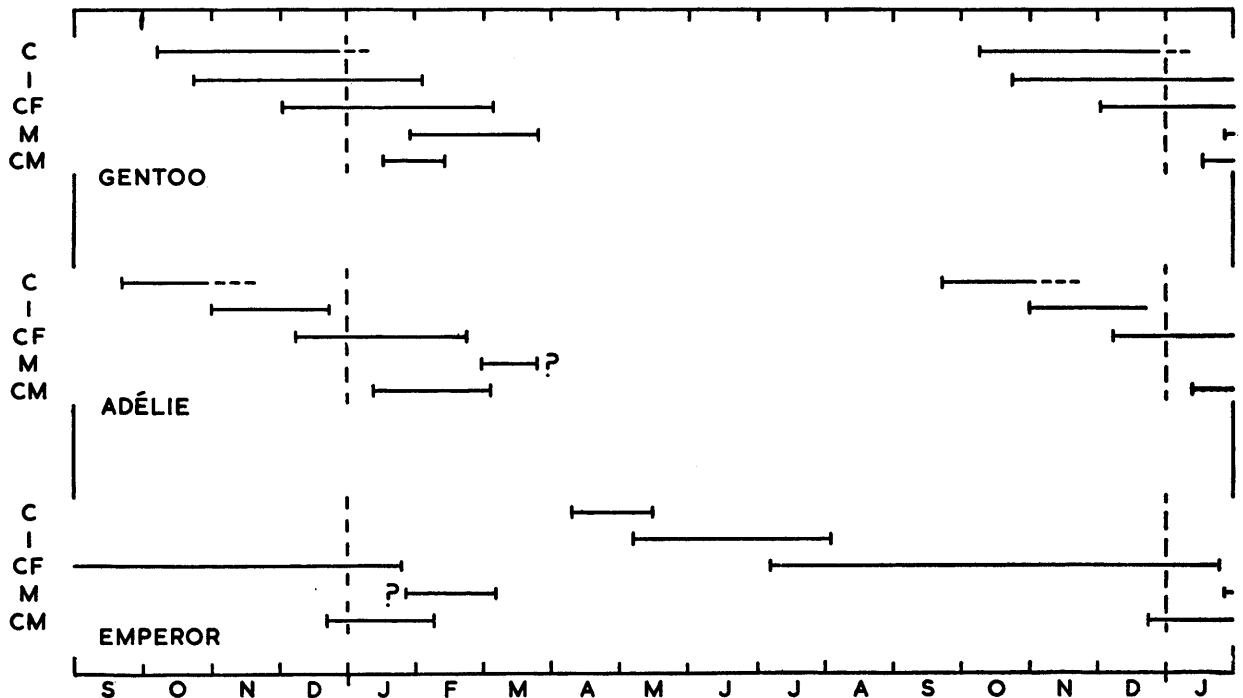


FIGURE 10. The annual duration of courtship (C), incubating (I), chick-feeding (CF), moulting (M) and chick-moulting (CM) in Gentoo, Adélie and Emperor Penguins.

all other genera) undergo a post-nuptial moult, the moulting of King Penguins is rather to be regarded as pre-nuptial. In the Emperor Penguin, moulting occupies the whole time between the end of one breeding cycle and the beginning of the next.

The complex situations found in King Penguin colonies during the breeding season may therefore be ascribed to two peculiarities of this species:

i. The length of the breeding cycle. Figure 11 shows the composition of a "typical" cycle generalised from over a hundred case-histories. After a period of fattening at sea lasting one or two weeks, the birds spend four or five weeks ashore undergoing a pre-nuptial moult. The moult is followed by a second fattening period at sea, usually of two or three weeks. On their return, the birds assemble in the breeding colonies to begin courtship which normally occupies two or three weeks but may extend to five or six. The single egg is incubated for 54–55 days, or nearly eight weeks. The chick is usually fed for a total of ten to thirteen months after hatching, and within three weeks of delivering their last feed to the chick the parents reappear in pre-moult condition. The breeding cycle cannot therefore be completed within a year; it usually occupies from fourteen to sixteen months and may extend over a year and a half. By contrast the Emperor Penguin rears a single chick in eight or nine months while the Pygoscelid penguins, like those of most other genera, rear two young in less than six months.

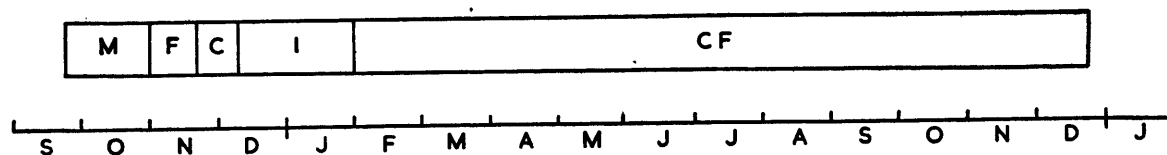


FIGURE 11. A typical breeding cycle in the King Penguin, showing duration of moulting (M), feeding at sea (F), courtship (C), incubating (I) and chick-feeding (CF).

ii. The length of the laying period. The King Penguin of South Georgia may lay its eggs at any time from late November to mid-April, a period of almost five months. By comparison, Gentoo Penguins in the same locality lay within two months and Emperor and Adélie Penguins (both with more southerly breeding ranges) complete their laying in less than a month. Of these, Adélie and Gentoo Penguins which normally lay two eggs may occasionally lay a third if one of the original clutch is lost. King Penguins normally lay one egg but seem capable of laying a second time in the same season if their first eggs are lost. In South Georgia, however, King Penguin eggs laid after the end of February are extremely unlikely to result in successful chicks, so that the "effective period" of laying (see below) lasts only about three months. The span is sufficient to allow the first chicks of the season to approach full size as the last hatch, and the courtship of late-forming pairs is often considerably disturbed by the arrivals and departures of earlier breeders feeding their young.

Few other birds compare with King Penguins in length of breeding cycle. The Royal Albatross (*Diomedea epomophera*) and Wandering Albatross (*D. exulans*) take a full year and breed only in alternate years (Harrison Matthews, 1929, p. 568; Richdale, 1942, p. 178; Sorensen, 1950, p. 19). The California Condor (*Gymnogyps californianus*), which also breeds in alternate years, takes sixteen months to complete a breeding cycle (Koford, 1953, p. 87). It tends its young for six or seven months after fledging. Richdale (1952, p. 142) summarises evidence suggesting a similar routine in the Andean Condor (captive birds, presumably *Vultur gryphus*). All are large birds, laying single eggs and rearing young which take many months to reach full size. None of the examples quoted, and no other species comparable in size, has an egg-laying period of more than two months. Only in the King Penguin is a long breeding cycle combined with a long laying period, and the reproductive disadvantages of the first are in part offset by the advantages of the second. Parents which fail to complete their breeding cycles in less than fifteen months are obliged, like the large condors and albatrosses, to miss the remainder of the year in which their chicks mature and to lay in alternative years. Those which complete their cycles in less than fifteen months, bringing their chicks to independence within the effective laying period of the second season, may lay again and so produce chicks in two successive years. Figure 12 shows the possible succession of cycles; it is clear that a third chick could not normally be reared in the third successive season. The King Penguin, then, is capable of breeding twice in three years; in this respect it is, so far as is known, unique among birds.

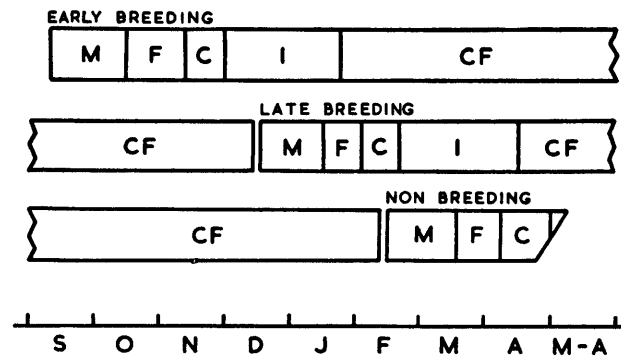


FIGURE 12. The succession of breeding cycles in the King Penguin, showing duration of moulting (M), feeding at sea (F), courtship (C), incubating (I) and chick-feeding (CF).

Observations in the Paul Beach colony, where this succession first became apparent, have shown also that individual birds vary considerably in performance. Some parents abandon their chicks before the chicks have started to moult, others feed them persistently until most of the down has been replaced. Some feed their chicks more frequently than others, and the more efficient parents are generally the first to be free of their chicks and complete their own moulting in time to breed again. The degree to which the routine of Figure 12 is achieved depends partly, therefore, on the individual efficiency of parents, and the more efficient ones will breed more frequently. Variations in the productivity of the sea from year to year may also effect the routine: in lean years fewer birds will dispose of their chicks in time to breed effectively before winter. The weather will affect the routine at critical times between March and May by altering the length of the effective laying period; thus, good weather late in autumn may allow more late breeders to rear their chicks, and warmer winters will allow the survival of more late chicks. These, and other factors which may influence the succession of breeding cycles, are discussed at greater length in the following sections.

b. The Colony: Non-breeding and Breeding Birds

Three classes of King Penguin were recognisable on sight when observations began at the Paul Beach colony:

i. Chicks. Growth stages of the chicks are described in sub-section 3c below. Throughout their first year the chicks are distinguishable by their thick covering of brown down. The mandibular plates remain black and leathery until shortly before the moult, when they harden and develop streaks of pink and blue. The rectrices and a few of the tail coverts appear precociously and are present from about the sixth week after hatching; they provide a prop for the chick when it settles back on its tarso-metatarsal bones.

ii. Juveniles. After the first year the chicks lose their furry down to disclose a juvenile plumage, distinguishable from adult plumage by the lemon-yellow auricular patches, grey-tipped feathers on the crown, and black mandibular plates more or less streaked with pink (Wilson, 1907, Pl. VIII). Birds marked as juveniles all moulted directly into adult plumage, suggesting that the juvenile plumage is worn for only one year in the wild as in captivity (Gillespie, 1932, p. 22). All moulted in December or January.

iii. Adults. All birds acquire the typical adult plumage at the beginning of their third year. Occasionally juvenile mandibular plates are found to persist for a few weeks after the adult feathers have grown, so that a few young adults can be identified by their combination of adult plumage and juvenile beak for a short period; generally, immature and mature adults are indistinguishable on sight. However, the completely asexual behaviour of immature birds is in many cases diagnostic. A few were ringed as juveniles immediately before their moult into adult plumage and were watched during the current and following breeding seasons. They were outstanding in the rookery as birds which, although in adult dress, did not respond to advances made by other adults at the peak of the breeding season and did not *mock-feed* (see section 2i) or otherwise

tend the chicks. They were seldom heard to call and did not initiate sexual behaviour by their calls; when handled for identification, painting or weighing they frequently broke into the shrill alarm calls of chicks. This reversion was most unusual, although not completely unknown, in breeding birds. The young adults disappeared from the beaches at the time when the juveniles and unsuccessful breeders migrated. Their weights and dimensions fell within the limits of those recorded for breeding birds, but their moults, like those of second-year birds, were concentrated in December and January. All unmarked birds which, although fully adult in appearance, showed no sexual activity of any kind in the colony, were assumed to be adolescent young. Others, including a few which were ringed as possible partners to previously marked birds, showed incomplete courtship behaviour and remained unpaired throughout the breeding season; these were assumed to be adolescent birds on the threshold of maturity. In captivity, King Penguins are believed to reach sexual maturity in their sixth year (Gillespie, 1932, p. 128).

c. Breeding Seasons and Breeding Categories

At any time of the year, most of the adult birds in a King Penguin colony are breeding birds, i.e. are involved in one stage or another of the long breeding cycle. Breeding adults particularly are responsible for the "spread" of moulting, the first appearing in pre-moult condition during the third week in September and the last completing their moults early in April. As courtship in this species is invariably preceded by moulting, the breeding season may be said to start with the arrival of the first moulting birds. During both years of study at Paul Beach the first eggs were laid on November 25th, and while so close an agreement is probably fortuitous it may be inferred that laying probably begins about the same time each year. In 1954, the end of the breeding season came with the onset of persistent cold weather in mid-May. The last eggs were laid in April; in early May courtship ceased, many of the remaining incubating birds abandoned their eggs, and by the middle of the month very few were left either incubating or brooding. At this time the first heavy snow of the season settled, and a cold blizzard cleared the rookery of all incubating, brooding and unoccupied adults. No further breeding activities, other than the feeding of older chicks and occasional inconclusive courtship movements, were seen until the following September.

By mid-May most of the current season's chicks were well developed and fat, and had for some weeks been left to join the crèche while both parents foraged independently. However, chicks which had only recently hatched were too small to be abandoned with safety by both parents, and lacked the reserves of fat necessary to sustain them between infrequent parental visits (see discussion on winter feeding). Many chicks of less than four or five weeks died during the early blizzards; some died of exposure, while others took shelter among the older chicks but were trampled to death or suffocated as the crèche packed tightly together. Survivors remained small and weak, their numbers decreasing steadily through the winter until the last died of starvation in August. It was clear that at least in the 1954 season, chicks hatched after mid-April stood little chance of survival, and therefore that eggs laid after the third week in February were unlikely to result in successful chicks. Thus, although the King Penguins laid eggs from late November to late April, in only about half that period was laying effective. The breeding birds could therefore be divided into the categories of "effective" and "ineffective" breeders, depending on whether or not they began their cycle within the first three months of the season. Although it was impossible to make accurate counts in so large a colony, it was estimated that between two-thirds and three-quarters of the Paul Beach birds bred within the effective period during 1953-54.

Effective breeders could again be divided into two groups—those which bred early and those which bred late within the effective period. During the 1953-54 season, while eggs were laid from late November to late April, two distinct waves of courtship and laying were observed, separated by a period of comparative inactivity. The first wave reached a peak during the second week in December, the second started about mid-January and reached its peak early in February. In the following season it became apparent that the first wave was composed entirely of birds which had moulted early (i.e. from mid-September) and were unoccupied during the previous winter. The second wave was composed of birds which had bred successfully in the previous season, had left their mature chicks about November, and had moulted during December and January. By combining the two seasons' observations it was possible to show the operation of a succession of cycles as illustrated in Figure 12. Birds marked as early breeders in the first season became late breeders in the second, while many of the late breeders of the first season were feeding their

chicks in January 1955 and during the second season could only have become ineffective breeders. Ineffective breeders of the first season became early breeders in the second, and were joined by those birds which had lost a chick through accident early in the first season. It may be noted that many of the early breeders, deprived of their eggs in December, paired with other birds and became late or ineffective breeders in the same season.

The effective breeders also included a few birds which bred in the period between the waves of early and late breeders. Some were early breeders whose normal courtship was known to have been broken for one reason or another. Others showed indecisive or incomplete responses to the sexual advances of other birds, and incubated only for a few days before abandoning or losing their eggs; these were believed to be young adults, perhaps attempting to breed for the first time. Few were marked, and little was learned about this group. Again, the size of the colony made accurate counting impossible, but it was estimated that late breeders outnumbered early breeders approximately in a ratio of 3 to 2, while intermediate breeders accounted for less than one-tenth of the total breeding population.

d. Migration and Dispersal

Effective breeders, raising their chicks successfully, were seen on the colony at intervals throughout the winter. Birds which lost their eggs or chicks before the end of winter generally disappeared from the colony altogether, returning in pre-moulting condition from September onward. Birds which completed their pre-nuptial moults too late to breed in the same season (and may be classed as unsuccessful breeders), also tended to leave the rookery for the winter. Of twenty-eight ringed males and twenty-six ringed females known to be in these categories, only five males and six females returned at intervals during the winter and early spring; the histories of these birds are summarised in Table V.

In addition, all juveniles and young adults left the Paul Beach area during April and May. On April 8th, between 2,000 and 2,500 adults were present at the rookery and 1,750 adults and juveniles were counted along the beach. A series of gales followed; by April 23rd all the beach population had disappeared and many of the rookery occupants had deserted their eggs and chicks. Early in May, when nearly all incubating and brooding had ceased, a second group of unoccupied birds assembled on the beach; these left during a gale which lasted from May 4th to 6th. During the remainder of the month smaller groups formed and disappeared successively, and an unusually high proportion of the birds present in the area spent their time in the immediate vicinity of the rookery. From June to September, the total number of adults present approximated to the numbers which would be feeding the chicks; there was no excess of unoccupied birds. However, the ringed birds which were known to have lost their chicks or eggs earlier in the breeding season did not all leave the rookery with the first wave of migrants. Figure 13 (abstracted from Table V) shows the numbers of unsuccessful breeders which may be assumed to have left in each ten-day period

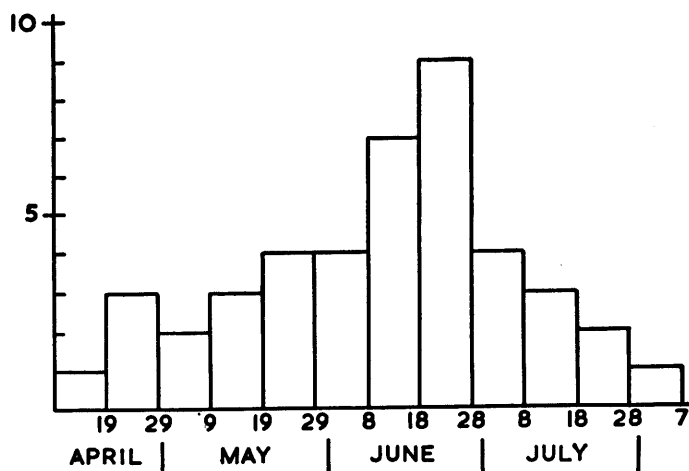


FIGURE 13. Dates of departure of marked adults migrating between 10th April and 7th August, 1954.

from April 10th to August 7th; it will be seen that the greatest numbers were last seen in June, long after the main waves of migration had passed.

The order of disappearance of marked birds bears no simple relation to the order in which they became unoccupied; thus No. 673, who lost her egg late in January, was last seen on June 26th after five months of wandering about the rookery, while 720, whose chick was abandoned shortly after hatching during the May gales, left the rookery early in June, less than a month later. This migration of unoccupied birds has not, apparently, been recorded previously; it is not known where the migrants spend the winter, but it seems likely that they leave the island altogether. From early May to mid-September, no juvenile birds at all were seen with the single exception of a crippled bird which appeared for short periods in August. King Penguins, perhaps more than any other penguin species, tend to gather in groups and it seems highly improbable that the birds would disperse about the shores of the island during winter without appearing in large numbers in so well populated an area as Paul Beach. It is estimated that over half the total adult population was permanently absent during the winter months of 1954.

Although over thirty chicks were ringed in the final stages of their down moult early in 1954, none returned to the Paul Beach rookery in the following season. Juveniles ringed or painted on the beach were not usually seen again once they had returned to sea; five which were marked in moult, however, did return a few weeks later in adult plumage and continued to associate themselves with the rookery. It seems that the second year, during which the juvenile plumage is worn, is a year of dispersal in which the young birds wander and finally attach themselves to a new colony. The colony in which the juvenile moults may be the one in which the bird subsequently breeds.

Unfortunately, few of the King Penguin rookeries of South Georgia are visited from year to year and the chances of recovering marked juveniles or young adults are remote, but by extreme good fortune one chick from Paul Beach was recovered at the Royal Bay rookery over a year after marking. This chick was ringed on January 15th, 1954, at the end of its down moult; although its juvenile plumage was complete the bird was in emaciated condition with a weight of 5.5 kg. (approximately half the normal weight for this stage), and was so weak that it could hardly support itself in an upright position. It was carried to the edge of the sea, and was engulfed in a party of adults which left for the feeding grounds a few hours later. On February 16th, 1955, the bird was recovered among a group of moulters in Royal Bay; it was in excellent condition and completing its moult from juvenile to adult plumage. This recovery (for which I am indebted to Squadron Leader Ian Brooker, R.A.F.) is of great interest in showing that a severely undernourished chick may survive if it is able to complete its moult and find its way to the sea. It also shows that a chick hatched in one colony of South Georgia might settle in a neighbouring colony and would not necessarily disperse to other parts of the species' wide-spread range. Finally, this recovery is the only case on record which shows positively that, in the wild, a juvenile loses its distinctive plumage at the end of its second year.

e. The Pre-nuptial Moult

On September 17th, 1954, the first moulting bird of the new breeding season was discovered in a sheltered corner a few hundred yards from the rookery. Others were found during the next few days, the condition of their plumage in some cases suggesting that they had already spent between one and two weeks ashore. Probably, therefore, moulting began during the second week of September at Paul Beach. By the end of the month between 200 and 300 moulting birds were scattered about the rookery, the cliffs and the beach, tending generally to avoid the main streams of traffic and to remain hidden in secluded corners. The numbers increased steadily throughout October, then seemed to decrease slightly as the first-comers completed their stay and returned to sea. A second wave of moulting birds appeared in December.

Between mid-September and mid-November, fifty-four ringed birds which had lost eggs or chicks or had failed to breed during the previous season were recovered in moulting condition. Very few successful breeders of the previous season began their moulting during this period (see below). A few of the ringed birds were identified only toward the end of their moult, being found by chance in wind-scoops or behind snow-drifts where they had perhaps spent two or three weeks in small, isolated groups. From their weights and from the condition of their plumage it was possible to estimate the dates on which their moulting began (see below). In several cases, ringed birds were missed altogether during moulting, but again it was possible to estimate the approximate dates of beginning and ending by comparisons with other birds, particularly by comparing the times at which they returned to the rookery to begin courtship.

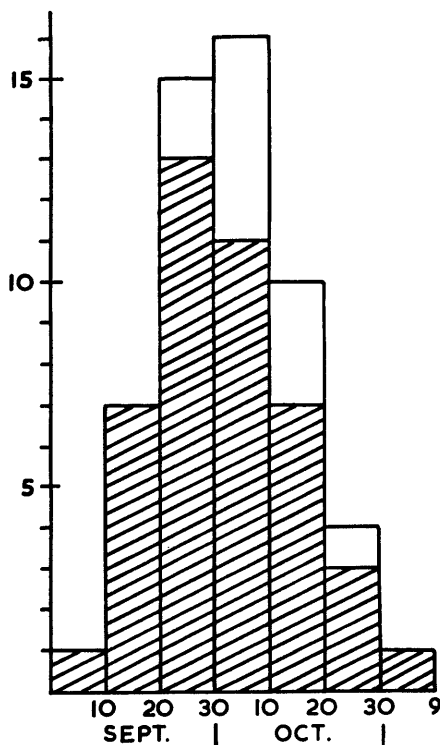


FIGURE 14. Estimated dates of onset of moult in marked breeding adults. The shaded blocks represent migrant birds.

Table V (col. 4) and Figure 14 show the estimated dates on which moulting began in the fifty-four marked adults previously described. For direct comparison with Figure 13, the shaded area in Figure 14 represents the forty-three migrant birds, and the unshaded area represents the six males and four females which reappeared at intervals throughout the winter. Although the birds dispersed in a period of 120 days, all returned within 70 days of each other. All known ineffective and unsuccessful breeders of the previous season had begun moulting by the second week in November, and it is believed that the first wave of moulters was composed almost entirely of birds in these categories.

Moulting birds were identified on sight, even before the feathers started to fall, by their marked obesity. Parents feeding their young emerged from the sea with weights varying between 14 and 17 kg., of which 2–3 kg. were accounted for by the crop contents. Moulting birds weighed from 19 to 21 kg. at the beginning of their moult; some were so fat as to be incapacitated once they had left the sea, and they could walk only with difficulty across the cobbles of the beach to the rookery. Much of the additional weight was contained in layers of sub-cutaneous and visceral fat, which was consumed rapidly as the moult progressed.

Four adults were confined in a snow pit and weighed daily throughout their moulting period. Their weights appear in Table VI and are shown graphically in Figure 15. The four were selected as being in approximately the same state of moult, and were believed to have spent between two and four days ashore when caught. Daily losses in weight were to a limited extent compensated by increases due to snow eating; it would be difficult to estimate an average figure for such increases, but observations suggested that they were not likely to exceed 0.1 kg. per day.

For about the first ten days ashore the moulting birds lost weight at an average of 0.2–0.3 kg. per day. During this time the colour of the faeces changed from white to green, the tail feathers were lost, and the contour feathers began to stand out at an acute angle to the body giving the birds an inflated appearance. Between the seventh and twelfth days the contour feathers began to fall; some birds preened actively and loosened the feathers in vertical tracts, others remained lethargic and preened very little. The feathers of the neck and head were generally the last to loosen.

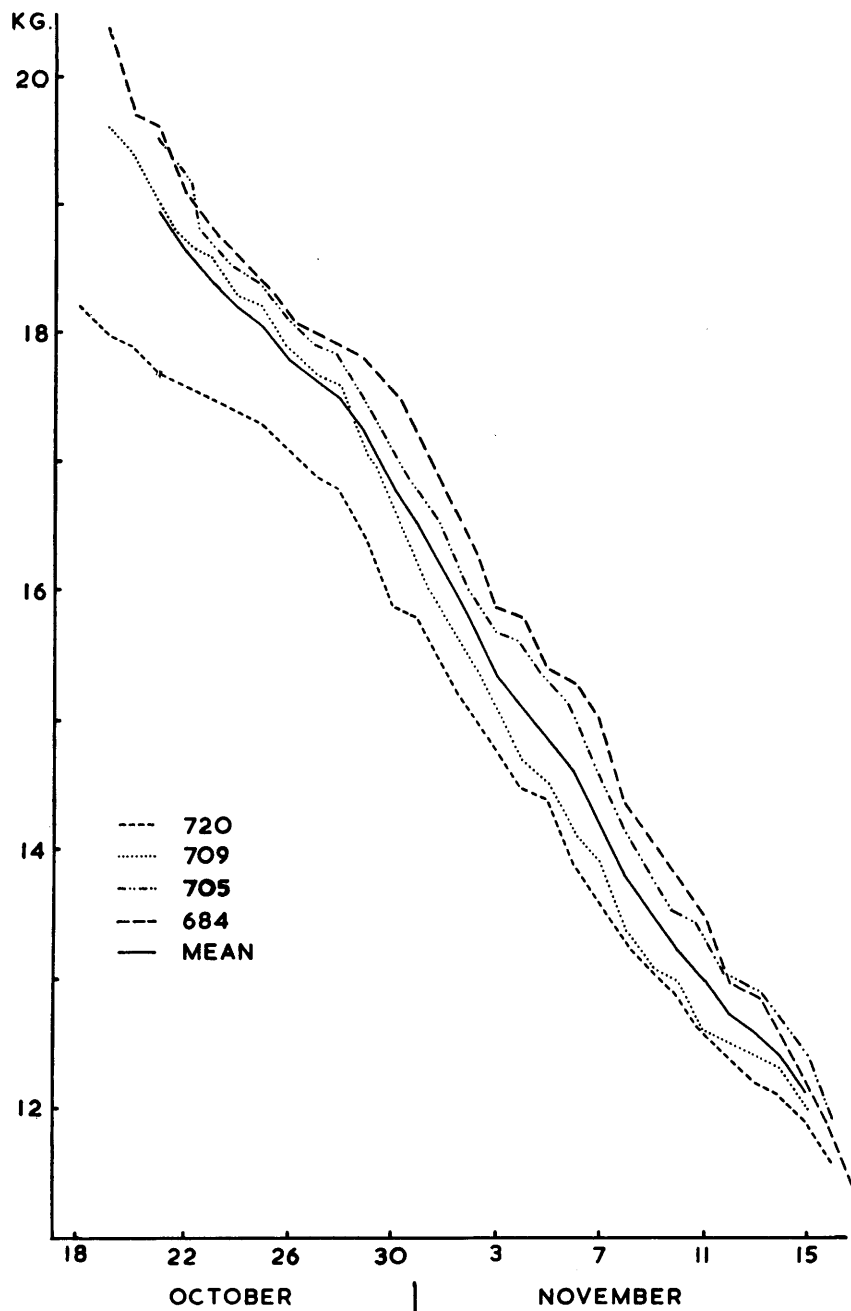


FIGURE 15. Weight losses (in kg.) of four adults during moulting.

As the feathers began to fall, the rate of weight loss increased slightly to average over 0.3 kg. per day. Growing tips appeared through the skin of chest and back, and the long feathers covering the trailing edge of the flippers loosened and fell. By the twenty-fifth day most of the contour feathers were replaced, only the neck and head remaining partially covered with patches of old plumage. Odd feathers persisted on the back and sides of the head long after all others had disappeared; these could not be displaced by routine preening, and were generally blown away or washed off when the bird returned to sea. The high average loss in weight was maintained to the end of the moult. After the last feathers had gone the birds tended to remain about the beach for three or four days, perhaps joining one or two daily swimming parties before finally leaving for the feeding grounds. The four confined birds were liberated when their weights fell below

12.5 kg.; all were recaptured in the following two days and re-weighed, and it is expected, by analogy with other birds, that their final weights before leaving Paul Beach would have been below 11 kg.

Other birds were weighed at irregular intervals throughout their moults, and found to conform to the pattern seen in the four confined birds. Table VII shows weight losses during the *maximum* period over which each bird was weighed. Column 9 shows the average daily losses, and Figure 16 summarises the daily losses of the 33 birds weighed. No attempt has been made to separate the results of the first ten-day period from the remainder; to reduce experimental errors only the greatest time interval has been considered in each case, so that the figures represent, as closely as the experimental conditions would allow, the over-all average daily loss in weight during moulting. These data will later be compared with similar figures obtained during courtship and incubation.

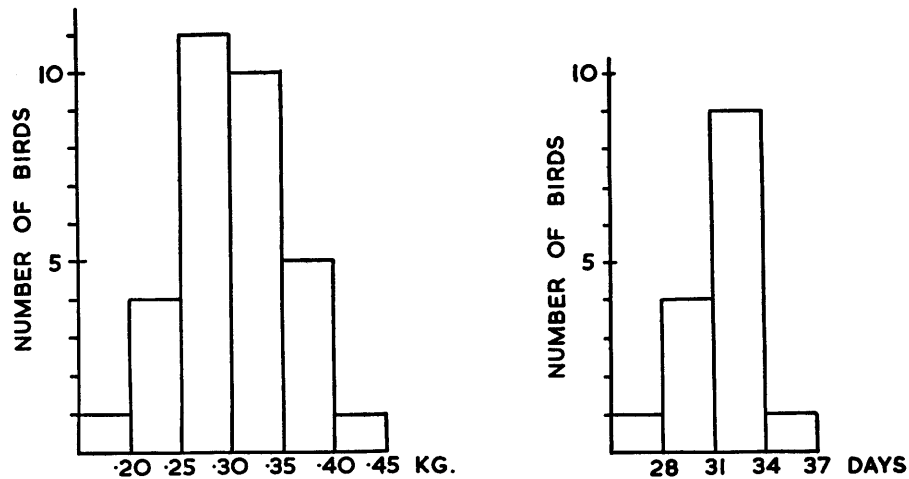


FIGURE 16. Mean daily weight losses (in kg.) of thirty-two adults during moulting.

FIGURE 17. Duration of moulting in fifteen adults.

The estimated dates on which moulting began were obtained by considering the weight and state of moult of each bird, if possible on more than one occasion during the moulting period. By comparing the data with the "average" curve in Figure 15 and with the known changes in plumage, a reasonably accurate estimation of the date of onset of moult could be attempted. For birds known to be larger and heavier than average throughout the year, an adjustment equivalent to one or two days was made. In cases where the actual average daily loss in weight was known, this too was taken into account; however, little importance could be attached to these figures in view of the variations shown where two successive moults were measured in the same bird (e.g. birds 685 and 718, Table V). The final estimations (Table V, col. 4) are believed to be accurate to within two or three days.

The dates on which moulting ended could in some cases be found directly; birds completing their moults usually spent the last two or three days on the beach and were consequently easy to catch. They were readily recognisable by the lurid blue and slightly dusty appearance of their new plumage and also by their extreme thinness: often the outline of the sternum could be seen and their weights generally fell to between 9.9 and 10.9 kg. at this stage. The last day on which they were seen along the beach could be taken as the last day of their moult. However, for most of the birds studied the end date was calculated. The mean total length of the moulting period was first estimated by comparing beginning and end dates in cases where both could be determined accurately. (Fifteen such cases are listed in Table VIII and the lengths of their moulting periods, grouped in classes of three days, are shown diagrammatically in Figure 17. The mean length from these data is 32.1 days, with range from 27 to 36 days.) The end date was then calculated by adding 32 days to the date, previously estimated, on which moulting began. The dates shown in column 5 of Table V are calculated in this way, except in the few cases where more direct evidence was available from observation.

Gillespie's observations on birds in the Edinburgh Zoological Park (1932, pp. 85–87) are unfortunately not directly comparable. Gillespie gave the dates of beginning and end of moulting in five birds over eight successive years. Two observations are missing, due to the death of one bird before the end of the period. The lengths of periods of moulting are shown in Table IX; it will be seen that the mean for all observations is 16.8 days, or slightly more than half the mean obtained for birds in South Georgia. It seems probable that Gillespie's figures refer only to the time when feathers are actually falling, although this is not expressly stated in the text. However the table may be interpreted, it is interesting to note the wide variation in average length of the period of moult from year to year; thus in 1922 the mean period for the five birds was 13.4 days, in 1919 the mean was 19.6. The mean lengths for each bird over eight successive years (six in the case of "Eric") vary only slightly in comparison.

Very little was discovered, during the investigations at Paul Beach, about the onset of moulting in successful breeders. Few birds feeding late in the 1953–54 breeding season (i.e. in January and February 1954) were ringed, and few ringed successful breeders of the same season had begun moulting by the end of observations in December 1954. Of twenty-four pairs of marked birds which raised a chick successfully during the 1953–54 season, only twelve pairs remained intact in December 1954. Only in four out of the twelve pairs had one of the parents begun to moult by the end of observations, but in each pair it was the female which moulted first. Of all successful breeders that were marked (including those whose partners were not known), twelve females but only two males had begun moulting by December 19th, 1954. These observations suggest a general tendency which was confirmed by further observations later in the breeding season (see section 2f: Courtship). It seems probable that chicks in the final stages of their growth, immediately before achieving independence, are fed by only one parent. Unless the pair has been separated or broken, the male continues to feed the chick while the female begins her moult. The single day's observations in January showed a number of males in moult, the partners of which had begun moulting in December; although none of the birds were weighed, it was clear that the males were moulting about a month later than their partners.

The onset of moulting in either parent is not related in any apparent way to the condition of the chick. The first marked successful breeder to moult, female 746, was known to possess both a flourishing chick (No. 16) and an active partner (male 658) when her moult began on October 17th. Female 746 returned to the rookery in breeding condition on December 6th and rested alongside her chick (which was still in full down) before joining in courtship activities. On December 19th she had settled with a new partner while the chick, still showing no sign of moult, continued to be tended by its other parent. The second banded successful breeder to moult in 1954 was male 668, father of a large but undernourished chick; the partner had not been seen since the previous July and was presumed missing. Male 668 had not fed the chick (No. 3) since mid-August, but began moulting about October 22nd with the chick still alive and active in the crèche. The fate of No. 3 is uncertain; it was apparently healthy when last seen in November, and might well have survived to moult successfully.

Two birds which are believed to have bred successfully in 1954 began their moults in November; their partners had not been seen for some months, but their chicks were believed to be alive. All the remaining marked successful breeders began moulting in December or later. Again, the time at which the parents began moulting could not in any way be predicted from the condition of the chick. Table X shows the dates on which ringed successful breeders began their moults, together with notes on the state of the chicks and the presence or absence of the partners.

Moulting was in every case concluded by the replacement of the pink mandibular plates, which were usually shed from one to two months later than the feathers. Variation in the colour of the plates, from mauve to salmon-pink, did not appear to be related in any way to the age of the plates or the degree to which they were attached to their sub-stratum. There was no definite period of moult for the scales of legs and feet.

f. Courtship and Pairing

The first indications of courtship behaviour appeared among birds which were completing their pre-nuptial moult. Those with head and shoulders still adorned by old feathers were frequently seen to respond to the calls of newly arrived birds in breeding condition; occasionally moulting birds responded to the

posturing of paired birds and became involved in triangular battles. However, no moulting bird was seen to form a partnership lasting more than a few minutes.

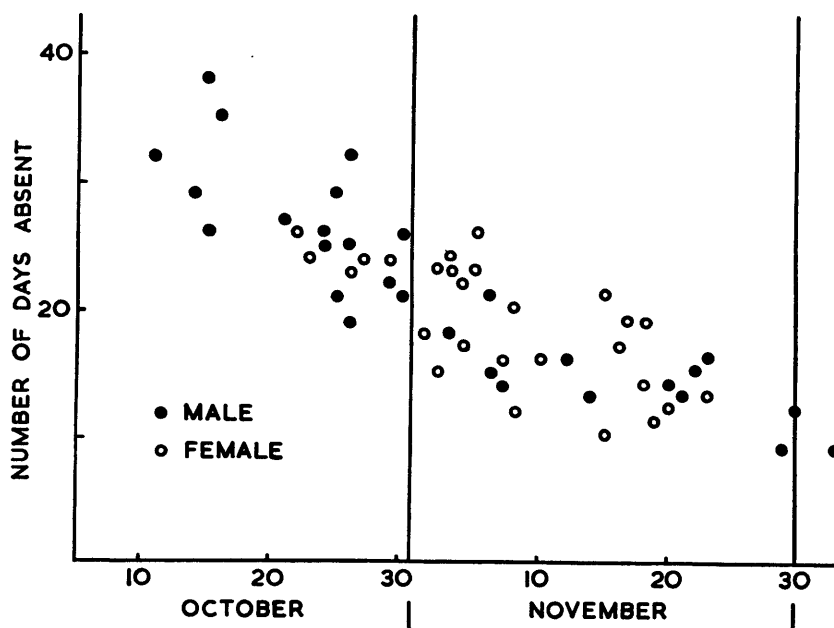


FIGURE 18. Length (in days) of absence before courtship plotted against estimated date on which moulting was completed, in fifty-six adults.

On completing their moult, the birds disappeared altogether from the rookery for a period of two to five weeks. At the beginning of the season, the earliest moulters stayed away for over a month; later, the time interval was shortened considerably. In Figure 18 the length of absence after moulting is plotted against the estimated date on which moulting ended; twenty-nine males and twenty-seven females are represented in the graph, including one of either sex (746 and 668) which bred successfully in the previous season. The data on which Figure 18 is based are included in Tables V, X and XI. It is believed that the period of absence between moulting and courtship is spent entirely at sea, enabling the birds to build up reserves of fat in readiness for courtship. Although the breeding urge of individual birds may develop more slowly in the early part of the season, the trend shown in Figure 18 is considered primarily to represent a gradual improvement in feeding condition between October and December.

On returning to the rookery the newly moulted birds were immediately distinguishable from all others by their combination of plumpness, immaculate plumage and tendency to court other adults. They were in excellent physical condition, normally weighing between fourteen and seventeen kilograms. Males were generally slightly heavier than females at this stage; in cases where the sex of a marked bird was unknown, its weight at the beginning of courtship was sometimes a useful guide, later to be confirmed by more critical differences in the breeding behaviour. The weights of twenty-seven newly returned birds are shown in Table XII and Figure 19. In cases when the first weighing was made some days after the bird's return, the weight on arrival was estimated by the addition of 0.17 kg. (males) or 0.23 kg. (females) for each day spent ashore. These figures were calculated from measured daily rates of loss in weight, which are discussed later. The mean weights of males and females on return to the colony after the pre-nuptial moult were 16.0 and 14.3 kg. respectively.

The dates on which marked birds returned to begin courtship appear in Table V, column 6 and Table X, column 7. Unfortunately, few dates of return were secured from successful breeders of the previous year; only two birds (both of which are believed to have moulted abnormally early) reappeared in new plumage before observations ceased. The results are tabulated in Figure 20; the forty-three migrant birds unsuccessful in the previous year are distinguished from the eleven non-migrants by shading, for direct comparison

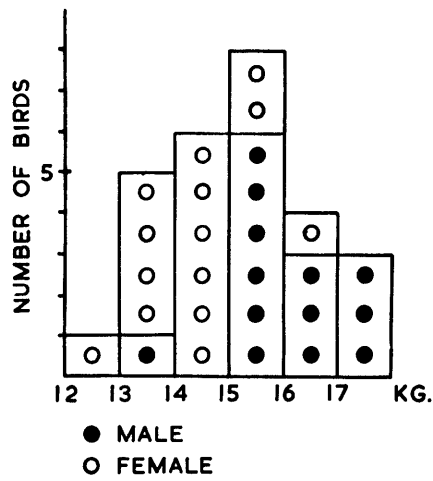


FIGURE 19. Weights of twenty-seven marked adults at the beginning of courtship.

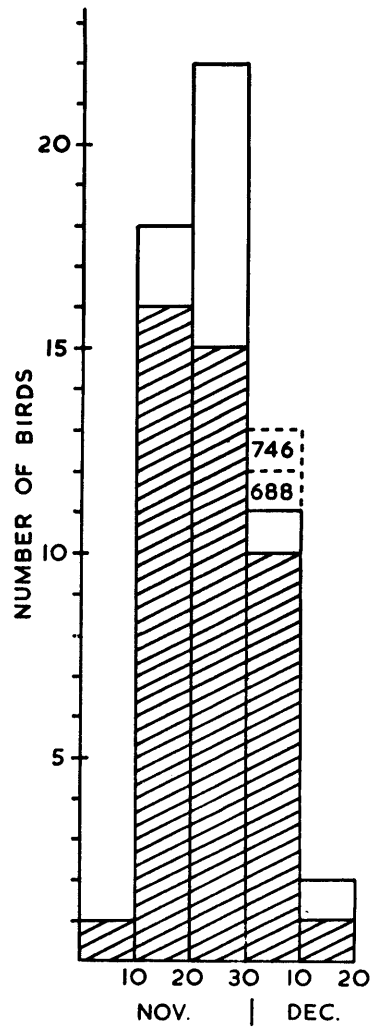


FIGURE 20. Dates of post-moult return in marked breeding adults. The shaded blocks represent migrant birds.

with Figure 13 and 14. All returned within fifty days of each other, the majority within 30 days; this is approximately a quarter of the period during which the same birds left the rookery in the previous winter.

Newly returned birds of both sexes made their way to the colony within a few hours of landing. They tended to congregate on the cliff tops above the colony, climbing and descending by the large drift which had formed in front of the cliffs during the winter storms. Here they were surrounded by fresh snow and unmolested by chicks or feeding adults; often the new arrivals slept at intervals during two or three days on the cliffs before starting their courtship activities. The first birds to return in breeding condition postured with moulting or feeding adults; later the proportion of newly returned birds increased enormously and courtship postures were less frequently misdirected.

For convenience the stages of courtship will be described under the following headings:

i. Attraction and pairing. Calls and postures typifying the first stage are directed to the colony as a whole, and serve to announce the arrival of a male or female bird in breeding condition. Responses from members of the opposite sex result in the formation of a pair, usually temporary; pairs eventually proceed to the second stage:

ii. Strengthening the pair-bond. Calls and postures are now directed solely to the newly found partner; partners become accustomed to one another and the pair-bond is slowly welded. A site is selected and defended.

iii. Mating. Further postures and calls lead to copulation and laying.

It must be stressed that the three stages are by no means clearly recognisable in the field; two birds may attempt copulation within a few moments of meeting and several hundred yards from the rookery, or seemingly well-established partnerships may break up after several days of apparent progress from stage *i* to stage *iii*. Again, individual birds may pass back and forth through the stages several times in a week. However, the sequence represents a framework on which, it is believed, most of the birds base their courtship behaviour. Together, the three stages correspond with Richdale's "pre-egg stage" (1951, pp. 143–198) in the Yellow-eyed Penguin (*Megadyptes antipodes*), but it may be noted that in the species studied by Richdale, pair-bonds are normally already established when the birds leave the water for breeding. Further comparisons are discussed in a later section.

i. Attraction and pairing. Newly returned birds in breeding condition advertise their presence by distinctive *short calls*, truncated versions of the typical, polysyllabic King Penguin call which can be heard on the rookeries at any time of the year. Figure 21 illustrates the differences between long and short calls used by the same bird at different stages of the breeding cycle. The displaying bird adopts a rigid *advertisement posture* with back slightly concave, head erect and beak horizontal, abdominal muscles contracted, neck fully extended and continuing the line of the back, neck feathers erect (i.e. ruffed out) and eyes half closed. The flippers are usually held closely in to the body. The bird raises its beak slowly to an almost vertical position, raises its tarso-metatarsi from the ground, stretches its neck to the fullest extent, inflates its air sacs and, with flippers held at a small angle from the body, gives vent to the short call. The eyes are almost completely closed at the end of the call, the head jerks forward, and the bird stands with beak horizontal for four or five seconds before subsiding to its normal relaxed stance.

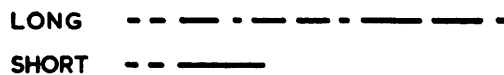


FIGURE 21. Sound pattern of long and short calls.

Male and female calls were not readily distinguishable to my ears; it is believed that female calls may be slightly longer and perhaps contain more long syllables than those of the male. There is no apparent constant difference in pitch. Yet it seems likely that the birds themselves have no difficulty in distinguishing the sex of an advertising bird from its call. A calling male is immediately pecked by the males of all pairs within reach, and all females within earshot seem affected to some degree. Those with partners raise their heads and turn toward the calling bird, while their partners frequently dart their beaks either toward the caller or toward neighbouring pairs. Nearby females with partners are sometimes seen to take a step

toward a calling male, while their partners interpose themselves between the females and the caller. This was seen frequently during the first few days in which courtship was observed; later, as the pair-bonds strengthened, females of the more firmly established pairs showed less interest in interlopers of the opposite sex. In newly formed pairs the females were occasionally seen to leave their partners and walk up to calling males, followed by their partners; in many cases, the original pairs did not re-form after such a disturbance. Similarly, when a female called, the attention of nearby males was drawn to the caller, while nearby females responded by pecking or lunging at the calling bird and at each other.

Unattached birds of the opposite sex are attracted directly toward a calling bird. Unattached birds of the same sex attack the caller, but do not usually step far out of their way to do so. Early in the breeding season, unattached females were occasionally known to cross the rookery floor, a distance of ten metres, in response to a call from a male; later, when more calls were heard and more pairs blocked the way, only birds within two or three metres of the caller were likely to respond.

The responder, on reaching the calling bird, usually adopts a similar stance, with chest thrust forward, abdominal muscles contracted, back arched and neck feathers ruffed. Facing inward at a right angle to each other, from one to two metres apart, the two make short, decisive movements with head and beak; the beak is held horizontally or pointing slightly downward, and the head rotates on a vertical axis, sometimes through as much as 120° in a single rapid movement. Usually the beak is directed away from the partner when at rest. The movements correspond, in description and context, to "head flagging" in Black-headed Gulls (*Larus ridibundus*; see Tinbergen and Moynihan, 1952, pp. 21–22); as in gulls, they form the antithesis of aggressive behaviour (see p. 28) and appear only in courtship. Head flagging may persist for several minutes after responder and calling bird have met, or may be punctuated by a series of antiphonal short calls from both birds. These generally attract the attention of nearby birds; on one occasion, a newly arrived male attracted no fewer than twelve birds of both sexes to his corner of the rookery after two or three preliminary calls and a similar number of responses from his first partner.

Partnerships established in this way are temporary and can be broken as easily as they are formed by newly arrived birds. However, at least some of the banded and marked birds were found in each other's company more frequently than random selection would have allowed. These birds seemed to know each other as individuals and to respond readily to each other's calls; an example is discussed later in this section.

After a period of head flagging and calling, one or other partner leads off with a characteristic strut, the *advertisement (attraction) walk*. The back is arched, the chest and abdomen are held as described in the advertisement postures, the beak points forward and slightly downward. The neck feathers are ruffed, the neck is extended and the eyes are half closed. The birds walk on their toes with flippers rigid and pointing to the ground. The most characteristic movement of the walk is, however, the pendulum motion of the head, which swings from side to side in a violent exaggeration of the normal counterpoise movement. At high intensity the head swings sideways through 90° , at the same time turning slightly from side to side so that when the head is farthest to one side the beak also points to the same side. One result is that the vivid auricular patches are demonstrated alternately, and to good advantage, from the rear.

Usually the male takes the lead, shaping a circular or elliptical course between neighbouring birds and returning to the point from which he started. The female may follow immediately, or may allow the male to make a circuit alone before following. If she fails to respond at all the male may call again and make a small circle, of two or three metres diameter, immediately in front of her. More than one female may follow a male; often fights between the females ensue when two or three try to follow a single male. Occasionally the male leads away in an almost straight line to another part of the rookery altogether, seeming to be aware all the time of whether or not the female is following. Should her attention be distracted by other birds he returns, calls and postures in front of her, and leads off once more. In following, the female adopts the rigid posture of the male. When the two are once again facing each other small head flagging movements show their mutual interest; the birds may lean against each other with breast feathers touching and heads well back.

Many instances were seen in which females, marked and unmarked, took the lead. The female version of the advertisement walk was similar in most respects to that of the male, but was never seen to reach the high degree of intensity shown by most males, for instance, during their third or fourth days of courtship. Occasionally, when a male had led an outward journey, a female would lead back across the rookery to

a previously occupied site. The journeys, whether led by male or by female, were seldom uninterrupted; bystanders frequently joined in and started running fights with the follower, and both birds were attacked if they ventured into parts of the colony where pairs and incubating birds stood closely together. The posture in the advertisement walk was well suited to pushing and also to edging rivals away from a coveted partner; with chest out, head held back and away from danger, the leading bird could barge its way through a crowd, beating with flippers and darting the beak forward effectively when opportunity offered. During the first few weeks of the courtship period, the rookery resounded with the hollow thumps of flipper edges beating against resilient breast feathers, a most characteristic and unmistakable sound which undoubtedly attracted other birds to the fights.

Leading and following usually resulted eventually in the isolation of a pair on a site where courtship could proceed without interruption. In crowded areas a newly arrived pair was seldom allowed to settle in peace, the pecks of neighbours urging them on and obliging them to spend more time in defence than in courtship. Although the display was also seen in moulting birds, in birds which had completed their moult but not returned to the sea, and in feeding birds during the winter, it was never seen to occur between chicks and juveniles.

The significance of the orange auricular patches as a releaser of following behaviour was demonstrated in experiments on two birds at the beginning of the 1954–55 breeding season. Male 693 was caught on the day of his return for breeding (Nov. 17th) and both auricular patches were daubed with black paint. Although the patches could still be seen through the paint, they appeared a dull, yellowish grey rather than orange. On the following day 693 was seen to give the advertisement posture before several birds, most of which could be identified as females. His calls attracted attention, but no female followed his walking. 693 followed several females, but did not appear to attract either the antagonism of males or the attention of females by his presence and postures. By November 20th he was still unpaired and was making no progress with courtship. On the night of the 20th heavy rain washed some of the paint away, and on the morning of the 21st the orange patches showed more clearly. On the same morning he was seen to attract females in advertisement walking, and by the following morning he was established with a partner on his final breeding site. The experiment was repeated with an unmarked male, the paint being renewed at intervals of three or four days. In spite of strenuous efforts the bird remained unpaired at the end of three weeks, but took a partner as soon as the paint was allowed to wash off.

Although leading and following tended to isolate pairs from the main mass of birds on the rookery, the pair-bonds were still weak at this stage and could easily be broken by the calls of new arrivals or by other disturbances. Thus, attempts to mark pairs early in the breeding season were seldom successful, as the disturbance caused in marking was generally sufficient to break the pair-bond. Even in cases where one bird was already marked, it was often necessary to mark two or three successive partners before the final breeding pair was established. Banded birds were, in any case, seen to take a succession of partners even if undisturbed by the observer. The following studies (transcribed from a tape-recording) show the complexity of relationships during initial stages of courtship.

Female 720 was seen on the rookery in the morning of December 13th, 1954; she was known to have returned in breeding condition six days earlier and had not as yet formed a permanent liaison. However, the condition of her breast and abdominal plumage suggested that copulation had already been attempted. She was standing with a large unmarked male (LM) when first noticed. 720 led off with a marked advertisement walk, gave a short call and was joined by LM. A second male (SM), followed by three fighting females, answered her call. Two of the females left the group; the third, which seemed attached to SM, attacked 720 and stood in close apposition to her partner. The two pairs head-flagged at a distance of one metre from each other. 720 led off again, followed by LM and by the other pair, with the second female trying to interpose herself between 720 and LM (i.e. behaving as though partnered with LM and in the presence of a rival female). The two pairs made a circuit of the eastern end of the rookery, covering a distance of 30 metres, then returned to the point at which 720 and LM were originally seen. Each bird stood with its original partner, leaning over to attack the other pair at intervals. A third male, blood-stained on flippers and chest (BM) postured in front of 720 and was attacked by LM, who also pecked 720 several times. BM led off across the rookery with a pronounced advertisement walk which attracted 720. After exchanging blows with her partner, 720 followed BM, who by this time was seven or eight metres ahead and lost in a crowd of pairing birds. BM turned, stood rigidly in an advertisement pose, and was joined by 720. BM again led off, this time closely followed by 720. LM rushed

forward to interpose himself between the two and again pecked 720 several times. Five minutes later the three birds were seen standing together, with 720 and BM close to each other, LM slightly apart.

As the incident seemed to be over, the observer's attention turned elsewhere, but ten minutes later

720 was seen to have returned to her old site, while BM remained where last seen and LM, who was unmarked, seemed to have disappeared. BM gave a long call and appeared to be searching about him. Moving nearer to 720's site he called again, this time with the short version of his call, and was attacked by a nearby pair. He was also pestered by a large chick, who solicited but was ignored. After several more short calls he was approached by a juvenile, who attempted to preen his neck feathers but was driven off. Meanwhile 720, after similar encounters with chicks and adults, moved over to the point where she had previously left BM. BM joined with another pair and was attacked by the male. When at a distance of two metres from 720 the latter suddenly stiffened and drew herself up into an advertisement pose, head flagging violently in the direction of BM. BM pushed past other pairs to reach her, and the two stood closely together, head flagging from time to time, for over an hour.

The observations showed the temporary nature of pair-bonds in the early stages of courtship, but also suggested that previous experience influenced birds in their choice of temporary partner. 720 and BM clearly recognised each other as individuals (i.e. not merely as members of opposite sexes in breeding condition) and showed affinities for each other in spite of 720's earlier preoccupation with LM. Many similar cases were recorded, of birds which associated constantly with two or three distinctively marked partners, or showed recognition of partners with whom they had been known to breed in the previous year. It is possible that 720 and BM had paired in the past; unfortunately BM's distinguishing marks were soon obliterated and his career was not followed; 720 settled with an unmarked bird three days after the events described, and was still awaiting her egg when observations ceased. The observations also showed the marked tendency of courting birds to congregate together, often in groups of four, six or eight, and conduct running battles between themselves, punctuated by intervals of courtship display. Thus the early stages of courtship are associated with continuous, violent activity, in which members of a pair may be seen attacking neighbours in their group at one moment, but attacking their own partners and exchanging partners a few moments later. A similar tendency appeared in feeding behaviour, when adults tending chicks during the winter usually stood in close proximity to each other and alternated feeding with bouts of antagonistic behaviour toward their neighbours.

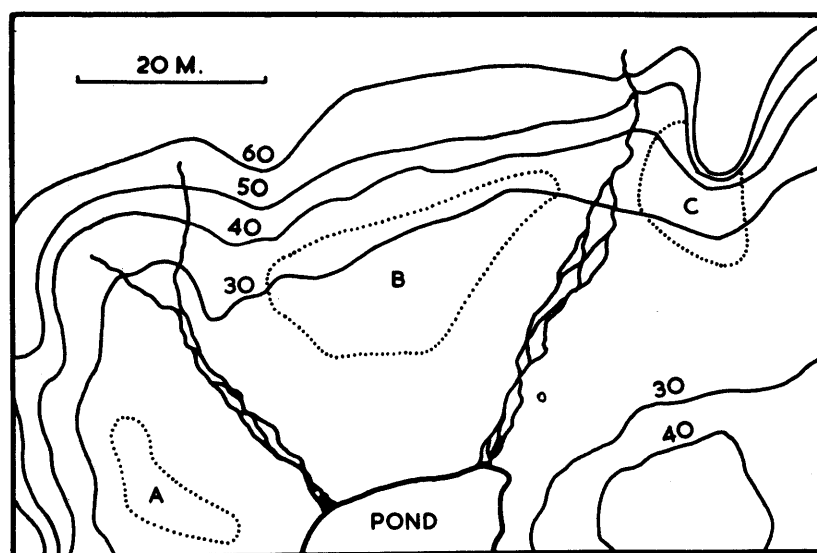


FIGURE 22. Three patches of dry ground (A, B and C) at Paul Beach on which the first breeders settled in 1953 and 1954. Heights in feet.

A third feature of courtship was also demonstrated in the behaviour of BM, 720 and LM. Each bird was apparently associated with a particular point on the rookery, to which it returned between bouts of courtship activity. Leading birds tended to lead their temporary partners toward their own "bases",

partners often tended to lead back to the point with which they were themselves associated. In many cases, ringed birds were seen to lead partners toward the site on which they had bred in the previous year, and it is believed that most sites owe their significance to an historical association of this kind. However, other factors influenced the final choice of breeding site in the current year, and the traditional site of one or other partner in a new partnership was not necessarily occupied again for breeding. The first breeders in both seasons settled on three patches of dry ground (A, B, and C in Figure 22; Plate IIIa), the three groups gradually spread and merged as the seasons advanced, and late breeders occupied inferior sites in stream beds or at the edge of the tussock grass. Many of the late breeders failed, and became early breeders in the following season. Although they began courtship at their sites on the fringes of the old groups, they moved inward to better sites as courtship proceeded, eventually laying in close company on one of the three patches of dry ground. Much of the apparently aimless wandering of courting pairs may be ascribed to indecision arising from the conflicting attractions of two or three sites, the traditional sites of the two birds forming the pair, and a new site on the best available breeding ground.

ii. Strengthening the pair-bond. The newly formed pairs may wander for two or three days before settling on a site, and may change their site several times before the final choice is made. Gradually, however, they become more closely welded together, and show more inclination to combine in defending the area about them. Still their behaviour is marked by the restlessness of early courtship; a site may be defended strongly for a day, abandoned for a few hours while the birds wander elsewhere, then taken up again after a series of battles with other pairs which have surrounded or occupied the area in their absence. The differences between the first and second stages of courtship are seen most clearly at the beginning of the season when the breeding areas are first occupied. After three or four days of battles, pushing, wandering, and strenuous calling, a proportion of the earliest breeders suddenly forms recognisable, static pairs, becoming the nuclei about which the rest of the colony eventually settles in the course of the breeding season. Although any pair may shift or wander, their behaviour is now centred on a site to which they are likely to return. Here their courtship develops, involving fewer calls and postures of general interest and attraction to unpaired birds, and more displays and postures directed exclusively to the partner sharing the site.

Advanced courtship is typified by two displays, *high-pointing* and *dabbling* (Plates IIIb and IVa). Either display may be seen in earlier stages, but both appear more frequently in pairs which have settled and are preparing to mate for the year.

High-pointing develops from the advertisement posture and frequently follows a prolonged spell of head flagging. The two birds stand closely together on their site, clearly aware of each other's presence and each responsive to the other's movements. One, usually the male, begins the display by lifting his beak vertically and extending his neck fully in a slow, deliberate movement. The partner follows exactly, until the two birds are standing, often on the tips of their toes, with beaks pointing to the sky and necks completely extended. The heads wave gently from side to side, sometimes turning decisively and weaving about each other, the eyes are almost closed, as in all courtship displays, but the birds respond immediately (by small movements of their own) to the movements of their partners. After a space of five or ten seconds the heads are slowly lowered, and both birds head-flag for a few more seconds before relaxing to the normal standing position. The display is silent, and does not seem to evoke the interest or antagonism of bystanders. Usually the head of the male is held slightly higher than that of the female, the birds thus exhibiting one aspect of their sexual dimorphism which cannot normally be measured in the living subject.

Dabbling, so called from its superficial resemblance to feeding movements in ducks, marks a further-stage in the development of the pair-bond. It is seen particularly when the birds are at peace with their neighbours and not immediately concerned with defending their site. The displaying birds stand facing each other, usually less than half a metre apart, and one or other begins the display by dropping its head sharply forward. The beak is opened and closed rapidly several times with an audible rattle; the tip of the beak may be directed toward the ground, or the displaying bird may lean slightly toward its partner and point the beak toward the partner's lower abdomen or feet. Frequently the tip of the beak makes preening movements among the bird's own abdominal feathers, or within the brood patch of the partner. On one occasion, a male was seen to dabble toward the ground and pick up a small pebble which it dropped again almost immediately. There were indications that dabbling was often, if not always, directed toward an irregularity or mark on the ground, on the bird itself or on the partner. Usually the partner responded

immediately with a similar movement. Either bird might initiate the display. Dabbling movements in the female were frequently followed by attempted copulation, in which the male advanced and tried to press the female downward with his weight on her neck and shoulders. The extended and curved neck of the female was apparently a stimulus for copulation; on many occasions males were seen to begin copulatory behaviour with females which bent forward to preen or to tend a newly laid egg.

The dabbling movements of one pair frequently stimulated the same behaviour in neighbouring pairs which had reached a similar stage in courtship; occasionally, when all was quiet in a corner of the rookery, a wave of dabbling would begin with one pair and spread to most of the breeding birds in the vicinity. Dabbling was occasionally seen when both members of a pair turned to each other after quarrelling with neighbours; for a few moments the two beaks would dabble in unison before the birds settled peacefully once again. Between well established partners the advertisement call of a new arrival would also be countered by dabbling; in consequence, at this stage neither bird would be likely to leave its mate to follow an advertisement call or walk.

iii. Mating. Birds which settle on a site for two or three successive days, and perform the displays of high-pointing and dabbling frequently during that period, may be considered as mated birds (Richdale, 1951, p. 7) joined by a permanent bond which will be maintained throughout the following months of incubating and rearing the young. Mated birds can be marked, with the assurance that the disturbance would not break the pair-bond. They defend their site stoutly against encroachment by other pairs, standing closely together with breast feathers in contact, darting their beaks in all directions and beating at passers-by with their flippers. Mated birds are generally invincible in their own limited territories, and will stand their ground if approached by human observers. Pairs which have not yet reached so advanced a stage in courtship are more likely to retreat in the face of determined attack, or at least to carry the battle to other parts of the rookery; they usually bolt when approached by man.

During the third stage of courtship the calls revert from short advertisement calls to the length more generally associated with identification of partner or chick. *Long calls* are heard frequently and are usually delivered antiphonally; when one member of a pair raises its head into the calling position the other follows immediately. Head and beak are elevated with neck fully extended, then, with air sacs inflated and eyes almost closed, the calls are given with full force. After calling, the head is jerked forward and down; with beak horizontal and neck extended the bird poses for a few seconds, then completes the ritual by lashing out with its beak, usually over the shoulder to left or right. The last movement is seen even when no other bird is within reach; any which happen to be standing by are pecked firmly, but the movement is ritualized and independent of the presence of bystanders.

Copulation usually begins two or three days after a mated pair has settled on its site. Although attempted copulation may be seen on the beach or among the tussock grass between birds which show no other signs of being mated and are probably strangers, successful copulation has been seen only on the rookery and only between birds which were likely to have conducted a normal courtship in the preceding few days. After a prolonged spell of dabbling, the male of the pair is sometimes seen to hook his neck over that of the female and press downward (Plate IVb). Alternatively, the male may approach the standing female from one side and lean forward against her back, pressing his beak into the feathers of the neck and head. Occasionally the male rubs the female's neck with the underside of his lower mandible. Any of these movements, or a combination of them, suggest that the male is ready for copulation. Females were occasionally seen to rub the neck of their partners with a lateral movement of the beak, or to preen the neck feathers of the partner after dabbling. However, the combined actions of neck-rubbing and pressing downward were confined to males. Occasionally the male bird would move sideways as though to mount the female during these preliminaries; usually the female side-stepped and the attempt was unsuccessful.

In successful copulation both male and female reach a high pitch of excitement, beginning with prolonged and agitated dabbling in which the male usually predominates. The female continues to dabble while the male places his beak over her neck, rubbing with the lower mandible flat against the female's shoulder. Simultaneously, the male moves round to the female's side, and stands close to her facing in the same direction. If willing to copulate the female bends forward and lies flat on the ground with flippers extended; if unwilling, she may extricate her neck from underneath that of the male, or may walk forward as he moves round to the side. With the female prone, the male climbs onto her back; his beak is placed firmly in the feathers of her neck and used as a pivot while he steps up and steadies himself with his flippers. The

male then shuffles gradually backward, depressing his tail under that of the female in a series of rapid flicks. The female shifts her tail sideways and protrudes her cloaca, which meets the cloaca of the male for not more than two or three seconds. The male steps off immediately after copulation and the female rises; the two birds usually dabble once again and pass their beaks outward in a wide circle to ward off the attentions of their neighbours.

Many copulations are thwarted by the behaviour of bystanders. Although the preliminaries (dabbling neck-rubbing, etc.) cause no appreciable excitement among neighbours, the sight of a male bird attempting to mount a female frequently leads to fighting, the mounting bird being compelled to defend his position against vigorous attacks from all sides. In a few cases the attackers, which are invariably males from nearby pairs or unattached males, themselves attempt to mount the prone female. In one isolated case witnessed early in the 1954-55 season, a strange male succeeded in mounting and was progressing toward a successful copulation while the rightful partner battled with two other males. Usually, however, the attacks seem to be acts of aggression directed against the mounting male, rather than attempts to copulate. Several males with firmly established partners were seen to move distances of four to six metres across the rookery to attack, returning to their sites after knocking over the offender and quarrelling with other pairs nearby. The females took no part in this behaviour, except to attack copulating females who lay with head or tail extending into their territory, and to attack fighting birds who came within their reach.

Rankin (1951, pp. 123-4) suggests that courting birds usually seek isolation immediately before attempting copulation, and that only in exceptional circumstances are attempts made in a crowded rookery. My own observations suggest, by contrast, that pairs almost invariably remain on the site to which they are attached throughout the final stages of courtship (except immediately before the egg is laid—see below) and that most pairs in copulating are therefore subject to attacks from a throng of neighbours. In some cases it was difficult to see how successful copulation could ever be achieved at all, so persistent were the neighbours' attacks. Lack (1939, pp. 295-6) quotes similar behaviour in the Blackcock (*Lyrurus tetrrix britannicus*) where males in adjacent territories attacked each other during copulation with a stuffed female, and records a case of aggression in captive Robins (*Erithacus rubecula*) in which a copulating pair was attacked by a second male in the same aviary (1940, p. 264). Similar behaviour in other penguin species is discussed in a later section.

Copulation was witnessed at all hours of the day; it occurred frequently in any pair which had reached the final stage of courtship, but it was not possible to maintain a constant watch on particular pairs and so obtain statistics on frequency of copulation before laying. In four marked pairs the egg was laid from four to eight days after the first copulation was witnessed, but previous copulations may in every case have passed unrecorded.

For the last few days of courtship the mated pairs sit closely packed together on the rookery, defending their sites and resisting invasion by wandering pairs. Two or three days before the egg is laid both male and female begin to adopt the incubating position, with back hunched, shoulders curved, and a large fold of feathered skin showing clearly below the abdomen. Their mutual behaviour is restricted to dabbling and occasional copulation. At this stage the egg may be palpated in the lower abdomen of the female. In several cases one or other member of marked pairs was found to wander during the last two days before laying, returning to the partner and site after making a circuit of the rookery and displaying spasmodically with other birds.

Eggs may be laid at any time; in several pairs the egg was laid at night or in the early hours of morning, and laying was also witnessed during late morning and afternoon watches. For about an hour before laying the female holds herself erect, relaxing her body from time to time, then tightening the abdominal muscles in spasms. Her movements provoke dabbling in the male, to which she may respond. After a series of spasms the egg appears point first at the cloaca, and may be held there for several minutes before finally being ejected. Immediately before laying, one female was seen to place a pebble on her feet, rolling it toward her with the tip of the beak; when provided with an egg she incubated it, but abandoned it at the next spasm of laying.

The newly laid egg lands forward between the female's feet, and is immediately held in the incubating position by the female. The male shows great interest, dabbling, hooking his beak under the female's abdominal fold, and occasionally attempting copulation when the female bends forward. Both give long calls frequently, and renew their attacks on neighbouring birds.

The total number of days spent in courtship (from post-moult return to laying) by nineteen males and twenty females is shown in Table XI and Figure 23. Males show greater range (12–29 days, females 8–18 days) and a greater mean length (19.1 days, females 13.9 days) of courtship. The stages of courtship were not studied in sufficient detail to provide material for statistical treatment. It is clear, however, that the differences in length of courtship shown between the sexes must relate to the period before settlement, i.e. before mated pairs have formed. Males, in effect, take longer to settle than females; whether this is due to a preponderance of males in the breeding population, and therefore to competition for females, is not known.

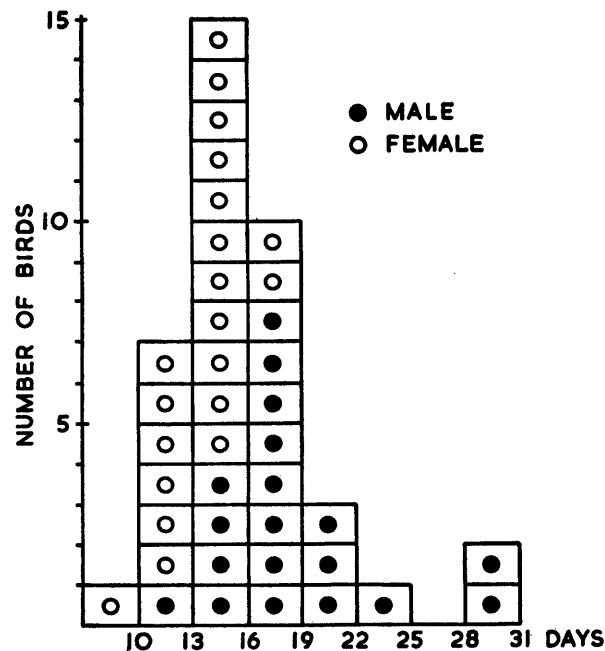


FIGURE 23. Length of courtship in thirty-nine marked birds.

Nor, with the data available, can any sound reason be given for the wide range in length of courtship shown by both sexes. It is known that male 605, who completed his courtship in the shortest recorded period (for a male) of twelve days, returned to the colony on the same day as his partner of the previous year and that the two formed a mated pair within two or three days of their return. Of the two males which took longest (twenty-nine days) over their courtship, No. 619 settled after about ten days and then had to wait an unusually long time for his partner to lay; 696 was unique in disappearing altogether from the colony for nine days during courtship, returning to settle and incubate normally after his absence. Of the females, 734 disappeared after eight days of courtship and possibly after laying, but unfortunately nothing was known of her partner or of subsequent incubation. Female 670 took eleven days in acquiring a new partner; her partner of the previous year was known to have been killed. She settled near her old site two days after returning and remained there until her egg was laid. Female 634, who took the longest time of eighteen days, wandered with a succession of partners for seven days before settling. Observations generally suggested that in most cases long courtship was due to indecision over partners or sites, and that 619's long wait after settling was unusual.

Of eleven pairs of marked birds which bred unsuccessfully during the 1953–54 season, seven pairs were broken by the disappearance (and presumed death) of one or both partners. In one other pair the female formed an alliance with a neighbouring family shortly after the loss of her egg, tending the chick through the winter and following spring as a third guardian (cf. the case of 748 described below): the male migrated for the winter, moulted, and formed a new partnership at the beginning of the 1954–55 season. Of the

remaining three pairs, two did not form again in the following season: in both, one partner returned to breed five days before the other, and all four birds established new partnerships. Only one pair of the original eleven (683-605) renewed its bond in 1954-55.

The weights of birds at the beginning of courtship have already been discussed; few were recorded during or at the end of the period, as handling tended to upset behaviour more during courtship than at any other stage. One male (641) was weighed on the fifth day of incubation and was found to have lost 2.2 kg. since his return from the sea eighteen days previously, a mean daily loss of 0.12 kg. As males tended to abandon their eggs if alarmed during the first few days of incubation, no further attempts were made to weigh marked birds. Five marked females were caught in the short period between laying and leaving for the sea; their weights are recorded in Table XIII. In two of these the weight at the beginning of courtship was also known; female 632 lost 2.5 kg. in ten days and female 646 lost 3.8 kg. in fifteen days (Tables XII and XIII). Both therefore showed mean daily losses of 0.25 kg. By comparing the mean weight of females at the beginning of courtship (Table XII) with the mean final weight obtained from Table XIII, a mean loss of 3.7 kg. is obtained. Using the figure for mean length of courtship (13.9 days) which may be calculated from Table XI, column 4, a loss per day of 0.27 kg. may be estimated.

g. Incubation and Brooding

During the first few hours of incubation the female takes full charge of the egg, crouching in the characteristic incubating attitude with back bowed, head lowered between the shoulders, flippers straight and almost touching the ground, and a fringe of abdominal feathers covering egg and feet. The egg rests athwart the ventral surfaces of the tarso-metatarsi; the bird sits back on her padded "heels" and tail, with toes raised in the air and lower abdomen resting on the egg. During incubation a brood patch becomes prominent in the mid-ventral line of the abdomen; a small ellipsoidal patch of skin remains free of feathers throughout the lives of birds of both sexes, but becomes dilated and prominent as incubation begins. The skin temperature of the brood patch was measured by clinical thermometer and Thermister probe, registering between 99°F. and 101°F. in five birds. Temperatures of eggs measured by the same methods ranged from 85°F. to 96°F., depending on how closely they had been held by the birds immediately beforehand. Frequently the upper side of the egg was 5° to 7° warmer than the lower side, both inside and outside the shell.

As the female incubates, the male takes up a position behind her; both lunge freely at their neighbours, dabble together, and frequently point their beaks toward the female's lower abdomen. Occasionally the female leans slightly back and raises her abdominal fold to display the egg; both give successive long calls and renew their dabbling on seeing the egg. After two or three hours (or occasionally longer) the female straightens up, stands once again on her toes and allows the egg to slip from her tarso-metatarsi to the ground. Either partner may take the egg by hooking the beak over it and drawing it towards the feet; usually the male succeeds, and he in turn adopts the crouching position. The females' interest in incubation may be prolonged for a day or more, but as she becomes restless, the male tends to incubate more closely until eventually the male retains the egg and the female wanders away. She may return several times to the breeding site, exchanging long calls with the male and dabbling excitedly when the egg is displayed. Finally she departs quietly and the male is left to incubate alone.

The female may wander to the beach on her own, or may join a party and spend up to forty-eight hours sleeping, preening, or swimming off shore in the company of other birds. Normally she leaves the area on the morning after her release from incubation (see Social Behaviour) and is not seen again until she returns to incubate, from twelve to twenty-one days later. Meanwhile, the male incubates constantly on the breeding site, defending his position against encroachment, sleeping, preening, examining the egg from time to time and normally remaining firmly within the space of about one square metre which constitutes his territory. Occasionally, incubating birds are compelled to move slightly as more and more pairs crowd into the breeding areas; the lone male is at a disadvantage against determined attacks from newly arrived pairs, and can defend only about two-thirds of the area previously held by himself and his partner. No measurements were taken, but my impression was that an incubating bird would be unlikely to move more than a metre from its original site in the course of incubation. No bird was known to abandon its egg because of overcrowding, although in two or three cases unmarked birds were seen to break their eggs while shuffling over rocks to avoid hostile neighbours.

On her return from the sea, the female usually spends one or two days on the beach before relieving the male. She may sleep in a group of moulting birds, wander aimlessly with other groups in the tussock grass, perhaps respond several times to advances from courting birds before finally making her way to the edge of the rookery. Standing at the edge of the breeding group in which her partner is incubating, she gives several long calls in succession. In spite of the general noise of the rookery, the partner usually hears and recognises the calls immediately; he responds by stretching upright and giving his own calls, which in turn are recognised by the female. The female then beats her way through the group of incubating and courting birds, apparently in the direction from which her partner was heard. She may stop two or three metres short of the breeding site, or may overshoot, passing the male and perhaps attacking him or being attacked by him on the way. She calls again, is re-directed by his response, and finally stands alongside him. The two give alternating calls, dabble, high-point, and lash out with their beaks at neighbours before settling together.

The egg is usually transferred within a few minutes of the female's arrival. As two birds now occupy the space previously occupied by one, the pair is attacked constantly from all directions; within two or three hours the male retreats, leaving the egg on the feet of the female. She adopts the incubating position immediately and, except for her clean appearance, is soon indistinguishable from the other incubating birds around her. The male wanders for several hours before leaving the area, in spite of having starved through two or three weeks of courtship and a similar period of incubation; his plumage is by this time muddy and bedraggled, and his weight is normally down to eleven or twelve kilograms. He makes his way slowly down to the sea with the swimming parties and, like the female, usually leaves with a feeding party on the morning after his relief. On his return to the colony from two to three weeks later, he identifies his partner by calling and the two exchange places as before.

By providing an extra egg during the change-over ceremony, the partners could be induced to incubate side by side. In one experiment the relieved partner incubated the extra egg for a further week before leaving; nothing was known of the history of this particular pair.

Incubation in the King Penguin takes from fifty-three to fifty-five days; nine reliable records were obtained within this range from Paul Beach (accurate to \pm one day) with a mean length of 54.2 days. Two records of fifty-six days and one of fifty-seven, also accurate to within a day, may be included to give a mean of 54.5 days. Records of fifty-eight, fifty-nine and sixty-one days, each accurate to within two days, may be taken into account but are considered doubtful in view of possible thefts, exchanges and substitution of eggs; although birds normally held their own eggs it was not unknown for two to be interchanged during fights, or for a bird deprived of its egg to acquire one mysteriously over-night. In comparison with the figures from Paul Beach, Richdale (1957, p. 35) quoted incubation records provided by the staff of Edinburgh Zoo, ranging from fifty-one to fifty-five days. Of these the seven quoted for 1954 seem most consistent, with a mean of 54.4 days, range from fifty-three to fifty-five days and estimated accuracy of \pm one day.

Table XIV shows the division of watches between males and females during incubation and brooding in the Paul Beach colony. The records are taken only from those pairs in which both partners were known. Most of the watches are accurate to the nearest day, but in cases of greater uncertainty the lengths of adjacent watches are combined and are not included in the mean figures. The first two watches (excluding the short preliminary watch of the female) are approximately equal in length, with mean lengths of 18.6 and 18.7 days. After his spell at sea, the male returns to incubate for a shorter period (mean length 12.2 days) and is replaced by the female for a shorter period still (mean length 9.9 days). The egg is normally hatched during the female's second long watch, a mean length of 4.3 days from the beginning. Males and females respectively incubate for 56% and 44% of the total incubation period.

Very little variation from this general pattern was seen among marked birds, although the lengths of individual watches varied considerably from the means. The length of a watch was, of course, determined by the absent partner and not by the incubating partner. The longest single watch recorded was that of male 618, whose unmarked partner failed to relieve him after her absence following laying. 618 incubated for thirty-five days, finally abandoning the egg. Female 604 incubated for thirty-four days in similar circumstances when the male failed to return. When both members of a pair took unusually long or unusually short spells at sea, the chicks would hatch while in the custody of a male, with no apparent ill-effects.

The time which a pair spent in incubation could be altered experimentally by substituting eggs at different stages of incubation; as the following examples show, the birds were able to accommodate themselves to feeding newly hatched chicks at any stage of the incubation cycle. The nature of the food is discussed in section 2i, on the care of the young. Relevant figures appear in the lower half of Table XIV.

i. Pair 608-609 were given an egg which hatched during the first few days of the male's second watch, presenting them with a chick two weeks before time. The male was able to feed the chick adequately (although the chick remained below normal weight) for twelve days before being relieved. The male returned after six days for his third watch, thus shortening the female's second watch (for which the mean length is 9.9 days). Similar results were obtained with female 625 who was given an egg which hatched toward the end of her first watch, i.e. about three weeks early. The chick probably received a little food from 625, but was taken over by the (unmarked) male on the third day and fed by him for fourteen days. The chick was healthy but undersized at the end of this period. 625 did not, apparently, shorten her absence after experiencing the presence of the chick; the male, however, returned for his third watch after four days instead of the expected eight or nine days.

ii. Pairs 614-716 and VIII-668 were given eggs which hatched abnormally late, during the males' third watches. Both chicks were fed satisfactorily. The females had not experienced hatching during their second watches but both returned after normal absences of eight days (mean for this watch, 7.3 days).

iii. For pair 740-616, hatching was postponed until the female's third watch. Again the chick was fed normally, and subsequent watches did not differ significantly from the means.

iv. The incubation of pairs 637-640 and 646-III was prolonged indefinitely, so that hatching did not occur. In both cases, the watches after hatching tended to remain equal in length, whereas those of normally brooding pairs tended to shorten progressively. 637-640 incubated for eighty-eight days; the egg was lost in a skirmish on the rookery and the incubating bird made no attempt to retrieve it. The second pair incubated for at least ninety-eight days, and may have incubated for ten or eleven days more, before their activities were observed. The egg was finally lost when the incubating bird took fright at one of my movements; the movement would not have affected it earlier in incubation, and the bird's urge to incubate was undoubtedly weak at the time. It returned to its site almost immediately but did not retrieve the egg.

Two cases were recorded in which the normal routine of incubation was disturbed by the intrusion of a third bird. Unfortunately in neither case was anything known of the intruder's history.

i. Pair 630 and 631 were marked on the day of laying. The male, 630, incubated for sixteen days, then disappeared before his partner arrived. No egg was found but it was assumed that 630 had broken or abandoned his charge. 631 appeared five days later, and was seen by the breeding site which was apparently occupied by an unmarked female. 631 wandered on the rookery for sixteen days. 630 then returned and took the place of the unmarked female, incubating for eleven days before being replaced by her once again. 631 continued to wander for four days after 630's return, but was not seen to incubate. The chick was hatched during the unmarked female's second watch, and was tended by all three birds. 631 and the unmarked bird (now marked 748) did not recognise each other as "partners" and would not surrender the chick to each other; 630 could take the chick from either and would allow the chick to be taken by both. The chick recognised all three "parents".

ii. Female 725 laid in mid-January and her partner, 684, began incubating. After four days 684 disappeared, his place being taken by an unmarked female. 725 returned to the site after an absence of eighteen days. Three days later 684 reappeared, took the egg from the unmarked female, held it for four days and then surrendered it to 725 who was standing nearby while he incubated. 725 incubated for twelve days while 684 disappeared. After returning, 684 incubated for a further four days, then passed the egg to the unmarked female who had returned to the site. After an absence of eight days, 684 returned to take over once again. The chick hatched nine days later but was found dead on the following morning.

Figure 24 illustrates normal and abnormal distributions of watches during incubation. In captivity, King Penguins incubate for comparatively short spells, usually of less than a week. (Gillespie, 1932, p. 102 et seq.). The incubating bird is often surrounded by others who are prepared to relieve it, and watches are changed frequently. In the wild, the absence of the partner would reduce the tendency for any bird to surrender its egg, and only in unusual circumstances (as in the cases quoted above) is the egg likely to be surrendered to a third adult.

Tests were made to see what range of objects incubating birds would hold, and to discover how rapidly the urge to incubate was lost after the removal of an egg. It was found that most birds would hold any object of suitable size in place of their egg. In twelve tests with different birds, plain white eggs (faintly

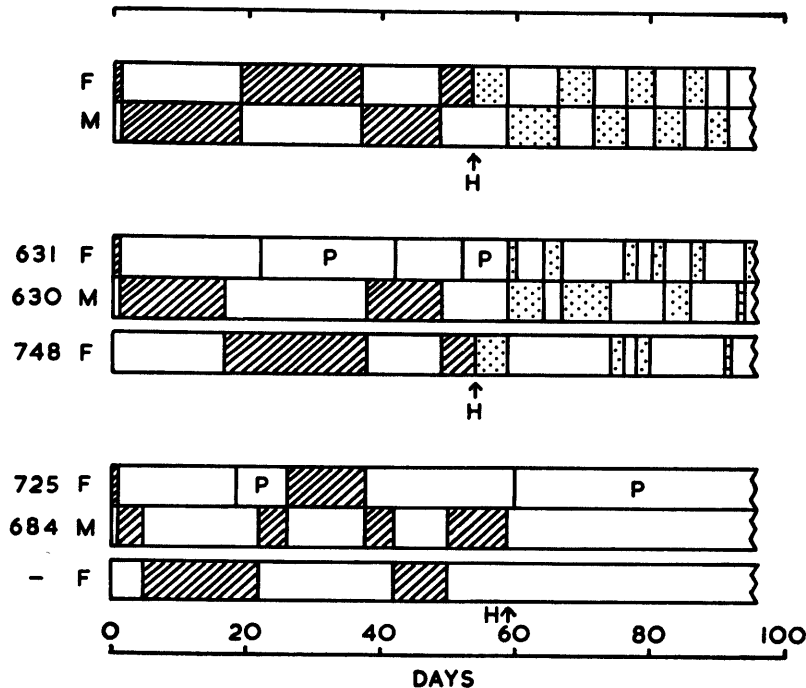


FIGURE 24. Normal incubation and brooding watches (top), compared with two abnormal cases due to the intrusion of third "parents". The normal case shows diagrammatically the means calculated in Table XIV.

Notes: Shading represents incubating, and stippling represents brooding.
 "H" indicates hatching.
 "P" indicates a bird present but inactive.
 The identification number and sex of the birds are shown on the left.

marked with mud) were taken in preference to striped or spotted eggs of the same size, and large eggs were taken in preference to small eggs if both were nearby. However, any egg of any colour or size was accepted on its own. With a selection of eggs at a distance (i.e. within one metre but further than the bird could reach without moving) tested birds always moved to the nearest egg in front of them irrespective of colour, pattern or size.

All the incubating or brooding birds were content to hold tins, bottles or stones of size and shape similar to eggs; one sat for three days with a cylindrical tin six inches long and three inches in diameter sticking out from the egg cavity like a ventilating shaft. Fragments of broken egg were also held, but bulk was apparently important; birds holding small fragments or the (smaller) eggs of Gentoo Penguins usually tried to sweep other objects into their cavities until a sufficient volume of material was being held.

Occasionally, birds were seen to roll a second egg toward them and try to place it under the fold while their own egg was already in place. Similar instances are quoted by Murphy (1936, p. 349) in which King Penguins, robbed by sealers, approached the piles of eggs to replace their losses and in several cases attempted to take two. In my own experience this behaviour was seen only in birds which had just succeeded in replacing their own eggs and were still in a state of agitation; the birds described by Murphy would undoubtedly have been in similar condition. Rankin (1951, p. 127, Plate 23) describes a case in which a bird attempted to take a second egg, apparently without previously having been deprived of its own. In several tests with settled, steadily incubating birds, I was unable to obtain this response; and the frequent occurrence of abandoned eggs on the rookery suggests that such behaviour would be extremely rare.

Incubating birds normally attack small chicks placed before them, but take up a chick in preference to an egg if given the choice while deprived of their own egg. Those deprived completely both of eggs and substitutes usually remain in the incubating attitude for two or three hours, frequently scanning the

ground and attempting to roll any mark or discontinuity towards them. After a time they adopt the more normal stance and begin wandering; a bird which reaches this stage can seldom be persuaded to incubate again, even if provided with an egg on its own breeding site.

As incubation progresses slight differences are noted in the behaviour of paired birds during the change-over ceremonies. Behaviour patterns associated with courtship (e.g. high-pointing and dabbling) become less prominent and are replaced by *regurgitation movements*. In these, one bird leans forward with neck extended vertically and beak horizontal, heaves its shoulders and thorax and opens its beak widely, as though feeding a large chick. Regurgitation movements in one of a pair stimulate the partner to similar activity; often the open beaks become crossed or interlocked, but neither bird feeds the other. Both seem to be directing their feeding to a non-existent chick. Normally no food is lost, although when the beak is held downward over the egg a small bolus of food is occasionally known to escape. The movements are slow and deliberate, lacking the final swallowing of complete feeding and *mock-feeding* behaviour (see section 2i). The birds regurgitate at the sight of the egg, and are particularly stimulated by the piping calls and movements issuing from a hatching egg.

Hatching extends over two or three days. The chick may be heard shortly after the first starring appears on the shell. No assistance is offered by the incubating parent, although considerable interest is shown. Boluses of food are frequently deposited on the hatching shell. A small number of chicks die while hatching, usually because the membranes dry and harden before the emerging chick manages to struggle free. A few which hatched on sites where the parent was standing in running water were drowned as soon as their heads were liberated from the shells.

After hatching, the spells of brooding become progressively shorter (Table XIV) until the parents are maintaining watch for only three or four days at a time. For the first week the chicks are interchangeable and any parent will brood and feed any chick; later the chicks become identifiable by their feeding calls and begin to recognise the calls of their own parents. A chick may then be brooded by a parent other than its own, but is evicted as soon as it gives a feeding call. The parent of a small chick will brood an alien chick very much larger than its own and may feed it if not conditioned to respond only to its own chick; if the parent has reached the stage of recognising its own chick's calls the alien is attacked as soon as it breaks silence. If agitated by the removal and restoration of its chick a parent may take a second chick onto its feet as well as its own, but a bird brooding peacefully will normally attack wandering chicks of any size. Wandering chicks find their parents by calling and following the sound of the parents' reply. They do not usually leave the parent until at least ten days old, and are then separated only if their group is disturbed by outside influences.

After about the fortieth day from hatching, nursery groups or crèches begin to form. Up to that age the chicks tend to hide under the nearest adult (usually their parent) if alarmed; only the head and neck may be accommodated in the egg cavity, leaving the relatively enormous body in full view outside. From the age of six weeks the alarm response alters and the chicks tend to join others of their kind when danger threatens. They also seek the company of other chicks if left temporarily by their parents, and so small groups of unaccompanied chicks appear among the incubating and brooding birds. The parents, no longer tied to the colony by the immediate presence of the chicks, tend to return to sea more readily after feeding. The groups of chicks amalgamate into the large crèches which characterise the rookeries from mid-February onward.

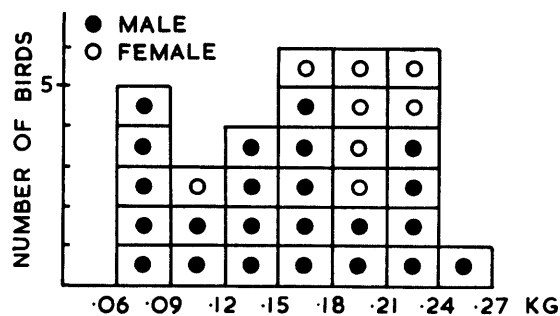


FIGURE 25. Mean daily weight losses (in kg.) of thirty-one incubating birds.

Table XV and Figure 25 show daily weight losses during incubation, recorded from twenty males and seven females. The initial and final weight was taken in each case during the same incubation period; those involving intervals of less than five days have been discarded to reduce the experimental error. Losses per day range from 0.23 kg. to 0.07 kg., with a modal value between 0.16 and 0.18 kg. and a mean for all observations of 0.15 kg.

h. Disturbed and Late Breeding

During the 1953–54 season several of the marked breeding birds were deprived of their eggs, which were removed after known periods of incubation and used for embryological studies. Other marked birds lost or abandoned their eggs from natural hazards, so that by the end of the season over forty cases could be studied in which breeding was stopped by the loss or removal of an egg.

Among these known unsuccessful breeders only fourteen attempted breeding again in the same season; their histories are summarised in Table XVI. All fourteen lost their eggs before the end of December, and all but one (male 650) had begun successful courtship before the end of January. This male courted unsuccessfully in December and again (after an absence at sea) in January; he was finally successful on returning a third time late in February. Males which lost their eggs during the first incubation watch usually wandered for a few days, left the area altogether, and returned as though for incubation after an absence of two or three weeks. Their second courtship began almost immediately. One male (730) completed his first watch without mishap, but returned after absence to find that both his partner and the egg had disappeared; he began courtship within a few hours and settled with a new partner less than a week after his return. Of the four females known to have lost first eggs, two (600 and 645) laid again early in February; after staying ashore for the remainder of the watch in which the egg was lost, they returned to sea for a spell of about three weeks and came up to begin courtship late in January. A third (639), whose partner lost the egg during the first watch, apparently stayed ashore unoccupied for only a few days, then returned to begin courtship after a further short period at sea. The fourth female, 631, is believed to have followed a similar pattern, but little is known of her movements between her departure after laying the first egg and the beginning of her second courtship.

As none of the original partners were marked, it was not possible to say whether birds generally took the same partners for their second breeding attempt. It seems likely that new ones were chosen, as the original partners behaved with complete independence after the loss of the egg and probably returned to begin courtship at different times. One case is known in which two birds (639 and 641) occupied adjacent sites during their first matings but formed a pair after the loss of their eggs.

Table XVII lists the histories of eight birds which lost their eggs before the end of the first week in January but did not mate again during the 1953–54 season. Three (male 618, females 670 and 683) showed no courtship behaviour and did not settle with partners. The remaining five courted with varying degrees of intensity from early January onward; some settled with partners but none produced an egg or incubated. Their courtship, where seen, appeared desultory and inconsequential. None of the birds which lost their eggs after the first week in January were known to lay or incubate a second egg. Some began courtship, but most spent their time in wandering with other unemployed birds about the rookery and beach.

Late breeders, however, continued to appear in breeding condition through February and March. Their courtship was no less vigorous than that of the early breeders, and seemed equally effective in the face of stronger opposition from the many settled and incubating birds. By the end of February the rookery was completely filled; new pairs were compelled to settle in the beds of the two streams which crossed the rookery floor, and a few colonised patches of open ground among the tussock grass. Their peace was continually disturbed by the movements of other birds entering or leaving the rookery. During March the demand for space was reduced, as many of the sites used by early breeders were no longer occupied, and some of the birds incubating among the tussock grass were able to move in toward the main rookery.

The 1953–54 breeding season drew to a close late in March. By March 26th only one adult remained in full moult, and by early April the last of the moulting birds left for the sea. Newly returning birds in breeding condition attracted partners, but seldom passed to the advanced stages of courtship. Warm, sunny days brought renewed posturing, but the birds became lethargic and inactive as the weather deteriorated. The last eggs to be laid by marked birds appeared late in March, but incubation tended to slacken; disturbed birds dropped their eggs readily and showed no inclination to pick them up. Small chicks were

left by both parents before they were sturdy enough to join the crèches, even before they had begun to develop the behaviour necessary for grouping with other chicks. Some were held temporarily by adults or larger chicks, but all were eventually trampled underfoot or killed by starvation and exposure. By April 9th very few incubating birds were left and abandoned eggs were found on the rookery floor each morning. During the last week in April, cold weather with snow and strong winds drove many unemployed birds from the rookery; the first waves of migration were seen and many of the remaining late breeders left their small chicks. The last of the marked breeding birds (late breeders of the previous season which had completed their moults in mid-February) abandoned week-old chicks early in May, as the winter drifts began to form across the rookery.

i. The Care of the Young

For about ten months after hatching the chicks are fed exclusively on material which their parents carry from the sea in their crops, together with mucus and other secretions from the crops which may amount to a significant proportion of the diet.

The newly hatched chick occupies the space, under the parent's abdomen, which previously held the egg. Its bulk is less than that of the egg from which it came, and the parent may frequently be seen touching the chick with its beak, pressing the chick back into the cavity as though dissatisfied with the sensation of a smaller object beneath it; similar behaviour is observed when, as described earlier, a small egg or other object is substituted for a normal King Penguin egg. The chick makes few sounds, occasionally giving a slight, piping whistle when touched. It normally lies across the parent's feet, with neck extended and head protruding slightly from under the parent's flank; sometimes it lies along the feet with neck curved to one side or the other. When exposed by the parent it raises its head and whistles. For the first two or three days after hatching the neck muscles are unable to support the weight of the head for more than a few seconds at a time, so that the head rises and falls spasmodically when the chick is disturbed. Later the same nodding movement appears in more vigorous form, and fully under the control of the muscles, as the chick begs for food. The nodding head and piping whistle stimulate the parent to regurgitate. When the neck is fully extended upward a swallowing reflex appears; the parent leans forward and opens its beak over the chick, which feeds by reaching up to the back of the parent's throat and (presumably) taking food from a bolus which the parent has lodged there by regurgitation. Small pebbles and grit are taken with the first feeds, and may be felt in the chick's crop from the first day. The chick feeds at intervals of two or three hours, and is usually stirred into activity only when the parent raises its fold of feathered abdominal skin. After about the fourth day, the chick has grown sufficiently for its head to protrude from under the lowered fold; at this stage it may initiate feeding by whistling and waving its head persistently.

The parent frequently gives long calls while feeding, and the chick responds with its characteristic whistle. The calls of the adult are associated with movements of the abdomen which must stimulate the chick directly; a mechanism of this nature may assist the chick in identifying the calls of its own parents.

If the chick is withdrawn from the cavity (e.g. for weighing) the parent normally shows agitation, scanning the ground immediately in front of it, pecking neighbours, and sweeping any loose objects under its fold. Some of the more placid breeding birds would attempt to retrieve their chicks from my hand, or from the canvas bucket in which they were being weighed. Timid adults tended to move away while the chick was being weighed, but would return immediately the chick was placed on the ground near the breeding site. The parent's retrieving action is similar to that used in replacing an egg; the beak is placed over the chick and drawn toward the body in a series of short scraping movements. Occasionally the adult shuffles forward slightly, thrusting its feet under the chick and rolling the chick aboard with a single movement.

If a newly hatched chick is left exposed on the ground, its slight movements and persistent whistles are powerful stimuli to all adults within sight or sound. An adult recently deprived of egg or chick responds immediately by sweeping the foundling onto its feet; usually it is the chick's own parent which retrieves it in this way. Occasionally parents which already hold a chick of their own will try to take the abandoned chick as well, but this behaviour is normally seen only if the birds are unsettled by the presence of a predator or observer or if they have recently been deprived of their own chicks. Incubating and brooding birds generally attack foundlings by pecking at them violently and throwing them in the air.

During their first week the chicks lose heat rapidly on exposure, particularly during cold weather; their

struggles and calls may be violent when first abandoned, but diminish in a few minutes as the body temperature falls. Moribund or dead chicks are seldom picked up by adults and may easily be trampled into the rookery floor; on a cold, windy day an abandoned chick's chances of survival decrease rapidly after five minutes of exposure. Unoccupied adults show interest in tiny chicks; two or three may approach a calling chick which has not been picked up immediately, point with their beaks, touch it gently with the tips of their beaks, and perhaps roll it onto their feet. A single unemployed adult soon loses interest, but the presence of two or three ensures that the chick is passed from one to another, warmed a little by each in turn, and kept alive. Unemployed marked birds which showed this behaviour were invariably unsuccessful breeders which had lost their eggs or chicks and were not attempting to breed again. None brooded for more than two or three minutes; the chick was always held uneasily and dropped frequently. Large chicks may also tend tiny chicks; as with the unemployed birds, their brooding responses are poorly developed, but are adequate to keep the foundling alive and active until its parent once again assumes responsibility. (Plate Va). The brooding urge of a parent dies quickly after the loss of a chick, but normally lasts for two or three hours, i.e. usually long enough for a lost chick to be recovered. It is clear that spasmodic brooding behaviour in older chicks and unemployed adults may save many small chicks which would otherwise die. The effectiveness of this behaviour rests in its apparent inefficiency; a temporary guardian which held a foundling chick for a number of hours would reduce the possibilities of its ever being recovered by the parent, and would find itself in charge of a chick which it could not maintain. Similar behaviour is seen in the Emperor Penguin (Stonehouse, 1953, p. 17-18, Plate 4 fig. b), in which unemployed birds struggle with each other to take charge of abandoned chicks, but lose interest almost as soon as they have secured one. Greater urgency is shown in the Emperor's behaviour, presumably in correlation with the lower temperatures experienced during its breeding cycle.

After the first few days the chicks are fed two or three times daily, beginning when the rookery stirs to life at first light. The amount fed is apparently regulated to the needs of the chick; an adult with a three-day chick will immediately increase its rate of feeding if a larger chick is substituted for its own. As the chick grows, its demands for food increase rapidly; at the same time the brooding watches are shortened, so that the parents alternate at intervals which decrease from five to three days (Table XIV).

After the first week of hatching, the change-over ceremony is complicated by the presence of the chick. The stimulus of the egg directly affected only one parent at a time, but the calls of the growing chick attract both parents simultaneously; neither can leave the site until a first feed has been given and the chick's calls cease. The two parents stand together with the chick on the feet of the newcomer; both regurgitate whenever the chick whistles, but only the holding bird feeds. After its feed the chick remains silent and the relieved bird wanders away. It returns immediately if still within earshot when the chick calls again, but usually escapes to the beach while the chick sleeps.

By the sixth week from hatching, the chicks begin to wander from their guardians and join the crèches. In their absence the guardians, too, wander from their sites and leave the chicks before relief arrives. The newly returned parent makes its way to the original site and gives long calls; its own chick responds and runs to the site to be fed. It is unusual for an alien chick to respond to a parent's call, although occasionally one makes the mistake and is soundly pecked. The chicks respond primarily to the combination of sounds which make up their parent's distinctive call; they turn in the direction from which the sound comes and run forward, orientating themselves next on the bird which appears in front of them in the extended calling posture. This is, of course, usually the parent, but if two adults are calling simultaneously and close together the chick may run to the wrong one. The chick utters its own call as it runs and the parent may begin to move in the direction from which the chick is heard. Usually chick and parent meet within fifteen seconds of the parent's first call; the chick may, however, find difficulty in reaching the parent through throngs of other chicks and incubating birds, all of which peck it as it passes. If the chick loses its bearing or is unable to identify the caller from its posture, it whistles violently and listens for a response from the parent. The parent may continue to move forward and actually pass the chick before calling again. However, if the chick is whistling and moving, the parent identifies it immediately and moves over to it. Chick and parent do not appear to recognise each other visually as individuals, at least during the first two or three months. They are attracted by sounds, movements and postures, which effectively bring the two together. Later in the year, visual recognition of the individuals may assume greater importance; after temporary separation chick and parent often identify each other by sight alone, although calls are always used to effect the first meeting when the adult visits the colony.

The parent calls several times while standing over the chick, and the chick responds by whistling. As the parent calls, the chick crouches in front of it with head lowered and beak pointing almost to the ground; as the parent's final note is given the chick raises its head sharply and, still with body crouched, waves its beak across the front of the parent's chest. The parent may respond immediately by regurgitating, or, if surrounded by hostile birds, may lead the chick off to a quieter corner of the colony. The chick follows in characteristic attitude, with head and shoulders bowed and flippers almost trailing on the ground. Usually feeding takes place within about five metres of the breeding site, and begins as soon as chick and parent have settled. Although the parent avoids places where constant defence would be necessary, almost invariably it selects a position alongside other feeding birds and alternates feeding with lungees at the neighbours.

The parent may feed for an hour, supplying the chick in this time with a kilogram or more of food. Towards the end it no longer responds to the chick's importuning by regurgitating; instead it preens the back of the chick's head, which appears to calm the chick and momentarily prevent further calling (Plate Vb). Preening and regurgitation may alternate for a time, then the parent becomes restless and moves away. The chick may remain behind and sleep or, more usually, may follow the parent and continue whistling. The parent stops to regurgitate or to preen the chick, then continues on its course, still closely followed. After preening and perhaps attacking the chick several times, it leaves the rookery and retires to the tussock or cliffs; the chick never follows beyond the boundaries of the rookery. On the following morning at first light, the parents return to the colony in a procession (see section 4d), call out their chicks and feed once again. They may feed again later in the day and possibly also in the next morning, but seldom remain in the area for more than two or three days. During this time the chick has received about three kilograms of food, composed mainly of finely triturated squid, complete with squid-beaks, small pebbles, and a quantity of mucus from the parent's crop.

After May, the parents appear less frequently, and remain in the area for longer periods. By the third morning after the parent's arrival, little food remains in its crop, yet feeding appears to occupy as much time as before and may be repeated two or three times during the day. A small quantity, possibly from fifty to one hundred grams, of bile-stained mucus is transferred at the beginning of each session; after this has been delivered, chick and parent continue with the motions of feeding but no material passes from one to the other. Both seem satisfied with the ritual of feeding, and may *mock-feed* for half an hour or more at a time. Mock-feeding is also seen between chicks and unemployed birds, among which were many of the marked unsuccessful breeders. At first this behaviour suggested that unsuccessful breeders were actually contributing food to the chicks of other birds; by weighing both chicks and adults after long sessions of mock-feeding, it was confirmed in many cases that no significant quantity of food passed. Mock-feeding behaviour of a parent and its chick cannot easily be distinguished from actual feeding. The chick importunes, the adult regurgitates, the chick reaches high into the adult's throat and both appear to swallow; only by close observation can it be seen that no food passes when the two are mock-feeding. Mock-feeding by an unemployed bird may also be deceptively similar to actual feeding, but is often less co-ordinated; both adult and chick may pass more slowly and casually through the motions of feeding, merely touching their beaks together and perhaps failing to swallow after each imaginary bolus of food has passed.

Mock-feeding is seen very frequently during autumn and winter. Some of the parents, on returning from the sea to feed their chicks, may stay ashore for a fortnight or more, mock-feeding once or twice daily after the stock of food has been delivered. Those unemployed birds which do not migrate for the winter may also mock-feed every day; they do not, unlike the parents, attach themselves to a chick early in the mornings, but frequently wander into the rookery later in the day and may then be importuned. Two important problems are presented:

i. Does the daily allowance of mucus have an appreciable effect on the welfare of the chicks? Unfortunately the weight of mucus supplied to chicks by their parents was approximately equivalent to the amount of snow which some of the chicks consumed daily. It was not possible to determine whether the chicks which received a daily ration (i.e. when one of their parents was present in the area) lost weight less rapidly than those which did not. The mucus, which is presumably secreted by the glands of the parent's crop, could conceivably contain quantities of protein and carbohydrate which would help to sustain the chicks on their starvation diet.

ii. It would seem that any bird which attempted mock-feeding with a full crop would almost certainly deliver food to the chick. Do unemployed birds, which may be importuned by chicks shortly after returning from the sea, carry food in their crops, and do they pass this to any of the chicks which they encounter? No marked unemployed bird was seen to mock-feed in these circumstances, but many could have done so without being observed. It is possible that the crop may remain full (i.e. digestion may be inhibited) for two or three days after arrival, while the parent sleeps (cf. return to incubate, p. 35). A parent, caught on its return from the sea, was confined in a pit with a hungry chick other than its own; the chick was not fed, and after three days the parent vomited quantities of the undigested food. Whether or not unemployed birds possess the capacity for retaining undigested food in their crops for a similar length of time is not known. If they can, it would seem that chicks in the crèches might from time to time receive considerable supplies of feed from adults other than their parents. The possibility that such feeding occasionally happens cannot be ruled out entirely; however, the chicks which I weighed at regular intervals showed an increase in weight (i.e. had received food) only when one or other of their parents came up from the sea, and apparently did not benefit from large feeds delivered by unemployed birds.

From June to September, the chicks receive food at intervals of two to four weeks. Their parents visit independently; both may by chance appear at the same time, but normally the visits are separated by irregular intervals. After delivering their supplies, the parents remain ashore for about a fortnight, then return to sea for a similar period. Parents meeting their chicks, or meeting each other at the breeding site, may call together, head-flag and high-point, but these displays are also seen frequently throughout the winter between birds which meet casually on the rookery and are known to be unpaired. In October and November, the rate of feeding increases slightly and the chicks, which have lost weight steadily during the winter, begin to fatten once again. By December, well tended chicks begin to moult and become independent of their parents; the female parents usually leave their chicks before the males (see section 2e: The Pre-Nuptial Moulting).

3. EGGS, EMBRYOS AND CHICKS

a. Eggs

The eggs of King and Emperor Penguins are closely similar in appearance; King Penguin eggs tend to be smaller but the extreme measurements overlap. The surface of the King's egg may be slightly smoother, with few calcareous nodules, but Wilson's description and illustrations (1907, pp. 29–30, Plates V and VI) of Emperor Penguin eggs from Cape Crozier would serve equally well for either species.

When freshly laid, the King Penguin's egg is white, with a soft, chalky surface. The surface later hardens and, within a few hours of laying, begins to assume a pale green colour. This gradually intensifies as incubation proceeds, and is usually marred by mud or faecal stains from the rookery floor. Dried shells darken to buff-green on storing. These colour changes are due to alterations in the cuticular layer, which may be removed completely by rubbing, scratching, or by the action of dilute acids. The substance of the shell contains small quantities of green pigment, most of which is concentrated in the inner layers and is therefore invisible at the surface; the ground colour of the eggs is white or very pale green.

The shape varies from sub-oval to pyriform. Dimensions of 69 eggs taken at Paul Beach were:

Mean Length	10.5 cm.	Range	11.7–8.6
Mean Diameter	7.6 cm.	Range	8.6–6.4

Wilson (op. cit. p. 30) provides measurements of twelve eggs taken at Macquarie Island:

Mean Length	10.1 cm.	Range	10.6–9.6
Mean Diameter	7.4 cm.	Range	7.8–7.0

Worth (1940) has shown that for most avian species an approximately constant relation exists between volume of egg and length of incubation. His graph (Text-figure 2, p. 48) indicates this relation for species ranging in size from humming birds to ostriches. The mean length of incubation for each size-range is shown by the straight line on his graph, and ecological conclusions may be drawn about those species the points for which lie far to left or right of the mean.

The volume of an egg may be calculated from the expression:

$$V=0.442 ab^2$$

(derived from Worth, *op. cit.*, p. 44) where *a* and *b* are the length and diameter respectively. The mean volume of the Paul Beach eggs, by this calculation, is 268 c.c. (range 382–156). Their mean weight (of eggs at all stages of incubation) was 319 g. (range 440–205 g.) The accuracy of Worth's formula when applied to King Penguin eggs is shown in Table XVIII, in which the length, diameter and volume of 13 eggs are listed, together with this calculated volume.

By comparison eighteen Emperor Penguin eggs measured by Wilson show the following mean dimensions:

Mean Length	12.0 cm.	Range	13.1–10.7
Mean Diameter	8.2 cm.	Range	8.6– 7.5

and a series from Terre Adélie (Etchécopar and Prévost, 1954, pp. 231–2, Nos. 29–42 and 10001–10037 in Tables I and II) shows the following:

Mean Length	12.4 cm.	Range	13.7–10.9
Mean Diameter	8.5 cm.	Range	9.1– 6.3

Prévost (1954, p. 249) gives a mean weight of 460 g. for an unspecified series of eggs. The mean weight of the forty-two specimens listed in Table I of Etchécopar and Prévost's paper is by contrast only 381 g. Of these, specimens 30–42 were collected in September 1951 some three or four months after laying, and had clearly lost weight during incubation. Considering only those collected in June 1951, a mean weight of 410 g. (range 539–255 g.) is obtained. From the mean length and diameter quoted by the French authorities, a mean volume of 396 c.c. may be calculated.

Taking the incubation period of the King Penguin as 54 days and that of the Emperor Penguin as 62–64 days (Prévost, *op. cit.* p. 153), and using the volumes obtained in the calculations above, it will be seen that both species incubate for about 15 days longer than the mean length appropriate to their egg volumes. The possible significance of this prolonged incubation is discussed in a later section.

The shells collected at Paul Beach, together with a series of Emperor Penguin egg shells from the Dion Islets (Marguerite Bay), have been passed to Professor C. Tyler for comparative studies of their physical and chemical structures (for methods see Tyler, 1956, and previous papers in the same series).

b. Embryos

Over one hundred embryos were collected in the course of the investigations. A small proportion came from eggs which had been incubated for known lengths of time, but most were from abandoned eggs of unknown age. A report on the embryology will be published in this series by Dr. T. W. Glenister, who previously (1954) published similar work on a series of Emperor Penguin embryos collected from the Dion Islets.

Forty-nine of the larger embryos were weighed and measured before fixing, in an attempt to discover a growth index by which age could be determined. Table XIX shows the weights and flipper lengths of these embryos, and in Figure 26 the weights have been plotted logarithmically against length of flipper. It is clear that these parameters, both of which may be measured with reasonable accuracy in older embryos, bear a constant relation to each other during growth; in combination, they provide an index which might be expected to fix the age of the embryo fairly accurately. Unfortunately, embryos of similar age vary considerably in size, the variation appearing most markedly in those approaching full term. Thus, in Figure 26 the embryo represented by point A was known to be five days older than that represented by point B. The time scale which has been added to the figure can only be approximate, and becomes inaccurate for embryos which are particularly large or small for their age after about the fourth week of incubation.

Some measure of an embryo's size in relation to its age might be obtained by considering the weight of the egg from which it was taken. In the previous section it was shown that King Penguin eggs vary considerably in size and weight, and a similar range is observed when newly hatched chicks are weighed. Large eggs give rise to large chicks. If the dimensions of an embryo could be adjusted by a factor based on the weight of its egg, it would be possible to devise a figure, similar to Figure 26, which might provide an

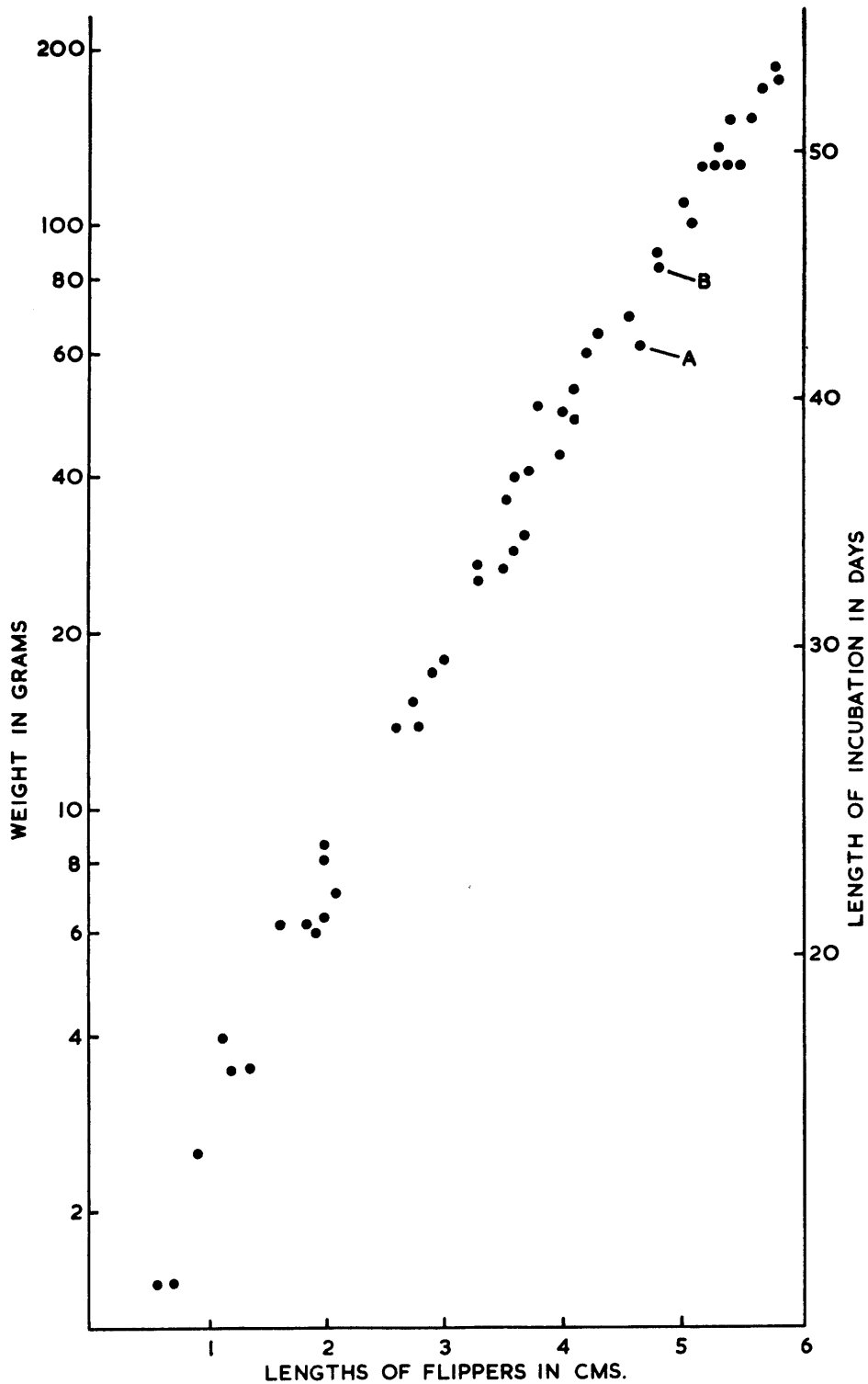


FIGURE 26. Weights of embryos plotted logarithmically against lengths of flippers, with approximate indication of length of incubation.

accurate guide to the age of any embryo large enough to be weighed and measured. Eggs collected during casual visits to rookeries in November and December would then yield information about the date on which breeding began, and from that date the whole calendar of the colony might be calculated.

The significance of the ratio between size of egg and embryo was not realised during the observations at Paul Beach; eggs were weighed and measured in batches before opening, and the relationship between egg and contents was not recorded. An additional factor, the loss in weight of an egg during incubation, might also have to be taken into account in assessing the ratio, but again no critical observations were made during these investigations to show how important this factor might be. However, the method is suggested for possible use in the future.

c. Chicks

Studies in the growth of King Penguin chicks, based on the mass of skeletal material from Paul Beach, will be published in a separate report. The following notes are based on field observations and measurements only.

The prolonged down stage of the King Penguin chick may conveniently be considered in three parts:

i. Initial growth. From hatching, the normal chick grows rapidly to a size only slightly below that of its parents, and to a weight of about 12 kg.

ii. Winter starvation. Growth almost ceases when the parents adopt a winter feeding routine, and the weight falls away to about two-thirds of the summer maximum.

iii. Subsequent growth and moult. In spring the parents feed their chicks more frequently, the lost weight is replaced, growth is completed and the chicks shed their down. So far as is known, only the Wandering and Royal Albatrosses are likely to share with the King Penguin the distinction of rearing chicks which effectively cease to grow for four months during their down stage.

i. Initial growth. The chicks emerge almost naked, with each feather papilla bearing only a single strand of fine grey or black down. The skin is dark grey and leathery, with the uniform pattern of papillae clearly marked. During the first three or four days coarser down begins to appear on flippers, rump, and head and neck; these are the parts most likely to be exposed as the chick alters position on the parents' feet. The chest and back remain bare, presumably to facilitate the transfer of heat from parent to chick. By the end of the first week brown mesoptile down begins to develop over most of the body, at first remaining thin over the chest and back; several wavy brown filaments emerge from each papilla, obscuring the grey of the skin and forming effective insulation. By the ninth or tenth day the chick is grey-brown all over. About the face and neck several of the filaments show grey tips, producing a pattern reminiscent of the face mask shown by the Emperor Penguin chick.

For the first week the chick remains hidden in the brooding cavity. After the seventh or eighth day it may begin to emerge, sitting upright on its parent's feet or on the ground in front for minutes at a time before retreating once again to the safety of the cavity. By the fourteenth or fifteenth day (when its weight reaches about 1 kg.) it may remain out for an hour, preening in the sun and calling for food from time to time. Chicks at this stage are grotesquely fat, pyramidal in shape and hung about with loose folds of skin. Their skin often shows scars and scratches, inflicted by the beaks of attacking adults, and may also be marked by a rash of small pustules, which presumably mark a bacterial infection. The colour of the down varies considerably from pale grey-brown to rich chestnut-brown, with head and neck usually paler than the body.

During the third week the chicks begin to move away from the immediate vicinity of their parents; they are attacked as soon as they approach the breeding site of another adult, and usually return immediately to their own quarters. By this time they are capable of navigating their way back to their own section of the rookery if carried experimentally to a distance of twenty or more metres; they appear to know the configuration of rookery landmarks, and finally "home" on the calls of their parents when near to their sites. They are active and alert, watching the passage of predatory birds overhead, and attacking other chicks which come within range. Their down grows steadily, and precociously developed rectrices appear through the skin of the tail. These lengthen rapidly, so that a chick four weeks old had an adequate "shooting-stick" support on which, like the adult, it may rest its weight. The rectrices are similar in appearance to those of a juvenile or adult, and are shed when the down is moulted toward the end of the first year.

During the fourth and fifth weeks the chicks grow steadily, and by the sixth week are tall enough to reach up to their parent's beak. Their flippers begin to lengthen and are used, together with the beak, in

effective defence. If alarmed they attempt to hide under the parent, but usually succeed only in forcing their heads into the brooding cavity, leaving the large rump exposed. (Plate VIa.)

After the fifth week the chicks begin to associate with each other. Their parents return to sea soon after delivering food, as previously described, and the chicks wander within a few metres of their breeding sites, joining and leaving loosely-knit groups of their contemporaries. Although the breeding sites retain their attraction and are still used by parents and chicks during feeding, they are more frequently deserted at other times and may even be occupied by newcomers for courtship and breeding. At this stage the crèches begin to form. In an undisturbed rookery the chicks usually remain widely spaced, or collect in knots of three or four; crèches become apparent only when danger threatens or when the weather deteriorates. If alarmed, or chilled by cold winds, the chicks congregate together in loosely-knit groups; adults are generally excluded and tend their offspring on the outside (Plate VIIa). Later in the year, when most of the chicks are unattended and few adults are about, the groups may coalesce until all the chicks (some 2,400 at Paul Beach) are contained in a single tightly packed mass (Plate VIIb). However, more characteristic formations during February and March would be the smaller groups of twenty or thirty, which form in the face of danger or cold. It may be stressed that at no time do the adults surrounding the groups act as guards; this question is discussed later.

From the seventh to the twelfth weeks growth continues. The down reaches a thickness of 5–8 cm. and the chicks approach the dimensions of their parents in height, girth and lengths of beak, foot and flipper. Those hatched late in January, the offspring of the earliest breeders, reach their maximum size and weight late in April. At an equivalent stage in any other species the moult into juvenile plumage would begin. In the King Penguin the chicks begin to settle into the routine which will carry them, as chicks in down, through the sub-Antarctic winter.

Figures 27–29 and Tables XX–XXII show various aspects of growth as measured in the Paul Beach chicks during 1954. Weights, and measurements of beak, foot and flipper, were taken from a total of eighty-three living chicks in the course of the year, and all dead chicks picked up from the rookery floor were weighed and measured where possible.

Table XX lists the weights, measured daily, of ten normal chicks during their first forty days of growth. These chicks were selected as examples of well tended, well nourished offspring; the uniformity of their growth suggests that all were receiving optimum feeding. Figure 27 shows the mean weights plotted logarithmically against time. It will be seen that weight increases exponentially for the first twenty days, after which the rate of increase falls off slightly. Not all chicks were equally well fed during their first forty days; thus No. 4 (not represented in the graph) was fed normally for the first week, remained approximately constant in weight for the second week, and by the thirtieth day weighed only 1.2 kg. instead of the normal 3.6 kg. The fluctuation in this case was due to the inattention of the mother, who apparently produced very little food for the chick during her first brooding, then left the male to brood for fifteen days instead of relieving him after about a week. The chick survived and reached a normal maximum weight by the end of April. Several similar cases were known. It is interesting to note that no marked parents were lost at sea during the brooding period, although many failed to return after May and June. The loss of a parent during the first three months after hatching could have resulted only in the death of the chick.

Although the data of Table XX are taken from ten chicks which hatched late in January (the chicks of the earliest breeders), the curve of Figure 27 would equally well represent the growth of chicks hatched later, except that those which hatched from late March onward showed a slightly reduced rate of increase between the twentieth and fortieth days. Late-breeding parents seemed to have little difficulty in feeding their chicks up to weights of 4 or 5 kg., but seldom managed to exceed these figures.

The continued growth of chicks from early breeders is represented in Table XXI, A, B, and C, and in the three corresponding curves of Figure 28. Table XXI B shows the mean weights at bi-monthly intervals of six normally tended chicks. The bi-monthly values were obtained by (a) estimating the mean of the four or five weighings taken nearest to the date on which each chick completed its second, fourth, sixth (etc.) weeks, and (b) averaging the six values so obtained for each bi-monthly period. It will be seen that the chicks achieved a maximum mean weight early in the fourth month, which in the case of the earliest-hatching chicks corresponded to early May. Table XXI C shows the weights of five chicks, each of which lost one parent before mid-June; as none of the parents was lost before the peak weight was achieved, curves B and C are closely parallel up to the peaks. Table XXI A shows the bi-monthly weights of the single chick, No. 27, which was fed throughout by three guardians (parents 630 and 631, and intruder 748). A greater

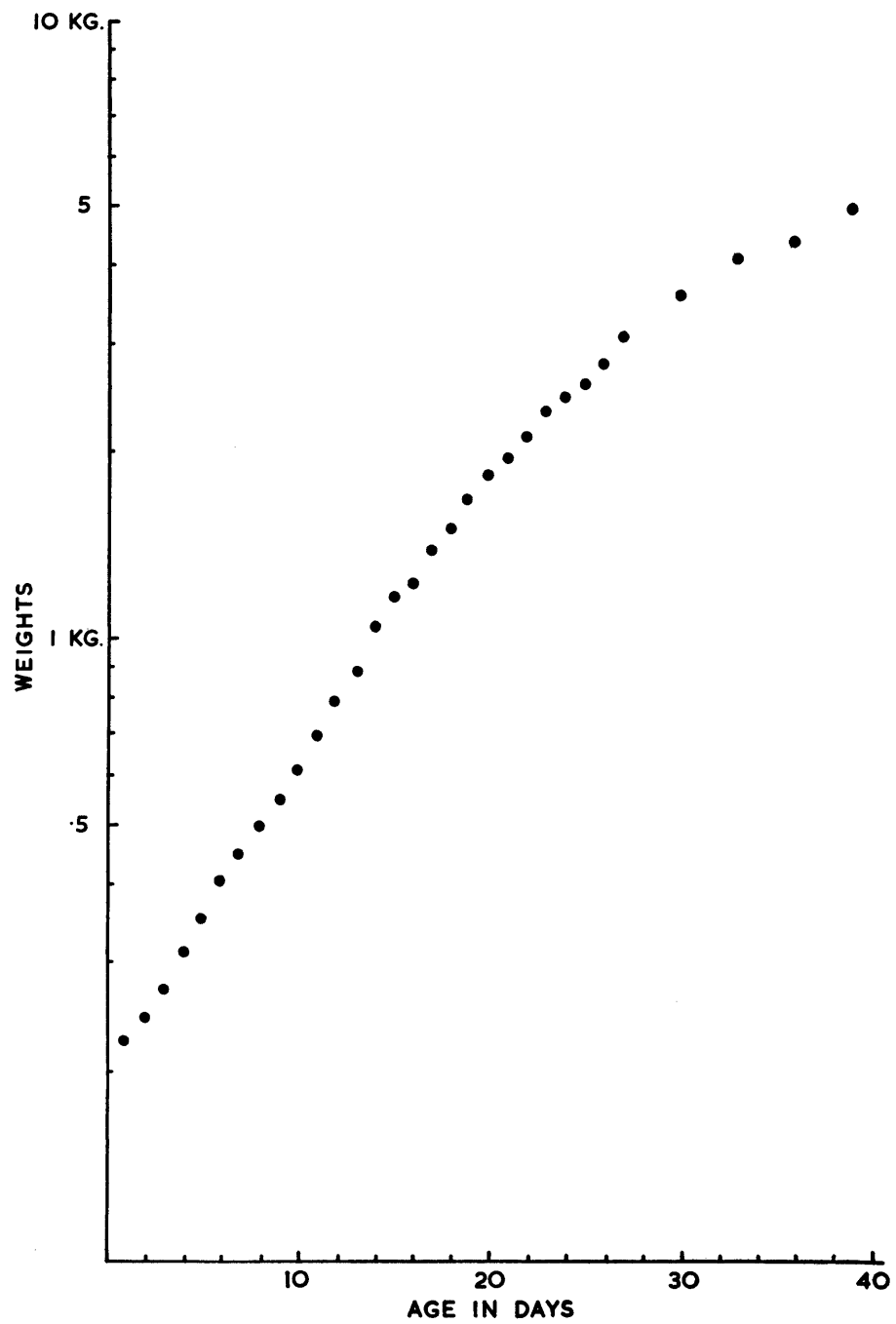


FIGURE 27. Mean weights of ten normal chicks during the first forty days of growth.

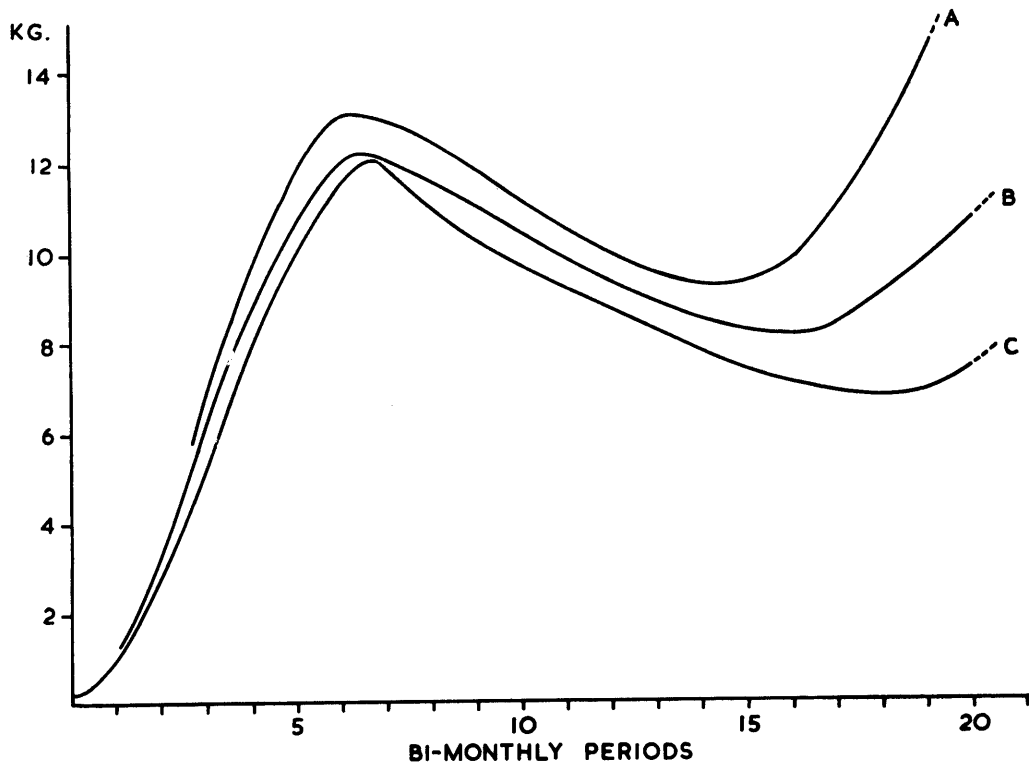


FIGURE 28. Growth of chicks. Mean weights (in kg.) plotted at bi-monthly intervals.

Notes. Curve A represents the growth of chick No. 27, fed by three "parents". Curve B shows the mean bi-monthly weights of six normal chicks, tended by both parents. Curve C gives similar data for five chicks, each of which lost one parent before mid-June (i.e. before period 20).

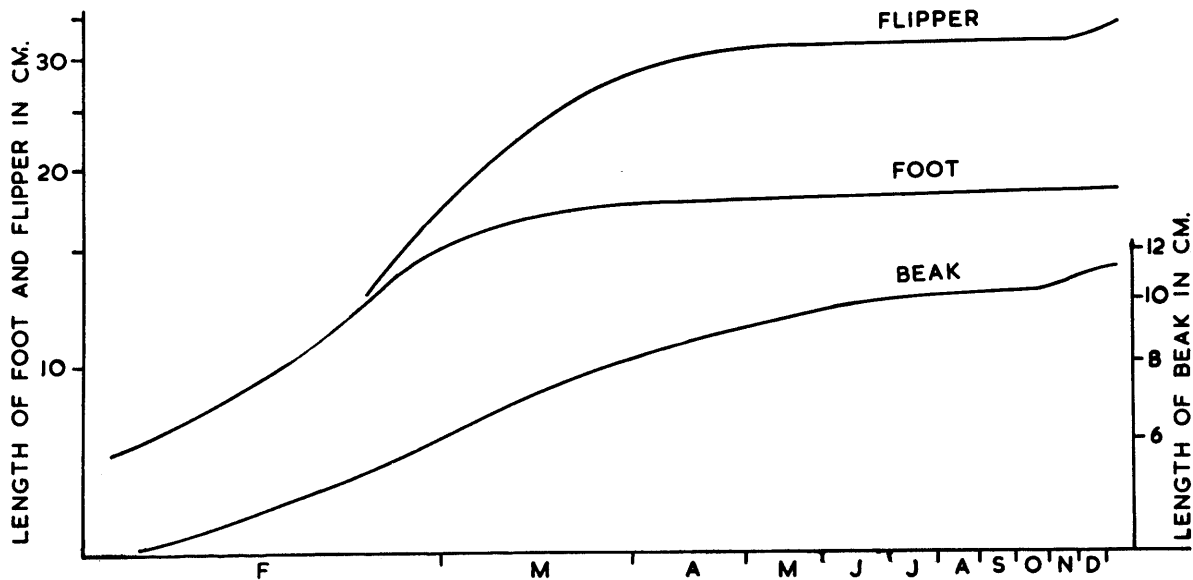


FIGURE 29. Beak, foot and flipper measurements (in cm.) of growing chicks. The curves represent mean lengths in twelve chicks all of which hatched between 20th-31st January. Scales are logarithmic.

maximum weight was achieved, and the weights at bi-monthly intervals were correspondingly higher at all stages during the first three months. Although No. 27 was a slightly larger and more sturdy chick than any other on the rookery, it may be noted that the differences indicated by curves A and B are probably excessive; No. 27 was fed more frequently than other chicks and was more likely to contain undigested food at each weighing.

Chicks hatching from mid-February onward did not generally manage to reach weights of 11–12 kg. They too achieved their maxima early in May, but usually at the level of 8–10 kg, or less, depending on the date of their hatching and upon the assiduity of their parents. Those hatching in April did not normally increase above 4–5 kg.

Table XXII and Figure 29 show rates of growth in a total of twelve healthy and well fed chicks, as indicated by measurements of beak, foot and flipper. The curves are made up of two sets of data. For the first forty days the mean measurements (taken at approximately three-day intervals) are recorded from ten chicks; for the rest of the period the mean monthly measurements of twelve are given. All the chicks concerned were hatched between January 20th and 31st, so that the weights at three-day intervals (which are grouped irrespective of date) continue until early March. The monthly weights are calculated for the end of each month, and the curves have been smoothed slightly.

In all three measurements growth is most rapid during February and March, the period in which weight also is increasing at the greatest rate. By April the foot has almost reached full size, but the beak and flipper continue to grow at reduced rates throughout May. After June only the beak shows slight growth. Growth ceases at the end of May, irrespective of the age or development of the chicks; thus, most of the chicks hatched by early breeders had by May reached the dimensions indicated; those from later matings tended to be smaller by the same date, more or less in proportion to their weights, and those which hatched in April reached little more than half size before their growth ceased.

ii. Winter Starvation. After early May, feeding was no longer maintained at the summer rate. Parents stayed for much longer periods about the rookery and also remained longer at sea than had been their habit during the summer. The weights of the chicks began to fall away, and fewer major feeds were detected by sudden increases in weight among those chicks which were weighed daily. Whether the decreased rate of feeding was due to a sudden shortage of food in the sea, to a decrease in the level of hormones responsible for feeding behaviour, or to a combination of these and other factors, is not known, but shortage of food was presumably the ultimate factor in any case. Courtship, incubation and brooding ceased at about the same time, and many of the smallest chicks died of neglect and starvation.

During the four months of June, July, August and September, the chicks were fed very infrequently and at irregular intervals. The parents worked independently of each other and met only by chance on the rookery; they remained ashore for periods of two or three weeks after delivering the bulk of their food, and some remained at sea for six or seven weeks at a time. Of thirty marked adults, twenty-seven made two or three visits each during the four winter months; the remaining three made one, four and five visits respectively in the same period. Chicks tended by both parents might have been visited by either of them approximately once every three weeks, each parent paying a mean of 2.6 visits in the four months. Although the visits were usually spread, there were times when the two parents arrived within two or three days of each other after both had been absent for five or six weeks. On these occasions the weight increase of the chick was less than might have been expected if the two parents had fed it at different times, suggesting that the chick was unable to make use of so much food in so short a period.

It is estimated that about 3 kg. of food were delivered during each visit. It was seldom found possible to weigh a marked bird both before and after it had fed its chick, and particular care was taken to avoid disturbing the birds while feeding was in progress. The most reliable records are of female 736; on October 9th this bird, probably fresh from the sea, weighed 17.8 kg. On the following day it weighed 15.0, and on the 11th the weight was down to 14.6 kg., a loss of 3.2 kg. in three days. Between October 8th and 10th the weight of the chick rose from 8.3 to 9.9 kg., and dropped back to 8.9 kg. by the 15th. Similar records exist for male 633, which lost 3.5 kg. in eight days, and female 726, which lost 3.5 kg. in 13 days. In none of these cases was it known for certain that the first weight recorded was the original weight of the bird as it came from the sea; it is possible, though unlikely, that some feeding may have taken place beforehand. It was usual for the weight of the chick to rise between one and two kilograms in the course of a visit, but to fall again to a point about 0.5 kg. above the original level after the bulk of the food had been delivered.

During the four winter months the chicks lost weight steadily. To investigate the basic daily loss, ten healthy chicks were labelled and confined in a shallow pit which was dug in the snow-drift below the rookery cliffs. The approaches to the pit were arranged so that a parent, returning from sea, would be able to find its chick without difficulty and enter the pit, but would then be unable to leave. In fact none of the parents returned during the twelve days for which the chicks were confined.

Although it was certain that none of the chicks were fed during their period in the pit, several gained weight from one day to the next; it was not unusual to record an increase of 100 g. (the limit of accuracy) overnight. Increases were mainly due to the habit of eating snow; the chicks nibbled at the walls of the pit throughout the experiment and removed several cubic feet of snow in the course of the twelve days. The amounts of snow and ice contained in the heavy down also affected the weighings; after snow-falls or strong winds many of the chicks showed an increase due entirely to ice in the matted down, and a corresponding decrease was shown when the ice melted or evaporated away. In addition to the expected losses in weight due to respiration and defaecation, an important source of loss was the habit of vomiting pebbles. All the chicks, including those which ranged freely on the rookery, from time to time vomited up small rounded pebbles which had been passed to them from their parents during feeding; by the end of the twelve days the floor of the pit was littered, and the loss in weight from the ten chicks probably totalled two or three hundred grams.

It was therefore not possible to establish an accurate figure for daily loss in weight of a starving chick. The weights of the ten chicks fell from 8.51 kg. to 7.69 kg. in ten days, providing a daily loss per chick of 0.06 kg. This figure compares reasonably with those quoted for weight losses in adults; inactive adults, weighing approximately twice as much as the chicks, lose approximately twice as much weight per day. A more significant finding was that the daily losses of chicks inside the pit (which were not fed or mock-fed) were very similar to those outside the pit where mock-feeding was possible. Thus No. 15, a free chick which was weighed daily throughout the period, lost 1.5 kg. between June 25th and July 25th (0.05 kg. per day), and No. 16, also weighed daily, lost 1.7 kg. between July 7th and August 6th (0.06 kg. per day). Both chicks were known to have been involved in mock-feeding with one of their parents for several days at the beginning of the selected period, and are likely to have "fed" from strangers later. Yet their mean daily losses were similar to those of the chicks in the pit, a fact which lends strength to the view that increases in weight from mock-feeding do not normally exceed those due to eating snow.

The effects of winter feeding appear in Figure 28. The chicks which were fed by both parents lost between three and four kilograms during the winter; those fed by only one parent lost slightly more but were not seriously underweight at any stage. No. 27, fed by three guardians, lost weight at approximately the same rate as the other two categories of chicks, and remained plump throughout. By the end of the winter nearly every chick on the rookery looked emaciated, in spite of the thick covering of woolly down.

Mortality among the chicks was high during the winter. Death was usually due to the ravages of Giant Petrels (*Macronectes giganteus*), several of which visited the rookery almost every morning from the third week in May to late August. However, early morning observations showed that the petrels were unable to catch healthy chicks; only the starved chicks which were too weak to run from them were in any danger (see later note on predators and parasites). As the corpses were usually skinned and eviscerated by the petrels it was not profitable to weigh them, but the lengths of beak, foot and flipper were recorded wherever possible. Chicks which were obviously on the point of dying from starvation were killed by a blow on the head, and could be weighed and measured accurately.

Table XXIII shows the numbers of chicks which died each month during the winter of 1954. The figures include only those which died as a result of weakness due to starvation, having been killed by petrels, by the observer, or by being crushed and trampled underfoot in the crèche. During this period only two others died from causes which were not connected with starvation: one choked to death during feeding and another, seemingly fat and prosperous, died after a fit of violent paroxysms to which no known cause could be ascribed. The mean flipper length of dead chicks is also recorded for each month, and for August, September and October the mean weights of undamaged corpses are given.

The smallest chicks died during April and early May, shortly after being abandoned prematurely by their parents. The very small ones which died in May were torn to pieces or squashed before they could be weighed or measured. A few aged three to four weeks survived for a few days but were the first of the larger chicks to fall to the Giant Petrels; these formed the bulk of the deaths recorded in May. In June and July deaths occurred mainly among a group of chicks which, having reached the age of six or seven weeks

(with corresponding weights of 3–4 kg.) by early May, remained at the same stage of growth but began to lose weight at approximately the same rates as the larger chicks. Eight of these chicks were weighed periodically before their deaths; in every case death occurred when the weight of the chick had reached between 2 and 2.5 kg. Some received at least one feed from a returned parent, but weighings showed that the food taken in was about half the amount normally received by a larger chick. Presumably the small chicks could not absorb a feed of 2–3 kg. in two or three days, and part of the parent's crop content would be absorbed or discarded. Although most of them died in June and July, a few survived until August. By the beginning of August several of the larger chicks were collapsing; these had reached weights of 6–8 kg. in May and had lost three or more kilograms in the course of the winter. Deaths of chicks in this group continued through September and reached a maximum in October. As is shown by the weights and measurements, these chicks were three-quarters grown but weighed, at death, little more than month-old birds.

iii. Subsequent growth and moult. Toward the end of September some of the chicks began to fatten slightly. During October an increase was seen in the mean weights of those which were fed by both parents, and the weight of No. 27, fed by three, soared rapidly. Adults were seen more frequently about the rookery, marked birds returned at intervals of two weeks or less, and the whole tempo of life on the rookery began to accelerate. The chicks which had lost one parent continued to lose weight for a further month, but began to increase once again in November.

The first signs of moulting appeared among the chicks during the second week in November. Tail rectrices loosened, and at the same time feathers began to appear on legs, flippers, chest and back. Generally, the largest and best fed chicks were the first to moult; the oldest chick on the rookery, No. 1, remained below average weight after the winter and did not begin moulting until early December, two or three weeks after the first chicks had left the rookery. All the marked chicks from early breeders, which had been fed by both parents through the winter, had begun moulting by mid-December when observations ceased. Marked chicks which had lost a parent tended to lag behind, but even those had developed loose tail feathers by mid-December and were expected to survive. No. 27, in spite of the constant attentions of three guardians during the final stages, was not among the first of the chicks to leave the rookery.

The moult was completed in three to four weeks, and the chicks made their way to the beach with the remains of down still clinging to the feathers of their head and neck. They seldom remained on the beach for more than two or three days. Newly fledged juveniles could easily be distinguished from those at the end of their second year, by the newness of their plumage and, usually, by their size and weight.

Chicks reared in captivity and fed directly, seem to mature only slightly more rapidly than those reared on a rookery. Gillespie (op. cit., pp. 132–148) provides records of a chick which completed its moult and was ready for swimming about seven months after hatching. This bird reached full adult weight (and approximately full size) after about eighteen weeks (i.e., six weeks later than in the wild), and was presumably maintained at full weight thereafter.

More deaths from starvation were recorded in November, mainly of chicks which had presumably lost both parents; others died during December and, by comparison with the previous year, the last would live on until the end of January or early February. A few of the well fed chicks died from other causes; six more developed the muscular spasms previously described and died in paroxysms reminiscent of epilepsy, and several suffered from an infection of throat, lungs and air-sacs which appeared eventually to suffocate them. Two died as a result of deformity; in both a ramus of the lower mandible failed to grow (possibly as a result of injury) and neither was able to close its beak properly. They fed well but could not preen and were eventually found in dying condition. About 2,100 chicks survived to mid-December, from an estimated total of slightly more than 2,500 eggs laid.

4. MISCELLANEOUS OBSERVATIONS

a. Mortality in Birds of Breeding Age

129 breeding birds (i.e., birds known either to have bred in the previous year or to have mated and begun incubating in the current season) were marked with permanent bands between November 1953

and March 1954. Sixty-eight were males, sixty were females (both figures include those marked as "doubtful" in the tables) and one was of unknown sex. Of these birds, fourteen males and eleven females and the bird of unknown sex disappeared between March 1st and October 31st, presumably being lost at sea. The dates on which the missing birds were last recorded appear in Table XXIV, grouped by months. It will be seen that twenty-one of the twenty-six disappeared during the three months of May, June and July, and that successful breeders tended to disappear during May and June.

Table XXV shows an analysis of the mortality figures. Among the successful breeders (i.e., those which were raising a chick when lost) 23.8% disappeared, including more males than females. Of the unsuccessful breeders, and of those which did not breed during the current season, only 16.7 were lost, including rather more females than males. The figures suggest that migration is a safer activity than breeding; it is likely that the high mortality among breeding birds in winter may be due to the constant presence of Leopard Seals (see below) immediately off shore, although nothing is known of the corresponding hazards encountered by migrant birds.

b. Predators and Parasites

Leopard Seals (*Hydrurga leptonyx*) are apparently the major predators of King Penguins at sea. From May to early November one or two seals were seen nearly every day, swimming back and forth along Paul Beach from fifty to a hundred metres beyond the surf. They chased both King and Gentoo Penguins and seemed able to take as many as they wanted from the constant streams of returning birds. Once caught, the penguins seldom managed to escape. They were apparently held under the water and crushed by the seals' jaws; if released momentarily they seemed unable to breathe or swim. The bodies were skinned by being thrown hard against the surface of the water; completely invaginated skins containing head and flippers, were occasionally washed ashore. However, the seals also ate quantities of feathers, which appeared in faeces when they rested ashore. During November the resident populations of Leopard Seals moved away from the rookeries, presumably to breed (Hamilton, 1939), and the species was seen only occasionally during the summer.

Ashore, King Penguins are comparatively free of predators, although several species of birds scavenge on the rookery during fixed seasons of the year. From the end of September to early May, the Paul Beach rookery was divided between two pairs of Brown Skuas (*Catharacta skua lönnbergi*) which removed abandoned eggs, cleared chick carcasses and occasionally attacked small, abandoned chicks. The Skuas did little damage among the King Penguins, and were beneficial in keeping all other scavengers away from the rookery (Stonehouse, 1956 b, p. 10). They were attacked, when patrolling on the ground, by groups of large King Penguin chicks which chased them slowly about the rookery and no doubt held their attention from predation. Adults lunged at any Skuas which came within their range, but otherwise tended to ignore them. As the territory-owning Skuas moved out in March, groups of young Skuas settled from time to time in the rookery, feeding on fallen chicks and abandoned eggs. The last disappeared in May.

Two other scavenging species began to occupy the rookery in March. Dominican Gulls (*Larus dominicanus*) fed throughout the winter on chick carcasses, but were never seen to attack living birds. A group of between twenty and forty Sheathbills (*Chionis alba*) also lived in the area from late March to September; the Sheathbills were ringed, and were found to divide their time between the rookery and the rocks at Markham Point, where they pecked over the marine algae at low tide. Their agility enabled them to move among the penguins without danger, although both chicks and adults lunged at them. They investigated any marks on the rookery floor (which for most of the period was snow-covered), pecked over skins, bones, faeces, opened eggs by hammering them with their beaks, and generally made a living from the most unpromising materials. Sheathbills recognised the possibility of obtaining food when chicks were being fed, and moved over to join parents and chicks engaged in feeding. They picked up any fragments of food which fell normally, and many possessed the interesting habit of flying up at the heads of chick and parent just as food was passing. The result was invariable: both feeding birds withdrew their heads and lunged violently, spilling food onto the ground. This the Sheathbill removed almost before the last had fallen, dodging out from behind one of the birds and scuttling away before they had time to redirect their attacks. The Sheathbills disappeared in September when the Skuas returned; none were known to breed at Paul Beach and it is likely that they moved elsewhere to take up their breeding territories.

The most serious land predator was the Giant Petrel which, as described earlier, made early morning attacks on the rookery throughout the winter. Although Giant Petrels were seen in the area throughout

the year, they seldom landed on the Beach except to pick at seal carcasses or other carrion, and did not visit the rookery at all during the summer. Towards the end of April the first birds were seen between the tussock grass and the cliffs, feeding on the remains of penguin chicks which I had left there. Later, in May, two or three were found on the rookery every morning at first light. They were unable to run more than a few metres at a time, but would make short rushes at the chicks which were herded tightly together in the crèche. The active and healthy chicks could move aside without difficulty, but occasionally the crèche would part to disclose a weakling or a fallen chick, which was immediately snapped up. The petrels combined to tear the carcasses to pieces. If left undisturbed they would probably have spent days together on the rookery, but my arrival every morning sent them flapping off over the snow-covered tussock grass and into the sea. In June and July it was not unusual for ten or more to gather; their attacks were unconcerted and, in spite of the numbers, seldom resulted in the deaths of more than two or three chicks. Very occasionally one of the healthy chicks received a wound on neck or flipper, but, as the measurements in Table XXIV indicate, few of the larger chicks were killed. It is probable that only those weakened by starvation would fall, and it was usually possible to predict which of the chicks would be taken during the following two or three days.

Two parasites, one internal and the other external, were noted. The internal parasite was a tape-worm, proglottides of which appeared in the faeces of most adults during the summer. They were not seen during the winter, and two adults killed in winter were apparently free from active tape-worms in the intestine. Sections of hind-gut and specimens taken during the summer have been preserved for examination. The external parasite was a small Mallophagan, *Nesiotinus demersus* (Kellogg, 1903), (largest specimens 0.5 cm. long), conspicuous from its prominent black and yellow abdominal bands. Specimens *in copulo* have been sent to the British Museum (Natural History). Lice were seen on most adults and chicks from November to May, but apparently were absent during the winter months. The two chicks with deformed beaks, mentioned earlier, were unable to preen properly and became very heavily infested; normal chicks and adults were only slightly infested.

Rats (*Rattus norvegicus*, according to Lönnberg, 1906, p. 21), are plentiful on South Georgia, but there was no evidence to suggest that they interfered in any way with the King Penguins. Carcasses of dead chicks were gnawed if left on the rookery floor in winter, but investigations of stomach contents suggested that the rats were mainly subsisting on tussock grass.

c. Feeding and Food Supplies

Although it is clear that cephalopods form the bulk of the King Penguins' food throughout the year, it has not been possible to ascribe species or genus to any of the cephalopod remains found in the crops of dead birds or on the floor of the rookery. Several species of squids are known to abound in sub-Antarctic waters; all are notoriously difficult to catch in nets but squid-beaks are found in the stomachs of Giant Petrels, King and Emperor Penguins and most species of Antarctic seals (personal observations). Laws (1956, p. 15) suggests that more than one species may form the diet of Elephant Seals (*Mirounga leonina*); a squid which he caught by hand off the South Orkney Islands is referred with some doubt to the genus *Onychoteuthis*, and it is probable that representatives of this genus are caught both by Elephant Seals and by King Penguins. Clark (1956, p. 256) records remains of *Moroteuthis ingens* in the stomachs of Sperm Whales (*Physeter catodon*) caught in Antarctic waters; some of the specimens were no larger than the *Onychoteuthis* caught by Laws, and again may be caught by King Penguins. I can find no information on the feeding habits of either species of squids, but it seems likely that they feed among the plankton and follow its migrations from season to season.

Fish remains were also recovered from the rookery floor at Paul Beach; they have been identified as vertebrae, fin rays and jaws, probably of adult specimens of *Notothenia rossi marmorata*. Adults of this species feed in the plankton during daylight, and are found in a belt from fifteen to thirty miles off the north-eastern side of the island (Olsen, 1954, p. 7).

Little is known of the feeding grounds of King Penguins. No feeding parties were seen among the kelp or elsewhere in inshore waters. It may be assumed that their prey congregates in areas where the zooplankton is richest, for example in the region of mixed water about thirty to sixty miles off shore from the Bay of Isles (Hardy and Gunther, 1936, p. 85-6), and that the birds feed in the surface waters at these distances from their breeding grounds.

The relative abundance of squids at different times of the year is not known. Foxton (1956, p. 210)

points out that in July, August and September the bulk of the plankton is concentrated below 250 metres, although the total standing crop of the plankton, measured over the whole water-column from 0–1,000 metres, is approximately constant throughout the year. Squids may be equally abundant during winter and summer, but may be more difficult to catch if they follow the plankton into deeper water during the winter. The relative abundance of plankton in the surface waters throughout the year may be judged from Table XXVI and Figure 30, which are based on Table 3 of Foxton's report. The figures show the volumes (in c.c.) of plankton taken in 50-metre hauls at depths of 0–50 metres and 50–100 metres, during each month of the year in Antarctic and sub-Antarctic waters. It will be seen that peaks are reached in December and March, with a marked decline in January. If the squids are more plentiful and easier to catch when plankton is richest in the surface waters, it is clear that the food of King Penguins will be most abundant in December and March, and almost as scarce in January as during the winter months. It is interesting to note that the demands of the chicks are probably greatest during the two periods when food is most abundant, and that the decrease in food supplies in January coincides with the time when most of the successful chicks of the previous season have completed their moults, while the newly hatched young are as yet too small to require large feeds. The importance of plankton abundance in relation to the needs of King and Emperor Penguins is discussed later.

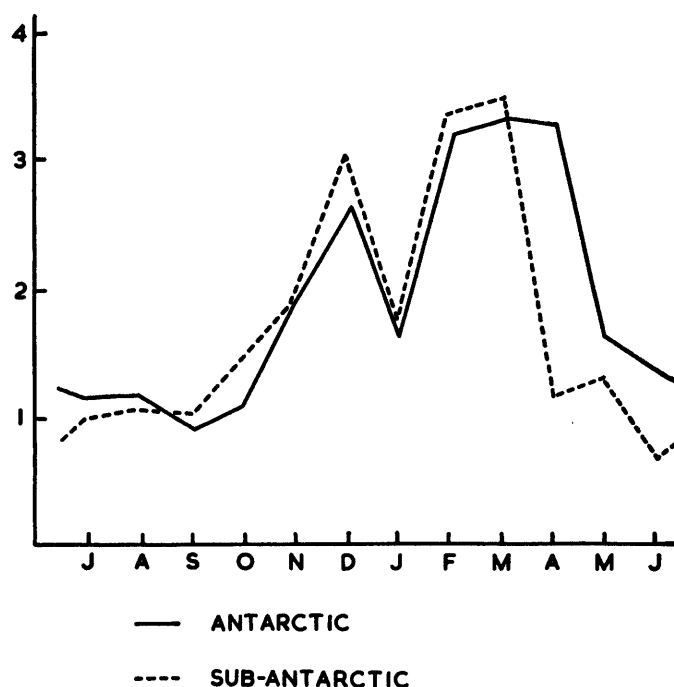


FIGURE 30. Abundance of plankton (in c.c.) in surface 100-metres of Antarctic and sub-Antarctic waters. The monthly totals plotted are taken from Table XXVI.

d. Social Behaviour and Swimming

Although all Antarctic species of penguins are sociable, the King Penguin supplies perhaps the most striking examples of social dependence. With the exception that the birds normally return singly from the feeding grounds, it is most unusual for a King Penguin to be seen on its own. One which has just arrived at the beach will call with a distinctive monosyllabic note to which other King Penguins within earshot reply immediately. The new arrival then joins the nearest group, guided in the direction from which the replies come. The call is also used frequently by birds which wander in the tussock grass; small parties, on hearing the movements of other parties which they cannot see, may call and eventually link up with the strangers.

Away from the rookery, any bird which walks with determination will almost certainly be followed by

others. A small party proceeding along the beach will attract other parties which, until its passing, were content to stand preening or sleeping. The most remarkable example of this concerted behaviour is seen in the early morning, when all birds which are otherwise unoccupied make their way in a procession down to the sea. The behaviour was first noticed during early morning watches in winter, and a typical example is quoted. During the night about 500 adults slept in groups at the western end of the rookery; the groups extended up the hillside to about 100 feet above sea level, and were limited seaward by the inner edge of the tussock belt (Plate VIIb). At first light several of the sleeping birds stirred and, from different points in the line, began moving slowly downhill toward the rookery. Within five minutes the whole column was awake and on the move (Plate VIIc). The leading birds pushed their way through the last of the sleepers onto the rookery floor, crossed over to the site of the frozen pond, then turned and headed toward the sea. As the following birds entered the rookery they stopped, gave long calls, and moved on; those which were joined by chicks left the column, while others passed onward across the belt of snow-covered tussock grass to the beach. The parents began feeding or mock-feeding, calling repeatedly and being answered by their chicks. Most fed for between fifteen minutes and half an hour; some left their chicks after about five minutes and rejoined the column. By the end of an hour about four-fifths of the adults had streamed across to the edge of the sea, and were heading westward in a long column stretching half the length of the beach. The remainder were standing in groups on the rookery, or had straggled out in small parties across the tussock belt; these birds seemed to have lost the initiative of the column, and were wandering slowly back and forth under the leadership of several individuals in succession.

The main column broke up into groups, each of about fifty birds, which followed the same pattern of behaviour but acted independently. Each group moved slowly along the shore, with all the birds packed closely together (much more closely than they normally allowed themselves to approach without fighting) and all peering out to sea. Those nearest the surf stepped seaward, until the low waves lapped about them, the remaining birds packed closely behind. The leaders then fell forward into the surf and began swimming, completely submerged. More entered the water behind them until most of the group was swimming. Then a sudden panic overtook the group, and with a tremendous clattering of flippers the whole party rushed out of the water and up the beach. Half a minute later the birds had composed themselves and were walking slowly seaward again, to repeat the performance several times.

After the swimming parties had been observed at different times during the winter, it became apparent that this recurring panic was induced by the sound of flippers hitting water; the sound could be simulated by striking the surface with a paddle or shingle of wood, and invariably caused the birds to rush from the sea after the first strokes. They were particularly alert on entering the water, and it seems likely that the "alarm" inducing this behaviour would nearly always be given accidentally by one of the birds in breaking the surface. The result was that, throughout the winter, all the birds remained on the verge of panic while swimming, and a group could be clear of the sea at a moment's notice. This was of particular importance in view of the presence of Leopard Seals; the birds would not enter the water if a seal (or a lump of dark, gritty ice resembling a seal) could be seen nearby, but they were also protected by a very efficient alarm system which called them out whether or not a seal was seen. On the few occasions when the resident Leopard Seal managed to approach a group without being detected, it was invariably defeated by an alarm which sounded equally effectively when the seal was basking in the surf half a mile away.

A marked contrast was later seen during the summer months, when the seals were no longer in residence. For the penguins, swimming remained a social activity and, as always, they entered the sea only in groups; but they swam with heads erect, washed and rubbed their feathers in the surf, spent four or five minutes in the water at a time, and showed none of the nervousness associated with winter bathing.

In winter, the swimming parties usually persisted throughout the morning. Sometimes the separate groups moved along the beach to amalgamate eventually near Markham Point, at other times most of the birds accumulated at the opposite end, near the edge of Grace Glacier. Small parties detached themselves from time to time and returned to the rookery; others would wander half way back to the rookery, meet a party heading in the opposite direction and follow it back to the beach. These small groups of aimlessly wandering birds were typical of the beach in winter. On one occasion, I was able to entice a group of twelve birds into the wind-scoop formed between a large erratic boulder and a snow drift on the hillside; the scoop was almost annular, with a diameter of about five metres (the radius of the boulder), and the little procession of birds followed its tail completely round the boulder two and a half times, in the manner of Fabre's caterpillars, before eventually breaking out.

The swimming parties were a daily event in the lives of most birds. Marked birds which had delivered a large feed to their chicks on several successive mornings were, on subsequent mornings, more likely to be found among the swimmers. The parties also formed nuclei from which groups left for the feeding grounds, and the behaviour leading to the departure of feeding groups was seen on several occasions. At first the party would proceed as described, then several birds would break off and begin circling in the water, swimming in close formation and remaining in the water after others had flapped out in alarm. The circles would widen, and eventually the group, of perhaps twenty birds, would head out to sea and disappear between Cape Buller and Albatross Islet. It was sometimes possible to predict when marked birds would leave, knowing how long they had spent on the rookery since delivering their last feed. However, some remained several days longer than expected, possibly because the swimming parties which they joined on successive mornings happened not to contain a nucleus of other birds which were ready to leave.

Three methods of swimming were distinguished:

i. While bathing in fresh-water pools or (in summer) among the surf, the birds swim with heads erect, propelling themselves along by small flipper movements. The body floats low in the water, but the tail and most of the back are visible.

ii. While bathing in the surf during winter, and while swimming rapidly to escape from a predator or from the path of a ship, the birds swim completely submerged, with flippers moving rapidly and neck fully extended forward.

iii. When swimming out to the fishing grounds or when seen far out at sea, the birds porpoise in and out of the water, usually in groups with co-ordinated movements. The groups leap out of the water at a shallow angle, traverse three or four metres while rising to a little over half a metre, and plunge again at a shallow angle; their path appears sinusoidal in a vertical plane, although the birds remain below water for two or three times the distance travelled in air.

The second method was most often seen in circumstances in which high speed was required, while the third method was used in long-distance travelling at lower speeds. From the cliffs at Paul Beach it was possible to pick out groups of penguins as they approached the rookery across the Bay. From their first appearance about 2 km. out, to within a hundred metres of the shore, they porpoised steadily and without halting. At about one hundred metres distance they usually halted, swimming back and forth in the water with heads erect, calling and responding to each other. Then all would disappear, and the final dash to the beach would be made with the whole body submerged, several birds emerging breathlessly from the water at different points along the beach. Those which came across the bay on their own usually porpoised all the way to the beach, diving only for the last twenty or thirty metres.

Bathing was inhibited only by heavy seas or by inshore ice. From time to time northerly winds brought a very heavy swell into the bay, producing enormous rollers which washed up the beach into the fringes of the tussock grass. On these occasions the swimming parties usually wandered beyond Markham Point before entering the water, and incoming birds swam outside the breakers to land through the calmer waters west of the point. A fall of ice from any of the nearby glaciers together with an onshore wind, frequently brought tightly-packed fields of brash ice along the beach, and these presented a more serious obstacle than breakers. However, the shelving bay west of Ample Bay, with its rocks and shallow water, usually kept the heavier ice away from the shore and provided a possible, if difficult, passage from sea to beach.

II. COMPARISONS, DISCUSSION AND CONCLUSIONS

1. THE EMPEROR PENGUIN

a. History of Research

A full account of early references to Emperor Penguins appears in Sapin-Jaloustre's paper of 1952 (pp. 144-166). Although the species was probably seen by earlier voyagers, the first specimens to be identified positively were collected in the course of the Ross expedition to the southern oceans, between 1839 and 1843. At about the same time a member of a French expedition, under the command of Dumont

d'Urville, picked up the first known Emperor Penguin egg from the broken sea ice near Terre Adélie. After an eventful history (Walter, 1920), this egg is now deposited in the Norwich Castle museum.

The first rookery was discovered during Scott's expedition of 1901-04 (Wilson, 1907, pp. 3-31). As *Discovery* entered the Ross Sea in January, 1902, many juvenile Emperor Penguins were encountered among the pack ice, and off King Edward VII Land, at the eastern end of the Ross Ice Front, a large group of moulting birds was seen on an extensive floe. In October of the same year, a party sledged eastward along the shore of Ross Island to Cape Crozier where they discovered a rookery of about four hundred adults with only thirty chicks. The rookery was revisited on November 8th when it was found that all the chicks had disappeared and most of the adults were leaving in the direction of the open water. From specimens brought back, Wilson, the junior medical officer, estimated that the chicks had hatched at the beginning of October. In the following year he took a third party to the rookery early in September, in the hope of finding eggs; to his disappointment all the birds were brooding young, which were only slightly smaller than the specimens brought back in the previous year. About one thousand adults were present, of which less than one hundred and fifty held young.

On October 12th Wilson returned to the rookery, and during a week of blizzards he watched a remarkable migration of unemployed adults, which filed out to the edge of the fast ice and were carried northward as the ice dispersed. The chicks, with a few guardians, remained under the cliffs of Cape Crozier, but only thirty survived the storm. It seemed probable that these would drift away shortly, and so account for the sudden disappearance of the same number of chicks early in November of the previous year. The chicks would therefore migrate with the ice before moulting into their juvenile plumage.

During Scott's second expedition (1910-13), a sledging party under Wilson visited the rookery in July and secured three eggs; the embryos were subsequently described by Parsons (1934). The party remained near Cape Crozier for three days, but bad weather prevented further observations.

The existence of a second rookery was deduced by the biologists of the German South Polar Expedition (1901-03), who reported the presence of many juvenile birds in the pack ice off Kaiser Wilhelm II Land. In the same region a rookery was actually discovered by members of the Eastern Party of Mawson's Australasian Antarctic expedition (1911-14) at Haswell Island, and a third was discovered by the present author in 1948, on the Dion Islets, Graham Land. During the winter of 1949, studies were made of the incubation and other breeding behaviour on the Dion Islets; it was found that the males were entirely responsible for incubation which lasted about two months, that they huddled tightly together during spells of bad weather to reduce heat losses, and that they were capable of feeding, from a crop secretion, chicks which hatched out before the return of the females (Stonehouse, 1952, 1953). Embryos collected during these observations were described by Glenister (1954).

In 1950, a fourth rookery was discovered at Pointe Géologie, Terre Adélie, and from 1952 to 1953 the French observer J. Prévost made daily observations on the rookery throughout a complete breeding cycle. Prévost's observations have not yet been published in full; a popular account by Rivolier (1956) supplies facts which are obviously based on Prévost's work but have not yet appeared in scientific journals.

The fifth known rookery was recently reported from Halley Bay, on the eastern shore of the Weddell Sea, and was visited from the British International Geophysical Year Base during the winter of 1956.*

b. The Breeding Cycle at Pointe Géologie

The rookery at Pointe Géologie has so far provided the fullest information on the breeding cycle of Emperor Penguins. Its position slightly north of the Antarctic Circle is at the northern extremity of the breeding range for this species, and its possible limitations as a "typical" colony must be borne in mind. Tentative comparisons with data from other colonies are made in the next section.

In 1952, the sea ice at Pointe Géologie began to form in March. On March 4th two adults were seen, apparently completing their moult; six days later the first of the new season's breeding birds began to arrive (Prévost, 1953, p. 142). By the end of the month five thousand birds (Rivolier, 1956, p. 103) had assembled, and the remaining seven to eight thousand took up their stations early in April (Prévost, 1954, p. 251). Courtship began at about the same time. Males at this stage were distinguishable by their voices, and also by their greater weight; Prévost (1954, Fig. 1) records mean weights of thirty-four and twenty-six

*See first footnote on p. 4.

kilograms respectively for males and females. During courtship the calls were made with the head pointing downward, in contrast to King Penguins which point their beaks upward and raise their heads as high as possible when calling.

The first copulation was seen on April 10th, and the first eggs were laid on May 5th. The males took control of the eggs and incubated for the full period of 62–64 days, while the females disappeared in the direction of the open sea and remained absent throughout.

The first of the returning females arrived at Pointe Géologie on June 30th, but most appeared between July 15th and 30th. They discovered their partners by calling, and took over the care of the eggs or chicks within a few hours of arrival. Chicks which hatched before the return of the females were fed from a crop-secretion by the males. The females fed the chicks for the first twenty to twenty-five days; the males left the rookery and presumably spent the intervening time at sea, returning eventually with more food for the young. At the age of about forty days, the chicks were left by both parents which returned independently to feed them through October, November and early December. By mid-December the chicks weighed about 15 kg. and were beginning to shed their down; at the end of the month the sea ice began to move out, taking the remains of the rookery with it.

The adults were assumed to complete their moults during January and February.

c. Comparisons with other Colonies

A summary of information from earlier sources is given in Stonehouse, 1953 (pp. 24–27), and forms the basis of the following comparisons:

i. Breeding site. Of the original five colonies described, four assemble on sea ice; only the Dion Islets rookery is based on a small island.* All occur at points where the sea ice is likely to disperse early in the spring or summer. At the Dion Islets, Haswell Island and Pointe Géologie the ice is weakened locally by contact with islets, by currents, reefs, etc.; at Cape Crozier an active glacier face breaks up the ice even during the winter. Reports from Halley Bay are as yet incomplete, but it is known that the rookery drifted out to sea early in the spring, which suggests the action of a similar force. As vast areas of sea ice remain *in situ* throughout the summer, it may be supposed that the birds gain an advantage in forming their colonies on unstable tracts. Most sea-birds which breed on the Antarctic mainland tend to congregate at rocky points or capes where the sea ice melts comparatively early in the season. They are thus provided early in the summer with several square kilometres of open water for local fishing, while elsewhere the sea ice remains unbroken. Emperor Penguins, by contrast, congregate at points where the ice may be expected to drift out in large floes early in the season.

ii. Date of breeding. At Pointe Géologie in 1952, the Emperor Penguins began to assemble before the sea ice was completely safe, and were present in large numbers by early April when courtship began. It was not possible to begin observations at the Dion Islets before early June because the sea ice was unsafe for sledging, but it was estimated that the birds assembled there during May. No information about assembly dates is available for other colonies. It is believed that laying began early in June at the Dion Islets in 1948 and 1949, and late in June at Cape Crozier during 1902 and 1903 (Stonehouse, 1953, p. 26). Thus, breeding may begin six weeks later at Cape Crozier than at Pointe Géologie, the two extremes of the range. It would appear that, although breeding cannot begin until the sea ice has formed, courtship is not actually initiated immediately after the formation of the ice; fast ice may be expected to form at Cape Crozier several weeks before Pointe Géologie is frozen up. Observations at the Dion Islets suggested that laying was completed in about three weeks, and a similar span is likely for other colonies.

iii. Incubation. I have suggested that the prolonged incubation by the males may be an adaptation made necessary by the great distance, during early winter, between the rookery and the open sea. The birds must breed on ice which will not break up before October or November, and must therefore assemble near the coast rather than near the open water. At mid-winter the edge of the ice may be from eighty to a hundred kilometres from the colony, and this long journey would have to be made periodically, through the worst weather of the year, if the parents relieved each other during incubation. Instead, the males

*Of the six colonies described by Willing (1958) five form on sea ice.

conserve their heat and energy by abandoning territorial behaviour and huddling tightly together (as seen in King Penguin chicks but not in the adults), while the females feed in more favourable climatic conditions far from the land.

iv. Hatching. The return of the females, after their complete absence of two months, coincides closely with the period of hatching. It is difficult to visualise any external factor capable of causing the females to return at the right moment; presumably the control is physiological. The males' ability to feed their young is a necessary safeguard, of use when the females are delayed; both King and Gentoo Penguins, from my own observations, feed their chicks in the same way if they remain unrelieved after their egg has hatched.

v. Growth of the chicks. Prévost's discovery that the females normally feed the chicks for the first twenty to twenty-five days after hatching (1954, p. 251), suggests that growth might be slower during this period than is the case in the King Penguin. A King Penguin chick fed by one parent for only twelve days was retarded in growth. It is possible that the males would have returned sooner if the edge of the sea ice had been nearer when the chicks hatched; at the Dion Islets open water was already in sight by this time, but, as a consequence, the observers had to leave the rookery before the return of the marked males could be checked. When returning to take control of the newly hatched chicks, the females were fat and their crops were filled to capacity. It is probable that the males fattened satisfactorily (as shown in Prévost's Figure 1), although food is unlikely to have been plentiful in the sea at this time.

At Pointe Géologie the chicks were left in the crèches at ages of thirty-five to forty-five days; King Penguin chicks enter the crèches at about the same ages, but are probably by that time heavier and more advanced in their development. Prévost also reported that Emperor chicks reached weights of about fifteen kilograms by mid-December, when their moulting began. They therefore moulted at less than three-quarters of the weight of a normal adult. Judging by Prévost's photograph (1954, Plate 6), they are also much smaller than the adults at this stage. My own measurements of a single captive Emperor Penguin chick may be compared (1953, Figs. 4 and 5, Tables on pp. 32 and 33); Prévost's figure suggests that this bird was under normal weight on moulting, although it had probably reached the normal size and was moulting at about the same time (late December) as its contemporaries in the rookery.

It is therefore apparently normal for Emperor Penguin chicks to moult when about three-quarters grown, and they achieve moulting weight and size about five months after hatching. By contrast, King Penguins reach full adult weight and approximate to full size within three months of hatching, and they do not begin to moult for a further seven or eight months. At full size and weight they are only slightly smaller and lighter than a moulting Emperor Penguin chick.

D. G. Dalgliesh, in an unpublished report from Halley Bay, makes the interesting point that an Emperor chick in full down is able to swim short distances. The chick would therefore not be at a disadvantage if the ice broke under it.

vi. Chick mortality. Both Prévost and Rivolier agree that mortality among the chicks was high at Pointe Géologie, although neither gives details of the causes of death other than in references to cold and starvation. It is unfortunate that Rivolier's statement (p. 125) that "... only a quarter of the number [of chicks] born will live to see the spring..." is not better substantiated. Later, he refers to the depredations of Giant Petrels which, if comparable with those at Paul Beach, would affect only the chicks whose death was already imminent. Mortality at Cape Crozier has already been mentioned; it is likely that conditions at the southern end of the breeding range would be very much more severe than elsewhere. On the Dion Islets in 1948 there was no indication that the chicks (which numbered about seventy in an estimated population of two hundred adults) were starving or suffering unduly from cold; no corpses were seen and none of the chicks were apparently diseased. Although a rookery of Giant Petrels was found nearby, the birds were not at that time (October) molesting the colony.* Mortality was also light during incubation and the early post-hatching stages in the following winter.

vii. Moulting. At Pointe Géologie adults were seen in moult from November 28th to January 30th (Richdale, 1957, p. 177, quoting Prévost *in litt.*). It is possible that the earliest moulters included juveniles and unsuccessful breeders. Wilson (1907, p. 19) records moulting birds in February. Richdale (*op. cit.*, p. 176) quotes lengths of moult from two sources, which range from thirty-two to forty days.

*A more recent visitor to the rookery has suggested that predation from this source might be more serious than my own observations implied; in October 1957 Proctor (unpublished F.I.D.S. base report, 1958) found three chicks killed and others wounded by Giant Petrels.

2. CONCLUSIONS

The genus *Aptenodytes* is distinguished from all other genera of penguins by several easily recognisable qualities. Emperor and King Penguins are considerably larger than all other species; their vivid orange or yellow auricular patches, conspicuously grey-tipped dorsal feathers, pink or purple mandibular plates and slender beaks, identify them on sight. Their prolonged trumpeting calls are unlike the calls of any other species. All other penguins prepare a nest and lay two or more eggs, while Kings and Emperors have no nesting behaviour and lay a single egg. All other species incubate in a prone position, with eggs held between feet and body. Kings and Emperors incubate with the the body upright and the single egg cradled on the tarso-metatarsi. Incubation is longer (Richdale, 1957, p. 35) in Kings and Emperors; the chicks take longer to reach juvenile or sub-adult size, and remain longer in the care of their parents (Richdale, 1957, p. 73).

Both species of *Aptenodytes* inhabit cold Antarctic water, probably spending their lives at sea south of the Antarctic Convergence. Their breeding ranges are different, however: King Penguins breed on the islands and shores of the sub-Antarctic region, while Emperors occupy the Antarctic coastline as far south as the sea extends. Both species are numerous and evidently successful in their respective breeding environments. Each has evolved a distinctive way of life, to overcome the difficulties presented by its environment. Presumably as a result of unusually strong and divergent evolutionary pressures, the two differ more in their breeding behaviour than any other congeneric species of penguins, or indeed than of any other two closely related species of birds.

The basic problems shared by King and Emperor Penguins may be summarised in the following terms:

i. Their chicks, like those of other penguins, cannot properly fend for themselves until their bones are fully ossified, and cannot complete ossification until they approximate to adult size. The chicks grow slowly, certainly no more rapidly than those of other penguin species, both before and after hatching, and must therefore be tended by the parents for at least two or three months longer than the chicks of any other penguin species. The slow growth rate is probably an adaptational response to uncertain and erratic food supplies in both species.

ii. Because of the long period of development, Kings and Emperors cannot fulfil a complete breeding routine in the time taken by Pygoscelid Penguins, which share their environments but complete their breeding cycles during the three or four months of summer.

iii. King and Emperor Penguins live in cold climates and feed in waters the wealth of which varies considerably from month to month (Fig. 30). Food is probably extremely abundant in December and again in March and April, but may be short or difficult to catch during the winter. Their chicks must be reared at the times when food is plentiful, and will probably benefit if their independence is achieved while food is still comparatively easy to catch.

Leopard Seals are known to haunt sub-Antarctic coastal waters throughout the winter and may provide a further reason why the chicks of King Penguins should not be released in May and June.

Emperor Penguins face one additional problem which is not shared by Kings: for over three-quarters of the year the sea near their breeding areas is covered with thick ice, and birds passing to and from the rookery must walk long distances to reach open water.

The two species have solved their problems of long chick development, variable food supply, and possible winter predation, in completely different ways. The relation of breeding behaviour to environment in the Emperor Penguin has already been discussed (Stonehouse, 1953, p. 25 et seq.) and new information may now be added from more recent work. To summarise briefly, the eggs are laid at mid-winter so that the chicks may be ready for the sea at about the time when the sea ice breaks up. Because of the great distances from open sea to rookery at this time, it is more economical for males to undertake all the incubating than for males and females to cross and re-cross the ice at the coldest time of the year. The incubating birds abandon all territorial behaviour and huddle tightly together, thereby reducing their total heat losses. I have estimated (op. cit., p. 9) that huddling saves about five-sixths of the heat which would be lost by individual birds standing alone, and have suggested that individuals would not be able to remain inactive for long periods if exposed to low temperatures without the protection of other birds. Incubation takes place at the time of the year when little other activity would be possible; there is no evidence to suggest that the incubation period has been shortened by natural selection, or that any

advantage would have been gained by such a shortening. The chicks are fed by both parents, which at first must travel long distances to collect food. At most rookeries the chicks and ice float away together while the chicks are still in down. The chicks moult while still below the size of adults, and presumably before their sternum is fully ossified; it is not known for how long after moulting, if at all, the chicks remain in the care of their parents. Their growth is highest and their demands for food are greatest at the time when food is most plentiful; they presumably achieve independence six or eight weeks before the sudden fall in plankton-volume which marks the end of the summer. Leopard Seals are likely to be scarce in southern waters at the time of their release, but more information on this point would be welcome.

Emperor Penguins succeed in rearing their chicks in a single season, by adopting the expedients of laying in mid-winter and reducing the period in which the chicks are dependent on their parents for food. King Penguins, by contrast, lay during the spring and early summer months, bringing their chicks to full size during the autumn peak of plankton production and keeping them alive, although at starvation level, throughout the winter. The chicks then take advantage of the plankton peak in the following December to fatten and complete their moult. Emperor chicks may be said to grow during the spring period of food abundance, and mature in the autumn; King chicks grow when food is plentiful in autumn and mature in the following spring. Emperor chicks moult when only three-quarters grown; King chicks grow almost to full size in a short time, and then are maintained for a further six months before the moult is achieved.

A consequence of these opposing methods of solving their problems is that Emperor Penguins (so far as is known) may produce one chick every year, while King Penguins certainly take more than a year to produce a chick. King Penguins would therefore appear to be comparatively at a disadvantage although living in a more favourable environment. It is interesting to examine the possible alternative ways of life open to both species, and to discover why each has accepted the advantages and disadvantages of the course which it now follows.

Simpson (1946) has suggested that penguins are primarily birds of cold temperate waters; their insulation has allowed some genera to penetrate southward and find success in sub-Antarctic and Antarctic environments. The forerunners of the genus *Aptenodytes* would presumably have colonised the sub-Antarctic region first, so it may be assumed that the breeding behaviour of Emperor Penguins has evolved from a system resembling that of present-day King Penguins and suited to a sub-Antarctic environment.

King Penguins lay from November to mid-April; they are presumably unable to lay outside these limits because of food shortage in the sea during the remainder of the year. If the fore-runners of Emperors were able to lay over a similar period, they would find, on extending their geographical range southward, that Antarctic waters remained rich for a further month or more at the end of the summer (Fig. 30) and that it was possible for them to lay as late as May or early June. However, they would also find that birds laying earlier in the summer (January or February) would produce their chicks just as the sea ice began to cut off food supplies, and those laying earlier still (November and December) would be unable to feed their chicks during the period of maximum growth, which would come between April and July. It now seems unlikely that Emperor Penguins have set back their breeding date from spring to winter as suggested in my earlier paper (Stonehouse, 1953, p. 31); it is more likely that the date has been set forward so that the birds are laying as late in the season as possible, and that selection has eliminated all which tended to breed earlier.

Perhaps a more interesting question is whether it would have been possible for King Penguins, in a sub-Antarctic environment, to evolve an annual breeding cycle. Again, Figure 30 suggests that food resources would be insufficient to allow laying before November, and the suggestion is confirmed for this species by Figure 18 which shows that adults fattening after moult take longer in October than in November. Chicks hatched from November eggs reach full size by May; if, like Emperor chicks, they moulted before reaching full size, they would be liberated in April and May when food was already becoming scarce. They would also encounter the hazard of predatory Leopard Seals, which are probably unknown to Emperor Penguin chicks further south. Nor would the evolution of laying dates similar to those of Emperor Penguins confer any advantage. Eggs produced in April, at the end of the season, are abandoned by the late-breeding parents. If they were retained and incubated, the chicks would require abundant food throughout July, August and September, when food is scarce and seal predation takes a heavy toll of parents.

So it is probable that King Penguins, like Emperors, have adopted the only mode of life possible to them. Only by lengthening the period of chick dependence has the species been able to fit the peak periods

of chick feeding to spring and autumn, when Leopard Seals are generally absent from inshore waters and food is plentiful in the sea. Lengthening the cycle has in turn eliminated the possibility of annual breeding, for in October and November the adults are fattening their chicks for moulting, rather than fattening themselves for breeding. However, the environment and system allow some latitude in laying dates, and King Penguins (unlike Emperors or Wandering Albatrosses) may breed at different times in successive years. By laying alternately early and late they fit two breeding cycles into three calendar years, and thus reduce the disadvantages laid upon them by their size and slow growth, their predators, and the seasonal fluctuation of their food supply.

SUMMARY

THIS report is primarily an account of field work undertaken in South Georgia, from October 1953 to December 1954, when the author was commissioned to study the present status of King Penguins and other species on the island.

The introduction includes notes on the nomenclature and history of the genus *Aptenodytes*, and the trivial names *patagonica* and *forsteri* are justified for King and Emperor Penguins respectively. Evidence of sub-speciation in King Penguins is discussed, and the geographical distribution of Kings and Emperors is outlined.

Section I gives an account of the observations on South Georgia. The rookery at Paul Beach, Ample Bay, is described, its situation and climate are discussed and methods of study are outlined. The characters of adults, juveniles and chicks are described, and evidence is given to show that, in any season, the breeding adults may be divided into the categories "early", "late" and "ineffective" breeders, according to their immediate breeding histories. It is suggested that birds normally follow the sequence of early breeding, late breeding and ineffective breeding in three consecutive seasons, and so raise two chicks in each group of three years.

Migration is described for the first time in this species, and evidence is cited to suggest that the birds do not generally settle to breed in the colony in which they were reared. Behaviour during the breeding cycle is described under the headings "Pre-nuptial Moulting", "Courtship and Pairing", "Incubation and Brooding", "Disturbed and Late Breeding", and "Care of the Young". The mean volume of a series of eggs from South Georgia is calculated, and is compared with the mean volumes of Emperor Penguin eggs. Weights and measurements of embryos are presented.

The long growth period of the chicks is described and divided into three stages: initial growth, winter starvation, and subsequent growth and moult. Newly hatched chicks are described and their growth is followed through the winter and spring months. Notes on adult mortality, predators and parasites are appended. The food of King and Emperor Penguins is considered in relation to the probable abundance of plankton throughout the annual cycle in Antarctic and sub-Antarctic waters.

Section II contrasts the markedly different ways of life adopted by King and Emperor Penguins. Published accounts of Emperor Penguin rookeries are summarised and an attempt is made to relate observations from rookeries in different latitudes and at different times of the year.

In conclusion, it is suggested that King and Emperor Penguins are faced with similar biological problems, in that both are attempting to raise large and slowly-growing chicks in regions where food supplies show marked seasonal variation. Under the action of divergent evolutionary pressures, the two species have evolved completely different modes of life in answer to these problems, the diversity arising from marked differences in their respective environments. Possible alternative modes of life are discussed, particularly in relation to the apparent disadvantages suffered by King Penguins, which cannot breed annually but succeed in breeding twice every three years.

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TABLES

Month starting	Mean Daily	Mean Max.	Mean Min.	Extreme Min.	Mean Wind (kt.)
1.12.53	39	43	35	27	7
29.12.53	39	43	35	30	9
26. 1.54	41	45	37	30	7
23. 2.54	38	41	35	30	10
23. 5.54	39	43	35	25	11
29. 4.54	36	40	33	23	9
18. 5.54	30	33	26	18	10
15. 6.54	32	35	29	16	12
13. 7.54	28	30	24	12	11
10. 8.54	27	30	24	6	11
7. 9.54	29	32	26	11	14
5.10.54	34	37	31	22	9
2.11.54	38	43	35	29	9

TABLE I. Summary of climate at the base, Bay of Isles, December 1953 to November 1954. All temperatures in °F.

Month	Maximum	Minimum	Daily
J	45	37	39
F	49	35	41
M	46	35	40
A	39	32	36
M	35	26	31
J	33	24	30
Jy	33	24	29
A	34	24	28
S	36	25	32
O	39	29	35
N	39	29	36
D	43	32	38

TABLE II. Mean maximum, minimum and daily temperatures by months, Grytviken, 1944-50. All temperatures in °F.

MALES				FEMALES			
No.	Beak	Foot	Flipper	No.	Beak	Foot	Flipper
605	13.8	19.0	34.2	683	12.4	17.8	33.6
608	12.3	17.9	33.6	609	11.9	17.3	33.0
616	12.6	18.4	33.6	740	12.5	17.5	32.5
617	13.7	18.6	35.0	620	13.1	18.8	32.9
621	14.2	19.4	36.6	736	14.2	17.8	33.7
624	14.0	18.4	34.2	745	13.4	18.0	34.0
630	13.6	18.0	34.1	631	12.2	17.6	32.9
641	14.0	18.6	33.8	639	12.5	18.8	33.7
643	13.8	19.0	34.2	642	13.4	18.9	33.0
III	13.2	20.0	35.2	646	13.5	19.2	33.6
647	13.3	18.0	34.2	648	12.7	17.5	31.0
658	14.4	18.1	32.8	746	12.6	17.2	32.4
665	14.0	19.3	34.0	731	12.2	16.6	32.6
671	13.3	19.0	33.2	670	11.6	17.6	33.8
676	13.7	19.9	34.7	735	12.9	17.6	32.5
688	13.2	17.5	33.2	729	13.1	17.2	32.9
690	14.2	18.2	35.8	742	12.6	16.8	32.6
696	14.2	19.1	33.6	627	12.7	17.0	32.3
706	13.1	17.8	32.3	628	13.3	17.6	31.2
707	13.5	17.6	32.9	610	12.9	17.1	32.9
708	14.9	19.0	34.3	613	12.9	18.9	34.2
719	14.1	18.6	33.4	601	12.6	18.2	31.8
728	14.0	18.3	33.9	737	12.8	17.6	33.8
XII	13.4	18.6	36.0	659	12.7	17.8	33.4
XIV	13.6	17.8	34.3	741	12.4	17.7	31.6
Mean	13.7	18.6	34.1	Mean	12.8	17.8	32.9

TABLE III. Beak, foot and flipper measurements of pairs of marked birds (in cm.).

MALES				FEMALES			
No.	Beak	Foot	Flipper	No.	Beak	Foot	Flipper
618	13.1	18.8	34.0	600	14.0	18.4	34.7
619	14.9	19.4	37.9	602	13.6	18.2	33.8
622	14.8	19.4	35.7	603	13.6	19.2	35.4
629	13.3	20.1	34.4	604	13.9	18.2	33.8
633	13.8	17.6	34.1	606	13.5	18.2	35.0
636	13.6	17.3	33.8	611	12.9	18.0	32.8
638	14.8	18.4	35.4	612	13.1	18.7	35.5
649	13.0	17.8	34.9	614	12.1	17.0	32.7
650	14.0	18.6	34.4	615	12.4	17.4	31.4
652	13.4	18.3	34.0	623	13.3	18.6	32.8
655	13.6	18.6	35.4	*625	12.9	18.2	31.5
657	13.8	17.8	32.8	632	13.2	17.1	32.3
663	13.1	17.0	32.8	634	12.8	18.0	33.0
664	13.4	19.6	34.8	*635	13.4	17.5	33.0
667	13.1	17.7	32.1	637	11.9	16.0	31.0
668	12.6	18.2	33.7	644	12.8	18.8	35.1
674	13.7	17.7	34.5	645	12.6	18.2	33.7
675	14.0	18.0	36.0	651	12.3	17.2	32.1
678	13.9	17.2	34.8	661	13.5	18.4	33.6
679	13.3	18.3	34.2	666	12.4	18.0	33.5
680	14.2	19.3	34.5	673	13.4	18.1	34.2
682	13.5	17.6	32.9	677	13.3	17.7	34.1
684	13.6	19.5	33.6	702	12.2	17.8	34.0
*685	14.0	18.8	35.0	703	12.6	18.1	33.6
686	13.9	17.8	34.2	*709	13.2	18.4	33.4
*687	13.0	18.6	34.6	713	12.7	18.0	32.8
689	13.2	18.2	32.4	*718	12.8	17.0	33.2
691	14.6	17.8	35.2	720	12.8	17.0	32.6
692	13.7	18.6	34.2	726	12.4	17.5	32.5
693	14.7	18.3	35.7	734	12.4	17.2	33.4
694	13.5	19.3	34.0	738	13.0	16.9	33.7
697	13.0	18.1	34.5	744	13.0	16.9	33.7
699	14.4	18.2	35.4	748	11.9	17.2	31.1
*705	13.0	18.6	33.8	XVI	12.8	20.2	34.1
712	13.8	18.9	34.1				
714	13.5	18.6	33.7				
715	13.5	18.2	34.6				
724	14.0	19.7	36.4				
727	13.9	19.2	33.0				
730	13.1	18.8	34.2				
V	13.5	19.0	35.2				
X	13.0	17.6	32.8				
XVII	14.0	17.7	34.0				
XIX	13.8	17.2	33.9				
XX	13.7	18.4	35.0				
Mean	13.7	18.4	34.4	Mean	12.9	17.8	33.2

TABLE IV. Beak, foot and flipper measurements of marked birds, excluding those listed in Table X (in cm.).

* sex doubtful.

MALES						FEMALES					
MIGRANT						MIGRANT					
No.	Date of departure	First seen in moult	Est. † start of moult	Est. † end of moult	Post-moult return	No.	Date of departure	First seen in moult	Est. † start of moult	Est. † end of moult	Post-moult return
605	28.6	10.10	24.9	26.10	27.11	604	19.5	6.10	1.10	2.11	25.11
618	15.5	30.9	21.9	26.10	20.11	606	12.6	23.9	20.9	23.10	16.11
636	4.6	14.9	14.9	16.10	20.11	623	9.7	21.10	30.9	1.11	19.11
641	29.4	30.9	22.9	24.10	18.11	628	24.6	6.10	30.9	3.11	27.11
643	30.7	1.11	20.10	21.11	6.12	632	29.6	10.10	25.9	29.10	22.11
655	21.5	19.11	22.9	24.10	19.11	634	6.5	8.10	7.10	8.11	20.11
657	28.6	24.9	24.9	25.10	23.11	639	11.6	23.10	6.10	7.11	23.11
663	23.6	10.10	10.10	12.11	28.11	642	12.6	29.10	9.10	5.11	1.12
664	12.6	24.9	24.9	26.10	15.11	644	12.6	24.9	20.9	22.10	17.11
674	9.5	13.9	13.9	15.10	22.11	645	24.6	26.11	3.10	4.11	26.11
675	25.6	30.9	30.9	30.10	25.11	646	28.5	6.10	3.10	4.11	21.11
684	30.5	19.10	19.10	20.11	4.12	661	5.7	26.10	22.10	23.11	6.12
*685	24.4	27.10	27.10	28.11	7.12	670	22.5	25.10	17.10	28.11	2.12
*687	17.4	10.11	6.11	3.12	12.12	673	26.6	5.10	23.9	25.10	17.11
689	13.6	10.10	1.10	2.11	17.11	683	20.6	27.11	2.10	3.11	27.11
693	28.6	28.9	18.9	21.10	17.11	702	18.5	25.10	14.10	15.11	6.12
696	28.7	13.10	27.9	29.10	20.11	709	27.5	19.10	19.10	20.11	2.12
699	17.7	6.10	28.9	30.10	20.11	713	10.6	11.11	15.10	19.11	30.11
*705	5.7	21.10	22.10	22.11	7.12	720	4.6	18.10	18.10	18.11	7.12
714	11.7	18.9	8.9	10.10	11.11	734	28.4	5.11	5.10	8.11	28.11
724	7.7	17.11	5.10	6.11	27.11	NON-MIGRANT					
730	7.6	19.9	14.9	15.10	10.11	611	—	13.10	27.9	27.10	20.11
XIX	27.7	12.11	12.9	14.10	12.11	612	—	6.10	2.10	3.11	21.11
NON-MIGRANT						677	—	28.11	4.10	5.11	28.11
619	—	30.9	23.9	25.10	15.11	703	—	1.11	14.10	15.11	25.11
629	—	6.10	6.10	7.11	21.11	718	—	21.10	13.10	16.11	3.12
667	—	3.11	27.10	29.11	11.12	735	—	9.11	9.10	10.11	26.11
686	—	5.11	4.10	6.11	21.11						
694	—	13.10	13.10	14.11	27.11						
(1)	(2)	(3)	(4)	(5)	(6)	(1)	(2)	(3)	(4)	(5)	(6)

TABLE V. Unsuccessful breeders 1953-54. Dates (1954) of departure, moulting, and post-moult return.

* Sex doubtful.

† Est. = Estimated.

Date	684	705	709	720	Mean
Oct. 1954					
18	—	—	—	18.2	—
19	20.4	—	19.6	18.0	—
20	19.7	—	19.4	17.9	—
21	19.6	19.5	19.0	17.7	18.95
22	19.1	19.2	18.7	17.6	18.65
23	18.8	18.7	18.6	17.5	18.40
24	18.6	18.5	18.3	17.4	18.20
25	18.4	18.4	18.2	17.3	18.07
26	18.1	18.1	17.9	17.1	17.80
27	18.0	17.9	17.7	16.9	17.62
28	17.9	17.8	17.6	16.8	17.52
29	17.8	17.5	17.1	16.4	17.20
30	17.6	17.1	16.6	15.9	16.80
31	17.2	16.8	(16.2)	15.8	16.50
Nov. 1954					
1	16.8	16.5	15.8	15.4	16.12
2	16.4	16.0	15.5	15.1	15.75
3	15.9	15.7	15.1	14.8	15.37
4	15.8	15.6	14.7	14.5	15.15
5	15.4	15.3	14.5	14.4	14.90
6	15.3	15.1	14.1	13.9	14.60
7	15.0	14.6	13.9	13.6	14.27
8	14.4	14.2	13.4	13.3	13.82
9	14.1	13.8	13.1	13.1	13.52
10	13.8	13.5	13.0	12.9	13.30
11	13.5	13.4	12.6	12.6	13.02
12	13.0	13.0	12.5	12.4	12.72
13	12.9	12.9	12.4	12.2	12.60
14	12.6	12.7	12.3	12.1	12.42
15	12.2	12.4	12.0	11.9	12.12
16	11.8	11.9	—	11.6	—
17	11.3	—	—	—	—

(1) (2) (3) (4) (5) (6)
TABLE VI. Daily weights (in kilograms) of four moulting birds.

No.	Sex	D ¹	D ²	Time (days)	W ¹	W ²	Loss	Loss per day
606	F	23.9	23.10	30	18.0	10.0	6.0	0.21
611	F	13.9	26.10	13	15.4	10.9	4.5	0.35
612	F	6.10	29.10	23	18.4	11.4	7.0	0.30
618	M	30.9	25.10	25	17.9	10.8	7.1	0.28
619	M	13.10	21.10	8	14.1	12.0	2.1	0.26
632	F	10.10	29.10	19	15.6	9.9	5.7	0.30
641	M	30.9	21.10	21	17.5	11.1	6.4	0.30
646	F	6.10	1.11	26	18.6	11.1	7.5	0.29
667	M	3.11	8.11	5	17.8	16.2	1.6	0.32
670	F	25.10	16.11	22	17.7	10.8	6.9	0.31
675	M	30.9	29.10	29	19.2	10.7	8.5	0.30
685	*M	25.1	12.2	18	18.4	14.2	4.2	0.23
„		27.10	19.11	23	21.0	13.4	7.6	0.33
687	*M	10.11	3.12	23	18.9	10.4	8.5	0.37
693	M	28.9	7.10	9	18.8	16.6	2.2	0.24
694	M	13.10	8.11	26	20.5	11.9	8.4	0.32
697	M	6.12	12.12	6	20.0	17.7	2.3	0.38
700	J	30.1	22.2	22	18.1	10.7	7.4	0.34
702	F	25.10	1.11	7	17.3	15.9	1.4	0.20
703	F	1.11	3.11	2	14.1	13.4	0.7	0.35
706	M	12.2	14.2	2	20.0	19.2	0.8	0.40
711	J	8.1	5.2	28	17.2	9.3	7.9	0.28
713	F	11.11	16.11	5	12.2	11.3	0.9	0.18
715	M	25.1	9.2	15	17.0	11.3	5.7	0.38
717	J	10.1	28.1	18	18.5	12.0	6.5	0.36
718	*F	30.1	18.2	18	17.4	11.5	5.9	0.33
„		21.10	16.11	26	17.4	10.5	6.9	0.27
720	F	26.1	11.2	16	18.6	13.4	5.2	0.32
746	F	8.11	16.11	8	13.2	10.0	3.2	0.40
684	M	19.10	11.11	29	20.4	11.3	9.1	0.31
705	*M	21.10	16.11	26	19.5	11.9	7.6	0.29
709	*F	19.10	15.11	27	19.6	12.0	7.6	0.28
720	F	18.10	16.11	29	18.2	11.6	6.6	0.23

TABLE VII. Miscellaneous birds. Daily loss in weight during moult.

D¹—Date of earliest weighing.D²—Date of latest weighing.W¹—First weight (kg.).W²—Last weight.

* Sex doubtful.

Note. Birds marked "J" in column 2 were juveniles of unknown sex, moulting from juvenile to adult plumage.

No.	Sex	First day	Last day	Interval (days)
606	F	20.9	23.10	33
611	F	27.9	27.10	30
618	M	21.9	26.10	36
628	F	30.9	3.11	34
632	F	25.9	29.10	34
636	M	14.9	16.10	32
657	M	24.9	25.10	31
670	F	17.10	18.11	32
675	M	30.9	30.10	30
687	*M	6.11	3.12	27
714	M	8.9	10.10	32
718	*F	13.10	16.11	34
730	M	14.9	15.10	31
735	F	9.10	10.11	32
746	F	15.10	17.11	33

TABLE VIII. Length of moult in fifteen birds (1954). * sex doubtful

	1918	1919	1920	1921	1922	1923	1924	1925	Mean
Andrew	16	15	17	18	14	19	19	14*	16.50
Bertha	16	16	21	16	16	17	16	12	16.25
Caroline	14	21	20	21	13	19	18	11	17.12
Dora	20	21	18	17	12	19	13	14	16.75
Eric	18	25	21	17	12	17	—	—	18.33
Mean	16.8	19.6	19.4	17.8	13.4	18.2	16.5	12.7	16.8

TABLE IX. Lengths of moult in five penguins between 1916 and 1925. Data from Gillespie (1932), pp. 85-87.

* Gillespie's final table suggests that in 1925 the moult observed by Andrew extended from May 5th to June 19th, a total of 54 days. If this were true some comment might have been expected in the text; it is assumed here that June 19th is a misprint for May 19th.

No.	Sex	Chick	Partner	Est. † start of moult	Est. † end of moult	Post-moult return
746	F	A	A	17.10	17.11	6.12
688	M	A	M	22.10	23.11	9.12
727	M	?	M	4.11	6.12	—
653	F	?	M	27.11	—	—
697	M	A	U	6.12	—	—
745	F	A	A	11.12	—	—
602	F	A	M	13.12	—	—
638	M	?	U	14.12	—	—
*748	F	A	A	14.12	—	—
603	F	?	U	16.12	—	—
742	F	A	A	17.12	—	—
659	F	?	M	18.12	—	—
737	F	A	A	18.12	—	—

TABLE X. Successful breeders 1953-54. Condition of partners and chicks, and dates (1954) of beginning of moult, end of moult and post-moult return.

* This bird formed the third partner in a trio, beginning her moult before either the male or the female (630 and 631) of the original pair.

† Est.=Estimated.

In column 4 A—alive
M—missing
U—unmarked

MALES			
MIGRANT			
No.	Length of post-moult absence (days)	Date of first incubating	Length of courtship (days)
605	32	9.12	12
618	25	10.12	20
636	35	7.12	17
641	25	2.12	14
643	15	—	—
655	26	7.12	18
657	29	11.12	18
663	16	14.12	16
664	19	10.12	25
674	38	—	—
675	26	14.12	19
684	14	19.12	15
*685	9	—	—
*687	9	—	—
689	15	3.12	16
693	27	5.12	18
696	22	19.12	29
699	21	7.12	17
*705	15	—	—
714	32	—	—
724	21	—	—
730	26	28.11	18
XIX	29	4.12	22
NON-MIGRANT			
619	21	14.12	29
629	14	10.12	19
686	15	12.12	12
694	13	—	—
667	12	—	—

(1) (2) (3) (4)

FEMALES			
MIGRANT			
No.	Length of post-moult absence (days)	Date of laying	Length of courtship (days)
604	23	10.12	15
606	24	—	—
623	18	4.12	15
628	24	11.12	14
632	24	6.12	14
634	12	8.12	18
639	16	7.12	14
642	26	—	—
644	26	3.12	16
645	22	11.12	15
646	17	5.12	14
661	13	19.12	13
670	14	13.12	11
673	23	2.12	15
683	24	8.12	12
702	21	—	—
709	12	—	—
713	11	14.12	14
720	19	—	—
734	20	6.12	8
NON-MIGRANT			
611	24	3.12	13
612	18	3.12	12
677	23	11.12	13
703	10	11.12	16
*718	17	—	—
735	16	13.12	17

(1) (2) (3) (4)

TABLE XI. Unsuccessful breeders 1953-54. Length of post-moult absence, date (1954) of laying or beginning of incubation, and length of courtship.

The figures in column 2 are calculated from columns 5 and 6 in Table I. Column 4 is derived from column 6 of Table I and column 3 in this table.

* sex doubtful.

No.	Sex	First seen on return	First weighed	Weight	Estimated weight on return	
					Male	Female
604	F	25.11	—	—	—	14.8
606	F	16.11	—	—	—	13.7
611	F	20.11	21.11	13.8	—	14.0
612	F	21.11	—	—	—	16.2
618	M	20.11	28.11	13.8	15.2	—
619	M	15.11	17.11	17.4	17.7	—
632	F	22.11	27.11	13.3	—	14.4
641	M	18.11	—	—	15.7	—
643	M	6.12	—	—	13.8	—
644	F	17.11	—	—	—	15.1
646	F	21.11	—	—	—	13.8
655	M	19.11	—	—	15.0	—
664	M	15.11	16.11	15.6	15.8	—
673	F	17.11	—	—	—	14.3
674	M	22.11	—	—	16.8	—
675	M	25.11	28.11	14.9	15.4	—
677	F	28.11	—	—	—	14.6
683	F	27.11	—	—	—	13.1
686	M	21.11	23.11	15.4	15.7	—
693	M	17.11	—	—	17.3	—
694	M	27.11	—	—	17.1	—
699	M	20.11	—	—	16.4	—
703	F	25.11	—	—	—	15.6
713	F	30.11	—	—	—	12.2
720	F	7.12	—	—	—	14.4
746	F	6.12	—	—	—	13.6
XIX	M	12.11	—	—	16.1	—
Mean					16.0	14.3

(1) (2) (3) (4) (5) (6) (7)

TABLE XII. Weights (in kg.) at beginning of courtship (1954).

No entry is made in columns 4 or 5 if the bird was weighed when first seen; instead the actual weight is recorded in column 7.

No.	Weight (kg.)
632	10.8
639	11.2
645	10.6
646	10.6
670	9.7
Mean:	10.6

TABLE XIII. Weights at end of courtship; five females.

PAIR	INCUBATION					BROODING										
	F	M	F	M	F	F	M	F	M	F	M	F	M	F	M	F
602-739	2	17	19	10	6	+ 5	5	7	3	4	3	4	3	3	4	3
610-707	1	16	21	10	6	+ 6	7	5.5	5	5.5	4	3	4	3		
729-688	← 33 →			12	9	+ 2	7	7	5.5	4.5	5	4	3			
601-719	0	21	18	14	2	+ 8	10	5	6	4.5	4.5	4.5				
613-708	1	22	← 27 →		5.5	+ 4	7	4	7	2	6	4				
648-647		17	19	11.5	6	+ 5.5	7.5	4	6	5	4	4				
659-XII	← 36 →			12	6	+ 4	8	5.5	3.5	5	4					
653-626		16	17.5	14	6	+ 5.5	8.5	5.5								
620-617		21	18	14.5	1	+ 9.5										
736-621					0	+ 8	6.5	5.5	4	5	3	4	3	4		
XVI-II					0	+ 8	6	5	4	4	3	4	3			
741-XIV						+ 1	9	6	6	4.5	4.5	5	4	3		
744-701						+ 6	6	6.5	5.5	5	4	2				
742-690						+ ← 11 →		5.5	5	3	3	4	3	2	3	3
Number of Observations	4	7	6	8	11	13	12	13	12	12	12	11	7	5	2	2
Mean length (days)	1.0	18.6	18.7	12.2	4.3	+ 5.6	7.3	5.6	5.0	4.3	4.0	3.9	3.3	3.0	3.5	3.0

PAIR	INCUBATION												
	F	M	F	M	F	M	F	M	F	M	F	M	
609-608	0	20	15	(4 + 12)	6	5	6	6	4	3			
614-716	2	14	18	11	11	(4 + 4)	5	7	3	4	4	4	
740-616	← 37 →			31	9	(0 + 7)	7	5	4	5			
VIII-668	← 47.5 →			12	(4 + 4)	7	6	5	4	4	4	4	
637-640	0	12.5	16	12.5	12	8	10.5	8.5	8	*			
646-III	← 7			16.5	14	9.5	13.5	7	7	7	8.5	8	*

TABLE XIV. Incubating and brooding watches.

The upper table represents normal brooding and incubation. The lower table shows conditions of abnormally prolonged or shortened incubation, effected by exchanging eggs. The sign + denotes hatching; figures immediately to left and right should be added to give the full length of the watch in which hatching occurred.

M—Male.

F—Female.

* Egg lost.

MALES							
	D 1	D 2	Time days	W 1	W 2	Weight loss	Loss per day
III	14.12	21.12	7	12.4	11.8	0.6	.09
"	9.1	21.1	12	15.8	13.7	2.1	.17
IV	3.1	12.1	9	14.1	13.4	0.7	.08
X	15.12	21.12	6	12.2	11.7	0.5	.08
"	16.1	1.2	16	16.2	13.2	3.0	.19
XIII	5.1	12.1	7	13.1	12.6	0.5	.07
XIV	30.12	12.1	13	15.2	13.0	2.2	.17
XVII	1.1	12.1	11	14.4	12.8	1.6	.15
617	4.2	11.2	7	13.8	12.7	1.1	.16
647	12.1	23.1	11	15.9	13.4	2.5	.23
658	29.12	9.1	11	13.4	11.4	2.0	.18
675	25.2	3.3	6	11.0	10.5	0.5	.08
676	5.2	22.2	17	13.4	11.4	2.0	.20
676	5.2	22.2	17	13.4	11.4	2.0	.12
688	1.1	12.1	11	15.3	13.6	1.7	.15
691	1.1	12.1	11	16.2	13.8	2.4	.22
694	1.1	13.1	12	15.7	13.8	1.9	.16
697	3.1	16.1	13	15.7	13.0	2.7	.21
"	31.1	11.2	11	15.4	13.2	2.2	.20
701	6.1	16.1	10	14.1	12.8	1.3	.13
704	6.1	18.1	12	11.4	10.2	1.2	.10
*705	6.1	21.1	15	14.0	12.7	1.3	.09
706	6.1	16.1	10	16.4	14.3	2.1	.21
707	7.1	14.1	7	12.8	12.0	0.8	.11
FEMALES							
VIII	16.1	26.1	10	15.2	13.2	2.0	.20
XVI	15.12	21.12	6	15.6	14.4	1.2	.20
"	16.1	21.1	5	16.7	15.8	0.9	.18
604	30.12	23.1	24	12.8	10.7	2.1	.09
637	14.1	28.1	14	12.2	10.3	1.9	.14
639	26.1	4.2	9	14.2	12.7	1.5	.17
646	22.1	28.1	6	15.2	14.2	1.0	.17
648	23.1	28.1	5	14.8	13.9	0.9	.18
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)

TABLE XV. Daily losses in weight (in kg.) during incubation, 1953 and 1954.

* Sex doubtful.

D 1—Date of first weighing.

D 2—Date of last weighing.

W 1—First weight.

W 2—Last weight.

No.	Sex	First egg laid	First egg lost	Second egg laid	Notes
600	F	30.11.53	26.12.53	4.12.53	1st egg removed. Returned c. 26.1.54. 2nd egg lost by partner.
626	M	30.11.53	30.11.53	c.5.1.54	1st egg removed. Completed "watch", returned c.21.12.53. Partner reared chick: 626, lost after June.
640	M	25.11.53	27.11.53	1.1.54	1st egg removed on laying. Wandered about rookery for few days. Absent, then returned and settled on 22.12.53. 2nd egg lost.
639 641	F } M }	c.28.11.53	c.1.12.53	6.1.54	Both bred early on adjacent sites. Paired c.22.12.53. 2nd egg taken late in incubation.
645	F	c.5.12.53	c.25.12.53	8.2.54	Lost egg during first long watch. Returned after absence to settle c.25.1.54. 2nd egg taken.
650	M	c.30.11.53	30.11.53	c.28.2.54	Returned late December and again in 3rd week January but failed to find partner. Eventually settled c.22.2.54. Raised foster-chick successfully.
651	F	c.30.11.53	?	7.1.54	1st egg lost by partner during 1st watch. Settled early January, raised 2nd successfully.
652	M	25.11.53	23.12.53	31.1.54	1st egg taken during 2nd watch. Returned after absence, settled c.21.1.54. Bred successfully.
657	M	30.11.53	c.3.12.53	2.1.54	1st egg lost. Returned 23.12.53 after absence. Partner lost 2nd egg.
664	M	27.11.53	1.12.53	16.1.54	1st egg taken. Returned 26.12.53 after absence. Chick abandoned soon after hatching.
667	M	29.11.53	?	7.1.54	1st egg lost early in incubation. Returned c.27.12.53 after absence. Chick lost during winter.
697	M	30.11.53	6.12.53	3.1.54	1st egg taken. Wandered for remainder of watch and paired immediately after return. Bred successfully.
730	M	1.12.53	?	8.1.54	1st egg lost by partner. Returned for 2nd incubation watch but paired instead. 2nd egg failed to hatch.

TABLE XVI. Marked breeding birds which lost their first egg and laid again in the same season.

No.	Sex	Egg laid	Egg lost	Notes
618	M	29.11.53	3.1.54	Abandoned after late courtship. Returned 18.1.54. No late courtship.
619	M	25.11.53	28.11.53	Egg taken. Returned 1.1.54 after absence. Late courtship mid-February unsuccessful.
629	M	17.12.53	c.18.12.53	Egg lost. Returned 10.1.54 after absence. Late courtship mid-January unsuccessful.
634	F	28.11.53	?	Egg lost by partner. Returned mid-January for second incubation watch; seen in courtship mid-February: unsuccessful.
670 671	F } M }	27.12.53	27.12.53	Egg taken on laying. 671 courted other females in January. 670 not seen to court on return. Neither formed second pair.
683	F	c.5.12.53	30.12.53	Egg taken at beginning of 2nd incubation watch. Wandered until 17.1.54. Returned 14.2.54. No late courtship seen.
693	M	30.11.53	6.12.53	Egg taken. Returned 1.1.54 after absence and again 26.1.54. Desultory and unsuccessful courtship.

TABLE XVII. Marked breeding birds which lost their egg but did not breed again in the same season.

No.	Length (cm.)	Diameter (cm.)	Volumes (c.c.)	
			measured	calculated
1	9.7	8.2	282	292
2	11.7	8.2	334	346
3	10.0	7.8	268	268
4	10.6	7.6	278	270
5	10.9	8.0	286	298
6	10.6	7.6	262	270
7	10.4	7.5	262	268
8	11.7	8.4	372	365
9	10.0	7.4	254	242
10	10.7	7.4	253	258
11	10.3	8.0	286	292
12	9.9	7.6	248	252
13	11.2	8.1	328	325
Mean			287	289

TABLE XVIII. Lengths, diameters and volumes of thirteen King Penguin eggs.

Embryo	Weight (g.)	Length (cm.)	Embryo	Weight (g.)	Length (c.m.)
30	13.4	2.8	61	40.0	4.0
31	6.4	2.0	62	125.0	5.4
32	6.4	2.0	63	52.0	4.1
33	17.8	3.0	64	100.0	5.1
36	1.5	0.7	65	170.0	5.7
38	13.5	2.7	66	90.0	3.8
39	6.2	1.9	67	47.0	4.0
40	36.0	3.6	68	25.5	3.5
41	37.0	3.8	69	125.0	5.5
43	70.0	4.5	70	135.0	5.3
44	48.0	3.8	71	65.0	4.3
45	27.0	3.6	72	180.0	5.8
46	17.0	3.0	73	170.0	5.4
48	3.5	1.3	74	185.0	5.7
49	6.0	1.9	76	150.0	5.4
50	26.0	3.3	77	150.0	5.2
51	7.0	2.1	78	125.0	5.1
52	3.5	1.3	81	2.5	0.9
53	15.0	2.8	83	19.0	2.6
54	46.0	4.1	84	4.0	1.1
55	85.0	4.8	85	60.0	4.4
56	24.5	3.3	86	8.5	1.9
57	39.0	3.7	87	110.0	4.7
58	33.0	3.5	88	6.3	1.6
60	135.0	5.3			

TABLE XIX. Weights and flipper lengths of forty-nine embryos.

Day	Mean Weight (kg.)	Day	Mean Weight (kg.)
1	0.22	21	1.94
2	0.25	22	2.11
3	0.27	23	2.32
4	0.31	24	2.45
5	0.35	25	2.57
6	0.40	26	2.79
7	0.45	27	3.01
8	0.49		
9	0.55	30	3.63
10	0.61		
11	0.69	33	4.10
12	0.79		
13	0.89	36	4.39
14	1.02		
15	1.16	39	4.99
16	1.22		
17	1.38	40	5.30
18	1.51		
19	1.67		
20	1.83		

TABLE XX. Mean daily weights of ten normal chicks during their first forty days of growth.

	A	B	C
Hatching	—	0.2	0.2
Months 1	1.1	1.1	0.9
	2.9	3.8	2.8
2	7.3	6.2	5.2
	9.2	9.0	8.3
3	12.2	10.9	10.1
	12.8	11.9	11.5
4	13.0	12.0	11.9
	12.0	11.5	11.1
5	11.5	11.1	10.2
	11.7	10.4	9.6
6	10.3	9.8	9.4
	10.3	9.3	8.8
7	9.8	8.9	8.3
	9.4	8.6	7.9
8	9.3	8.5	7.6
	10.3	8.2	7.1
9	10.6	8.4	7.0
	12.6	9.2	6.6
10	14.7	11.1	6.8
	—	10.8	7.5

TABLE XXI. Bi-monthly weights (in kg.) of King Penguin chicks.

- A—Weights of Chick No. 27, fed by three guardians.
 B—Mean weights of six chicks fed normally by both parents.
 C—Mean weights of five chicks, each of which lost a parent before mid-June.

	Beak	Foot	Flipper	
Days	2	3.2	5.2	5.3
	5	3.5	6.0	5.8
	8	3.8	6.9	6.8
	11	4.1	7.5	7.3
	14	4.5	8.5	8.2
	17	4.5	9.5	8.8
	20	5.0	10.2	10.1
	23	5.2	12.9	12.3
	26	5.4	13.5	13.5
	29	5.9	13.9	15.0
	32	6.2	15.5	18.1
	35	6.5	16.0	19.5
	38	6.6	16.3	21.0
	41	6.9	17.0	22.9
	Months	March	8.0	17.6
April		9.0	18.1	31.0
May		9.5	18.2	31.4
June		9.8	18.4	31.7
July		10.0	18.4	31.7
August		10.2	18.4	31.8
September		10.2	18.4	31.8
October		10.2	18.4	31.8
November		10.8	18.4	32.4
December		11.0	18.4	33.2

TABLE XXII. Mean lengths of beak, foot and flipper in twelve growing chicks. (Measurements in cm.).

Months (1954)	Number dying	Mean weight (kg.)	Mean flipper length (cm.)
May	15	—	12.3
June	17	—	19.3
July	19	—	19.3
August	21	2.9 (12)	20.5
September	40	3.2 (33)	26.0
October	46	3.3 (44)	27.1
Total	158		

TABLE XXIII. Numbers, weights and measurements of chicks dying from starvation during the winter months.

Months (1954)	Successful Breeders			Total	Failed or Non-Breeders			Total	Grand Total
	Male	Female	Unknown		Male	Female	Unknown		
March	—	—	—	0	—	1	—	1	1
April	1	—	—	1	—	—	—	0	—
May	4	2	—	6	—	1	1	2	8
June	4	—	—	4	2	—	—	2	6
July	—	1	—	1	1	5	—	6	7
August	—	—	—	0	1	—	—	1	1
September	1	—	—	1	—	—	—	0	1
October	—	1	—	1	—	—	—	0	1
Total	10	4	0	14	4	7	1	12	26

TABLE XXIV. Final dates, summarised by months, on which 26 missing adults of breeding age were last seen.

- Notes. 1. All were known to have bred (i.e. laid or incubated) since November 1953.
 2. All were marked between November 1953 and February 1954.
 3. Successful breeders were those known to have been feeding a chick shortly before their disappearance.

	Males	Females	Unknown	Total
Successful Breeders:				
Safe	26	22	—	48
Lost	10	4	1	15
Failed and non-Breeders:				
Safe	28	27	—	55
Lost	4	7	—	11
Total	68	60	1	129

TABLE XXV. Mortality in birds of breeding age.

- Notes.* 1. All were known to have bred (i.e. laid or incubated) since November, 1953.
 2. All were marked between November, 1953 and February, 1954.
 3. Successful breeders were known to have been feeding a chick shortly before their disappearance.

Region	Depth (metres)	Months											
		J	F	M	A	M	J	J	A	S	O	N	D
Sub-Antarctic	0-50	0.94	2.42	1.84	0.60	0.72	0.34	0.47	0.37	0.55	0.71	1.28	0.99
	50-100	0.79	0.96	1.63	0.52	0.58	0.34	0.52	0.68	0.46	0.71	0.63	2.03
	Total	1.73	3.38	3.47	1.12	1.30	0.68	0.99	1.05	1.01	1.42	1.91	3.02
Antarctic	0-50	0.89	1.73	1.93	2.12	1.00	0.63	0.49	0.75	0.54	0.37	0.52	0.96
	50-100	0.77	1.45	1.37	1.12	0.62	0.69	0.67	0.41	0.43	0.72	1.43	1.65
	Total	1.66	3.18	3.30	3.24	1.62	1.32	1.16	1.16	0.97	1.09	1.95	2.61

TABLE XXVI. Abundance of plankton in sub-Antarctic and Antarctic surface waters (vol. in c.c. per 50-metre haul).

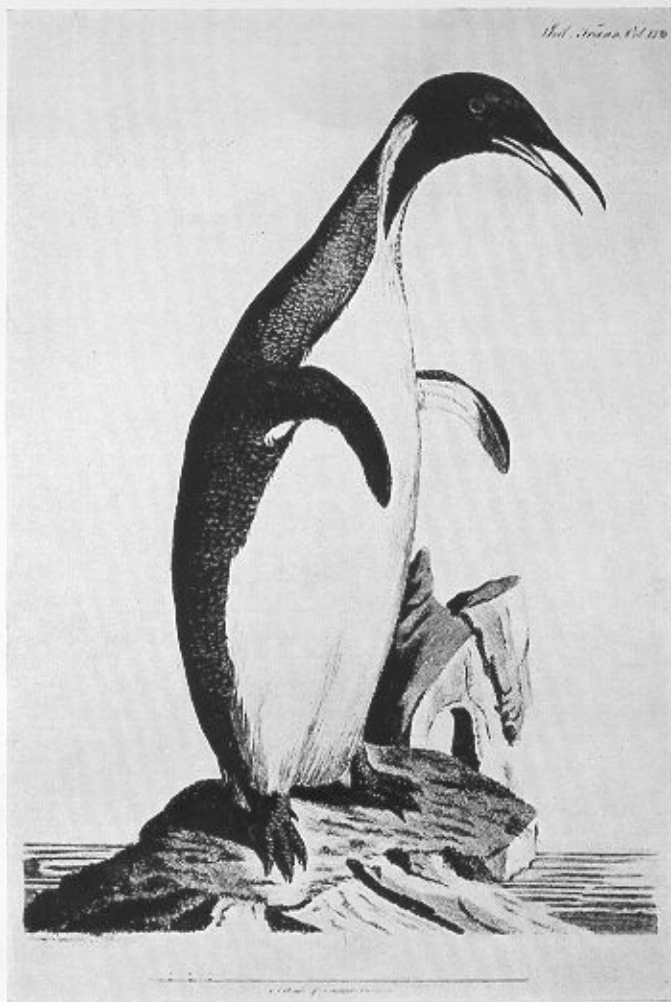
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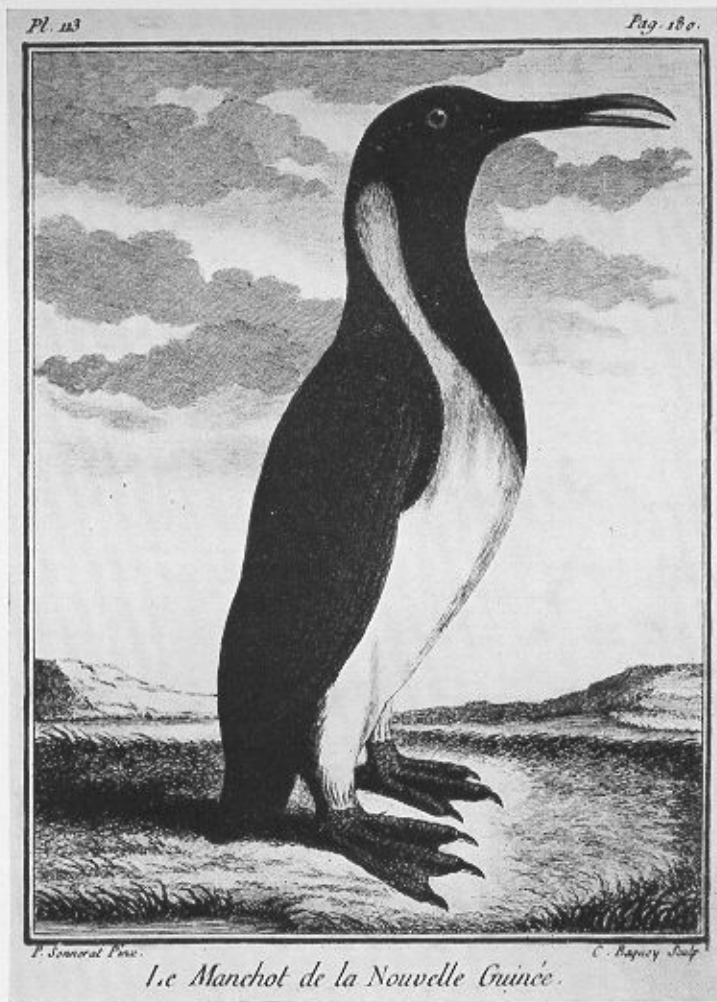
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PLATE I

- a. Illustration of King Penguin from Pennant (1768), the first specimen to be described.
- b. Sonnerat's "Manchot de la Nouvelle-Guinée" (1776, PL.113). Probably redrawn from sketches by Commerson.
- c. Miller's *Aptenodytes patagonica* (1777 or 1778). This photograph is taken from Miller's later publication (1796), but the same plates were used for both works.
- d. Forster's *Aptenodytes patagonica* (*patachonica* in text) dated 1781.
- e. Pennant's illustration published in 1781. The same name is used as in his earlier description (1768), but the bird is drawn from a different model.



a



b



c



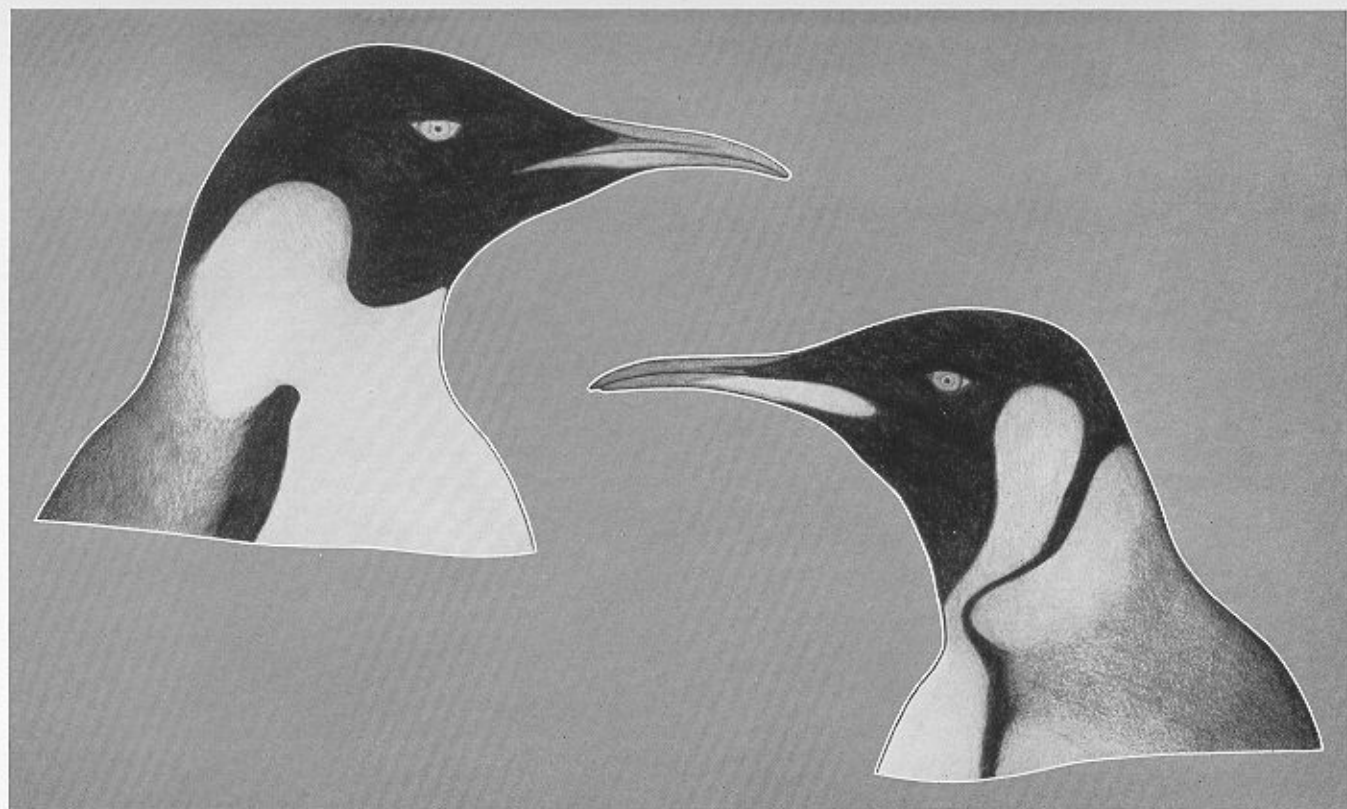
d



e

PLATE II

- a. Heads of Emperor (left) and King Penguins, redrawn after Wilson (1907). In life, the length of the King Penguin's head is slightly less than that of the Emperor. Note the unfeathered mandible and unbroken post-auricular bar of the King Penguin.
- b. General view of the eastern end of the Paul Beach rookery. (Late March).



a



b

PLATE III

- a. Formation of the first pairs. (Early November).
- b. Pair formation; head-flagging. The bird on the right is dabbling.



a



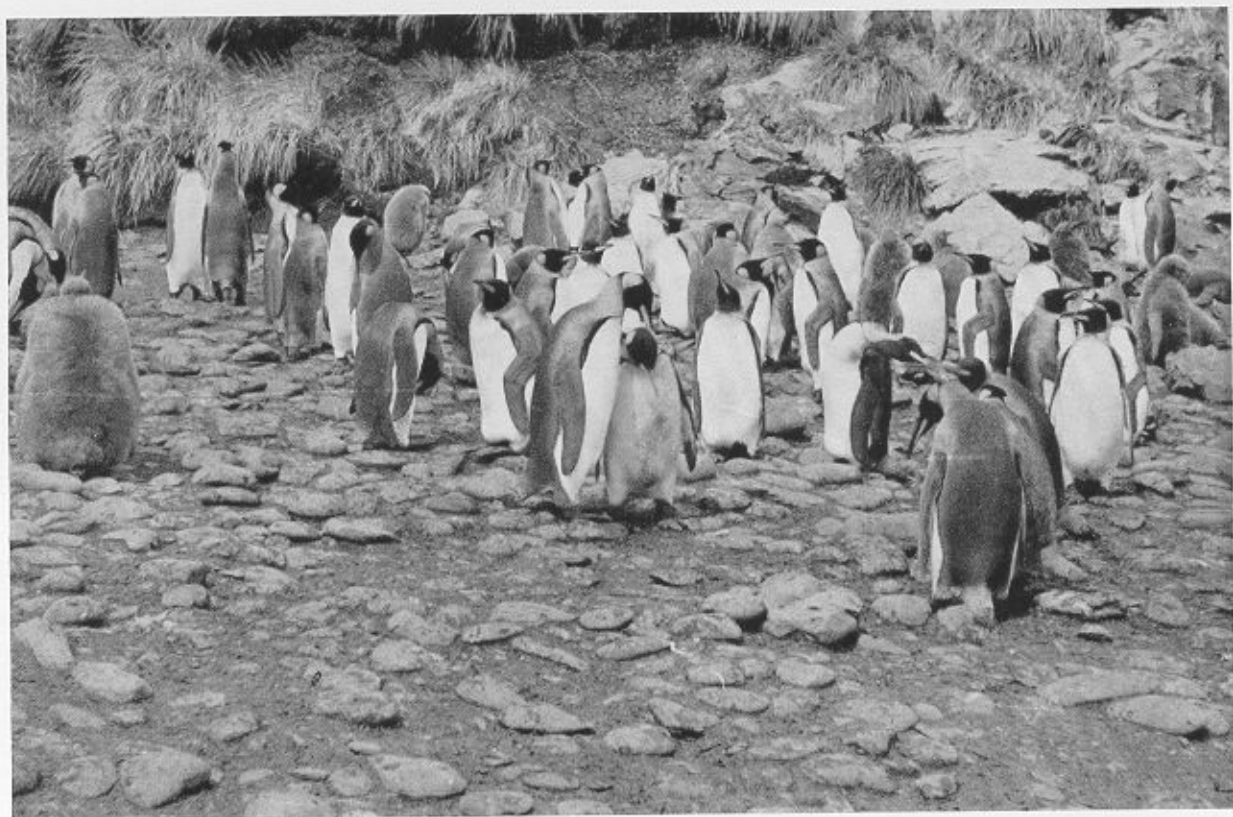
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PLATE IV

- a. Pair formation; high-pointing.
- b. Pair formation; attempted copulation.



a



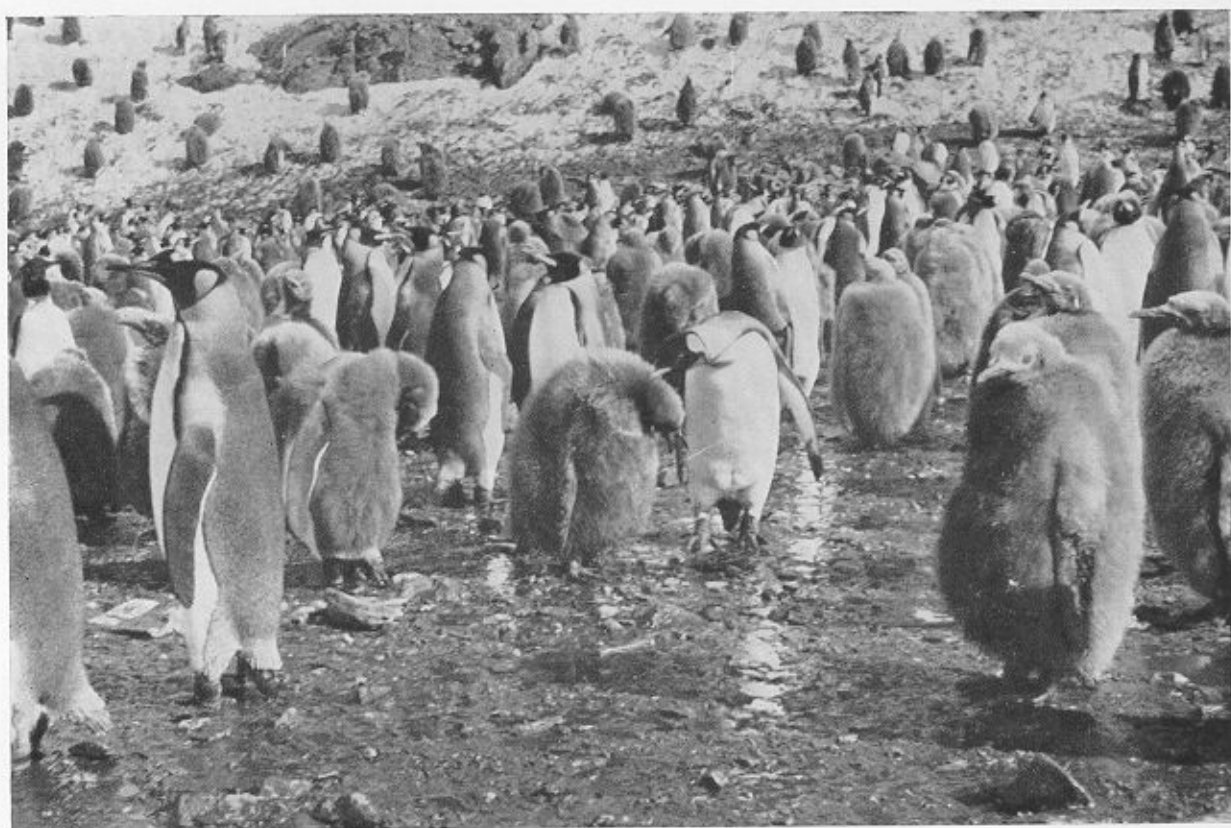
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PLATE V

- a. Chick of 2½-3 months tending a temporarily abandoned chick of 3-4 weeks.
- b. Adult preen-pecking a chick after feeding.



a

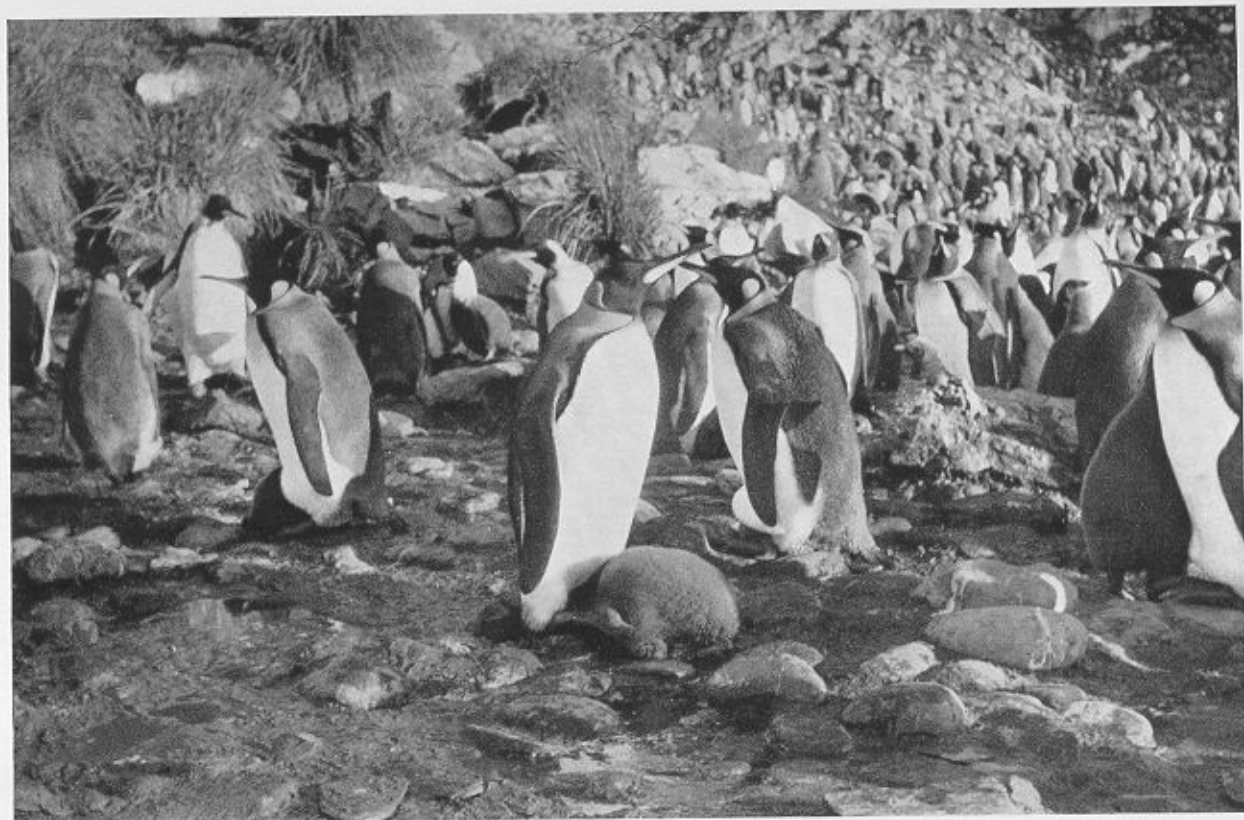


b

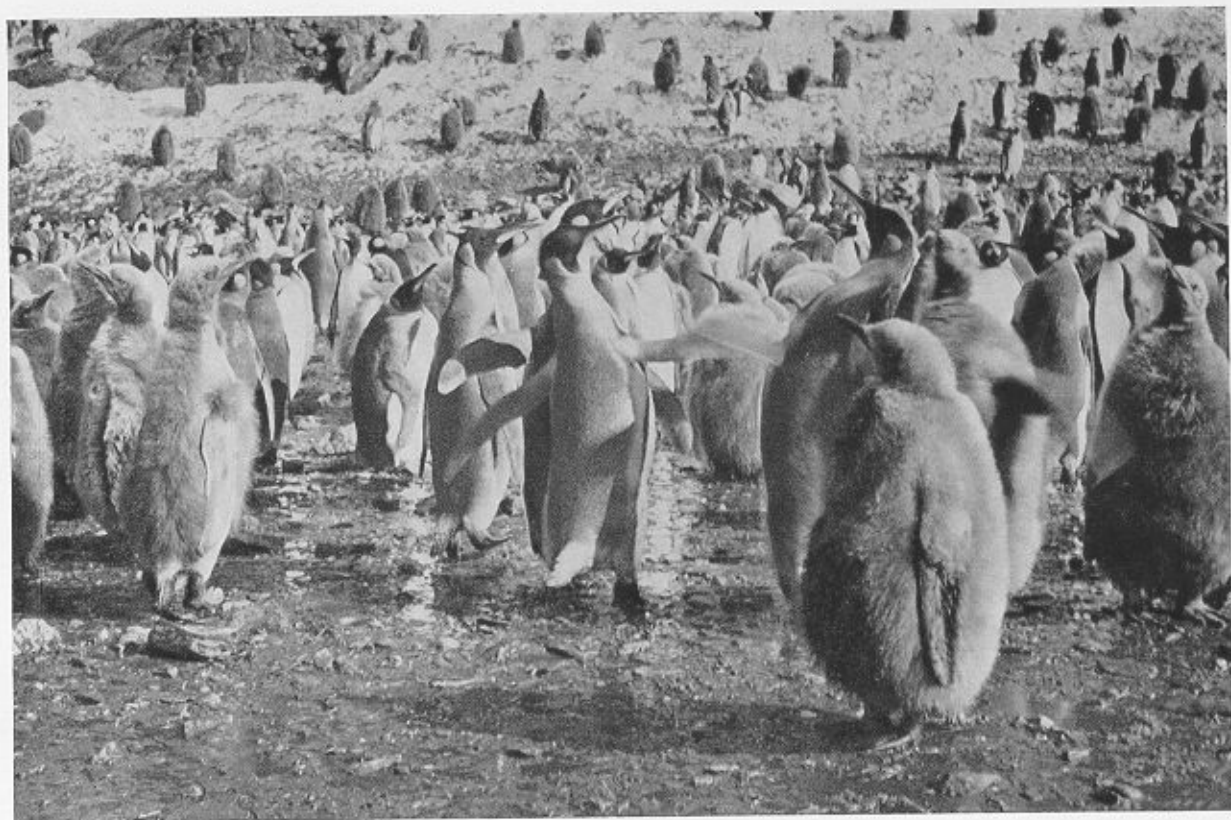
PLATE VI

a. Adult with chick of 5-6 weeks.

b. Pair formation; flipper fight. Note moulting chicks from previous year's brood.



a



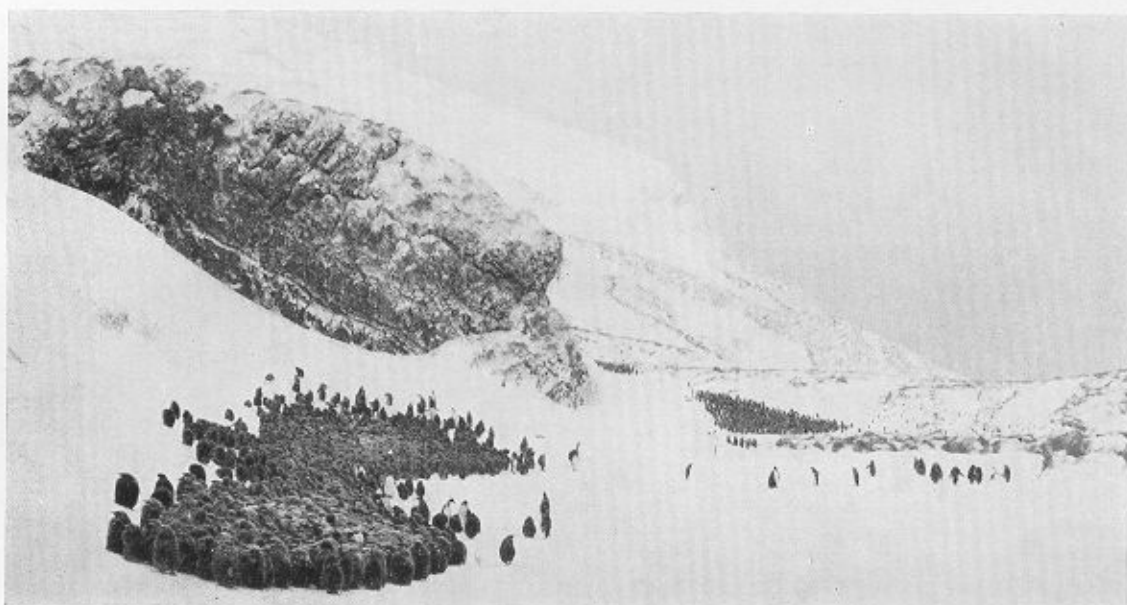
b

PLATE VII

- a. Crèche, with a few adults tending chicks.
- b. Chicks in crèche, with adults grouped on slopes in background. (August).
- c. Morning promenade from slopes to beach.



a



b



c