

FALKLAND ISLANDS DEPENDENCIES SURVEY

SCIENTIFIC REPORTS

No. 17

THE PYGOSCELID PENGUINS

I. METHODS OF STUDY

II. THE ADÉLIE PENGUIN

Pygoscelis adeliae (Hombron & Jacquinot)

By

WILLIAM J. L. SLADEN, M.B.E., M.D., D.Phil.

*Falkland Islands Dependencies Scientific Bureau
and Edward Grey Institute, Oxford University*



LONDON: PUBLISHED FOR THE COLONIAL OFFICE
BY HER MAJESTY'S STATIONERY OFFICE: 1958

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(Manuscript received December 1954*)

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* This report has been available at the Edward Grey Institute, Oxford, for use by students of ornithology since it was submitted for a thesis for the Oxford degree of Doctor of Philosophy in December 1954. For example, it was used, with due acknowledgements, by Dr. L. E. Richdale in his recent and very complete work on penguins (Richdale, L. E. 1957. *A Population Study of Penguins*. Oxford).

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SUMMARY

THE three Pygoscelid Penguins are the Adélie, *Pygoscelis adeliae*, the Chinstrap, *P. antarctica*, and the Gentoo, *P. papua*.

Two rookeries were studied between 1948 and 1951, one at Hope Bay, Graham Land, and the other at Signy Island, South Orkneys. At both of these there survived a small number of birds that had been ringed two seasons before. A further 338 Adélies, 213 Chinstraps and 207 Gentoos were ringed, and more than 1600 temporarily marked with coloured rings and/or paint. About 2000 that were fed to sledge-dogs or used for human consumption, were dissected. Some of the Gentoos studied were breeding in the Falkland Islands.

PART I. METHODS OF STUDY

The value of *marking birds* for any life history and behaviour study is discussed, and three points are stressed: the importance of mastering methods and technique from the beginning of the study, of studying a large sample so that allowance can be made for individual variation, and of devoting much of the work to birds of known age (i.e. those marked when young).

The various methods used for marking the Pygoscelid Penguins are described in detail, including a new method of marking them with *flipper-rings*.

Methods used for *marking colonies and nest-sites* so that they can be located in later years, and methods used in *dissection and skinning*, are also given in Appendix B (p. 92).

The value of *photography*, both still and motion, is discussed briefly. The ciné-camera is particularly valuable for recording the actions and movements going on in a community of birds which cannot be taken in all at once by the field worker. Some of the difficulties encountered in carrying out photographic work in the Antarctic are discussed in Appendix C (p. 93).

The use of large-scale maps, showing individual breeding colonies, is also discussed.

PART II. THE ADÉLIE PENGUIN

Methods of sexing Adélies are described. The only certain way, other than by dissection, is to mark breeding birds before egg-laying and to continue observing them during the early part of the breeding season. Casuals and non-breeders cannot be sexed unless marked and recovered breeding in another season.

The diversity in behaviour of a penguin community appears to be due to three factors which are often inter-related: *variation among individuals*, differences in "*intensity*" of behaviour, and differences in *age and breeding experience*. Emphasis is laid on the differences in age and breeding experience, and some evidence is given from field observations and dissections to show that this is an important factor.

Suggested age groups divide a population seen at the rookery into five categories: the experienced (established) breeders, the inexperienced (unestablished) breeders, the non-breeders ("wanderers") in adult plumage, the non-breeders in immature plumage (yearlings), and the nestlings.

The *established breeders*, probably four or five years old and over, come back to their former nest-sites

independently of their former mates. Such a bird may "keep company" with another bird of the opposite sex until its true mate returns.

The *unestablished breeders* have first to establish themselves and pair off. Their behaviour differs somewhat from that of the established birds, though with some overlap due to individual variation. They often arrive back later than the established breeders, and take up territories on the periphery of the colonies, or fill vacant places within them. They are the cause of most of the fighting. Courtship behaviour is more prolonged, egg and chick mortality higher, and breeding efficiency lower.

The *non-breeding "wanderers"* in adult plumage are two or three years old and can be seen wandering around the rookery in small parties, and even visiting rocky outcrops up to 1000 ft. above sea-level far away from the breeding area. Some of them build poor nests, or occupy vacant sites for a short time before moving elsewhere or being turned out by older birds. Of the wanderers which were dissected, some showed undeveloped gonads despite their adult plumage. It is this age group which, together with some of the unestablished birds, will, under favourable conditions, occupy new ground and thus extend the range of the species. They will also quickly take the opportunity to fill any gap in the colonies, and may during the re-occupation period occupy territory in anticipation of the following season.

The *yearlings*, which are easily recognised by their white throats, normally live among the pack ice, but are occasionally seen at the rookery where they associate with the wanderers. Several were seen building nests in a half-hearted way on the edge of colonies, but, like the wanderers, they never stayed in one place for long.

The displays and postures of the Adélie are classified. During the first and second fasting periods the *ecstatic display* is confined to the male, its most important function appearing to be in pair-formation. A lone male by this display can attract a nearby female to its nest. After the eggs have hatched (or should have hatched), it is also seen in females, though on a diminished scale. It is more commonly seen among the younger and unestablished breeders or non-breeders, than among the established breeders.

The "*bill to axilla*" display, described for the first time, appears to be closely related to the ecstatic and is probably also associated with pair-formation. Its resemblance to one of the attitudes of threat suggests that this display has in it a greater element of repulsion for the same sex and less attraction for the opposite sex than has the ecstatic. The possible relation to nervous strain of the ecstatic and "bill to axilla" displays in some situations is mentioned.

Bowing is described as a posture and a display, and it is suggested that the display is associated with early pair-formation, and is possibly a form of appeasement ceremony.

For convenience, the *mutual display* is divided into two phases, the loud mutual display (high intensity) and the quiet mutual display (low intensity). The situations in which it is seen are described, the most frequent being between pairs before egg-laying, during the nest-relief ceremony, and between parents and nestlings.

The Adélie is the most aggressive of the Pygoscelid Penguins. Its *aggressive postures* are described under the headings of threat, attack, fighting and pecking.

The Adélie has a number of *postures and noises which suggest nervousness*. These include flipper movements, raising of the forehead crest, head movements, the use of the call-note "aark", when walking between nests and sometimes in the mutual display. The possible association of these postures and noises with displacement activities is mentioned. *Copulation* is described.

Both sexes share the duties of *nest-building*. The Adélie's habit of *stealing stones* is discussed and it is suggested that it serves a useful purpose in distributing stones throughout a colony from the outside towards the centre, thus reducing the necessity for long treks.

A number of other postures and movements are described. Of particular interest is the behaviour of Adélies before *departure to sea* when their fear of the Leopard Seal is plainly noticeable.

Some *displacement activities* are mentioned, though the writer was not aware of this aspect of animal behaviour when carrying out his field work.

The breeding season starts when birds return to the rookeries in September and October and occupy nest-sites. They may have to travel 200 miles or more from their winter quarters, the last stage being over many miles (up to sixty) of rough sea ice. The *occupation period* is the period from arrival until the last egg has been laid. Evidence is given from marked birds that, once established, Adélies are, on the whole, very faithful to their old nest-sites from year to year, and keep the same mates. Nest-sites are often covered by a foot or more of snow, yet Adélies appear to come back to the same spot; the explanation of this is discussed.

The normal clutch is two eggs, the interval between the first and second being from 2–4 days. If eggs are removed as soon as laid, a third one is sometimes produced. Adélies are single-brooded. The average *incubation period* (from the day of laying until the chick is completely out) is thirty-five days with a range of thirty-three to thirty-eight days.

Fasting periods, two for each member of a pair, start at the beginning of the occupation period and continue until the end of the incubation period. Four reliable ways of telling that Adélies are fasting are described. Both birds are together until the eggs are laid, and then the female goes off to sea (and not the male as supposed by previous workers) leaving the male incubating alone until she returns. Some males have sufficient body reserves for a first fast of at least six weeks, and females for over three weeks. The length of the male's first fast is known to be exceeded by only one other species of bird, the male Emperor Penguin. The loss of weight during these first fasts is about 40%. The female starts the season lighter than the male, and loses weight more rapidly during her shorter fast.

Care of young is divided into three stages: the *guard stage* when one of the parents is at the nest to care for and feed the chicks while the other is away collecting food; the *crèche stage*, when the chick is left alone at an age of about four weeks and groups with others to form crèches of 100 or more chicks, and, later, the *dispersal of the crèches*. Evidence is given from a study of marked adults and chicks, that parents feed their own chicks in the crèche, feeding others only under exceptional circumstances. There are no adult "guardians" of the crèches. These two facts are contrary to previous literature on species of penguins whose chicks group together in crèches. Three possible factors which contribute to crèche formation are discussed, predation by the Skua appearing to be the most important.

During the chicks' eighth week the *dispersal of the crèches* starts, chicks tending to lie in or near their old nest-sites, though bunching together when frightened. During their ninth week most of them start assembling along the coast and usually depart to sea independently of adults. There is no fasting period prior to departure. The *plumage* and *process of moult* are described, and the *increase in the weight* of the birds is given.

Breeding birds break off the normal routine if eggs or chicks are lost, and go to sea to feed. They usually return and re-occupy their nest-sites for a period of fasting, but do not lay eggs again. The second rise in population seen between the time of chick-hatching and crèche formation is due not only to the parents guarding and returning to feed their chicks, but also to the return of these *unsuccessful breeders*. This phase of the breeding season has therefore been called the "*re-occupation period*". In addition, there are the non-breeding wanderers endeavouring to stake a claim on territory. It is these unsuccessful breeders and non-breeders, which have been mistaken as "guardians" of the crèches.

The Adélie's habit of "*keeping company*" (i.e. the partnership of two birds of opposite sex at a nest-site which may, or may not, lead to the establishment of a mated pair) is believed to have survival value in facilitating the formation of new pair-bonds should the original mate of an experienced breeder fail to return, or return very late.

Roberts' (1940) "trial and error" theory of *sex recognition* is discussed and evidence given that it does not apply to Adélies.

Pair formation is discussed and defined, and some of the associated displays described. The importance of affinity of one bird for another is emphasised, and an example given from Richdale's (1951) work.

Most Adélies *moult* away from the rookeries among the pack ice. The yearlings moult first. Little is known about the *winter movements* of the Adélie, but the birds appear to stay in the pack ice and visit land in winter only when gales break up the fast ice and bring the pack close to the land.

When considering *mortality and predation*, it is suggested that more attention should be paid to the possible effect of age and breeding experience. The adult Adélie has no predator on land, but the Skua and Sheathbill attack eggs and chicks. The Skua appears to select the weakling or stupid chicks. But if a chick, even though starved and weak, puts up a bold front, it will not be overcome by a Skua. There were only ten breeding pairs of Skuas for a population of over 100,000 Adélies at Hope Bay. The fact that the Skua does not have unlimited supremacy over its prey might well be the most important factor in limiting the Skua population. The *Sheathbill* is a scavenger and does not kill Adélie chicks. Other less important enemies are the *Giant Petrel* and the *Dominican Gull*. The effect of predation by *man* and *sledge-dogs*, and some of the dangers to a penguin population that might result from indiscriminate killing are discussed. It is most important that dogs should be kept chained, as they kill for the sake of killing, and even apart from killing, the constant disturbance does untold harm to a breeding community.

Interference on land by inter-specific and intra-specific competition and by Elephant Seals may be responsible for a small mortality of eggs and chicks.

The only important predator at sea is the *Leopard Seal*. A study of available literature suggests that, like the Skua, the Seal's predation is selective, a healthy, alert and experienced Adélie being able to outmanoeuvre the seal in the water. The Leopard Seal takes a heavy toll of young when they enter the water.

The effect of *weather and ice conditions* on the mortality of eggs and chicks is discussed. The greatest danger to eggs and young chicks is burial of the nest and incubating bird under snow. Mortality figures for eggs and young chicks were between 80–90% for Hope Bay, 1948–9. The most exposed and windswept colonies were the most successful because they were comparatively free from snow.

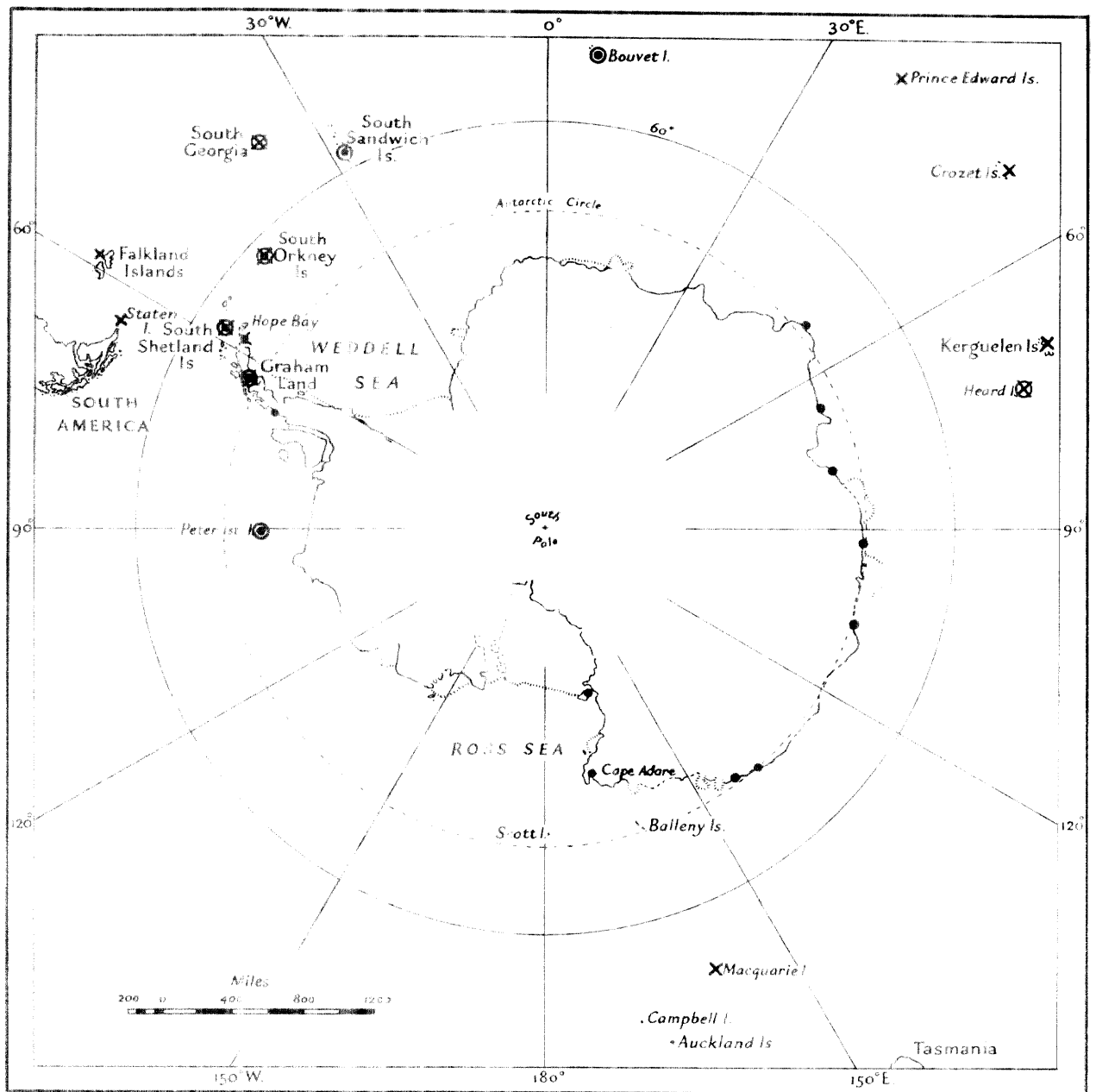
The last chapter provides evidence of the importance of *individual recognition* in an Adélie community. Undoubtedly the two birds of a pair recognise each other from the time they are paired before egg-laying up to the time when the chicks go into the crèche. Parents also recognise their chicks in the crèche, and established breeders appear to recognise each other when they return to the rookery, even after separation during the winter months. Territory brings both members of a pair, and parents feeding chicks, back to known ground. Several examples observed of marked pairs shifting their nest-sites and yet remaining together suggest, however, that individual recognition is a more important factor than territory. In the writer's opinion, *visual and auditory recognition* between adults, and parents and chicks, is the most important factor. In the chick, recognition is slowly acquired during the guard stage and fully developed by the time the chick goes into the crèche. The great variation in character, appearance, deportment, voice, etc., between one bird and another contributes much to this recognition. Finally, the function of the *mutual display* is discussed and evidence given in support of its being a true "*greeting ceremony*" and not an appeasement ceremony. It is also suggested that the mutual display serves as a confirmation, re-enforcement and "reassurance" of individual recognition.

Special attention is paid to *photographic illustration*. The Plates illustrate most aspects of the behaviour and breeding routine of the penguins. A ciné-film, *Life History of the Adélie Penguin* (see Film Bibliography) is also referred to in this report, as the writer believes that many of the actions described are better illustrated in motion. It is of particular value in illustrating the text on important and often controversial points such as departure of young, landing of adults in rough seas, predation by the Skua and Leopard Seal, and individual recognition of parents and chicks during the crèche stage.

INTRODUCTION

THERE are three Pygoscelid Penguins: the Adélie, *Pygoscelis adeliae* (Hombron & Jacquinot*), the Chinstrap, *P. antarctica* (Forster), and the Gentoo, *P. papua* (Forster). The Adélie is Antarctic and circumpolar in its distribution, but does not breed north of the South Sandwich Islands and Bouvet Island. It is the most abundant and widely distributed of all the Antarctic penguins. As a non-breeding straggler it has been recorded from South Georgia (Matthews, 1929), Heard Island (Law & Burstall, 1953) and Macquarie Island (Gwynne, 1953). The Chinstrap is also an abundant species, but has a much more restricted distribution, being confined to northern Graham Land and the outlying islands of South Shetlands, South Orkneys and South Sandwich and further east to Bouvet Island; it also breeds in small numbers in South Georgia, Peter 1st Island (Holgersen, 1945), and Heard Island (Law & Burstall, 1953) which are the northern limits of its range. The Gentoo, though never breeding in such vast numbers as the Adélie or Chinstrap, nevertheless has the widest distribution of all, and is circumpolar in the zone of the westerlies. Its southerly limit is on the west coast of Graham Land, and it breeds as far north as the Crozet Islands and the Falkland Islands. Map I shows the main breeding areas of the Pygoscelid Penguins.

* Falla (1937) and Roberts (1940) consider that the Adélie's bill and plumage characters warrant generic distinction from *Pygoscelis papua* which is the type species of *Pygoscelis*. They have therefore called the Adélie *Pucheranphus adeliae*. To be consistent, *Pygoscelis antarctica* should also be separated, for *P. antarctica* and *P. adeliae* are more closely related anatomically and behaviourally to each other than either is to *P. papua*. In fact, *P. papua* seems closer to *Megadyptes antipodes* the Yellow-eyed Penguin than to *P. adeliae* or to *P. antarctica*. For the present, therefore, I prefer to keep all three Pygoscelid Penguins in the same genus.

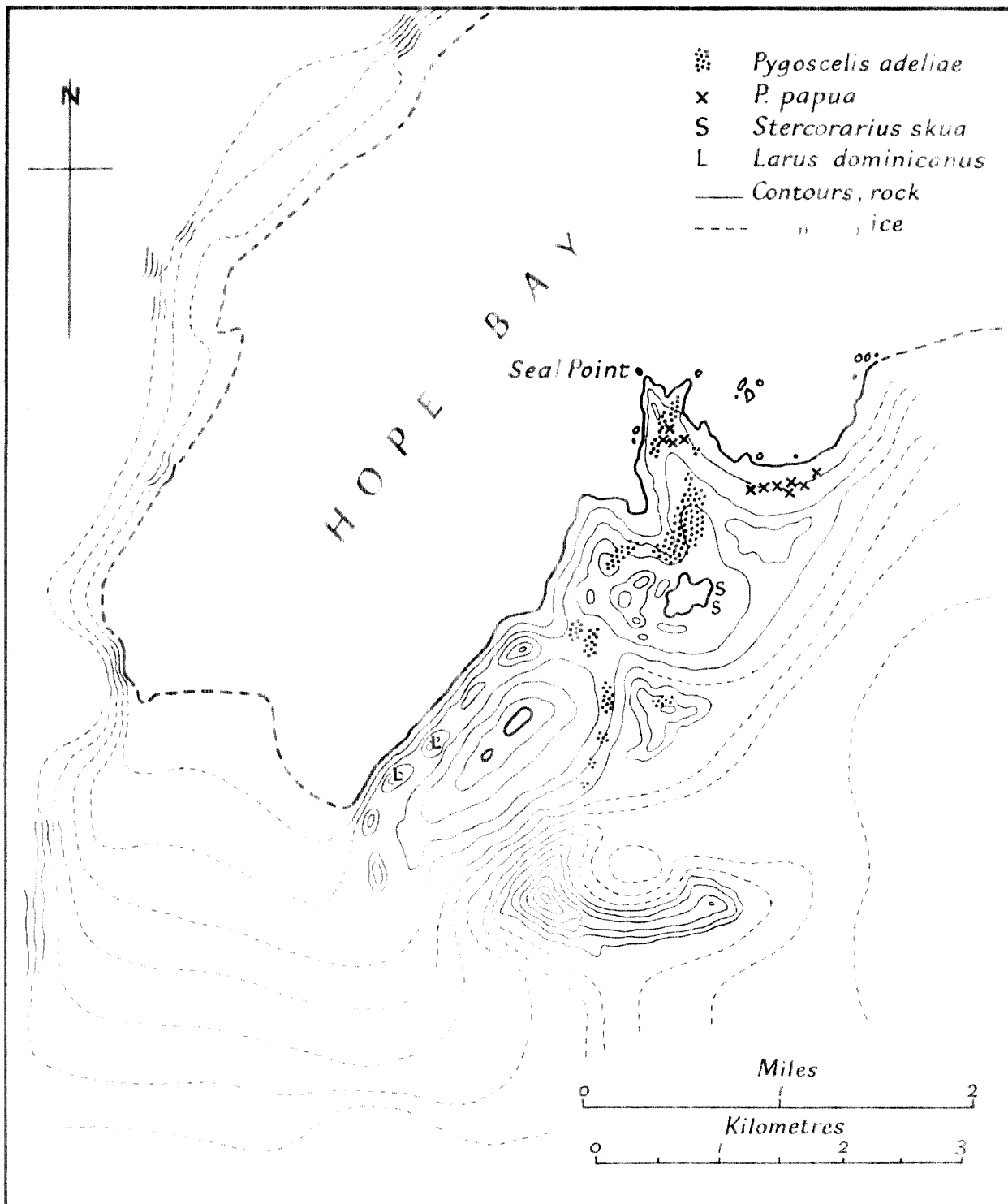


Distribution of the Pygoscelid Penguins

- Adélie Penguins ○ Chinstrap Penguins × Gentoo Penguins ● Adélie and Chinstrap
 ⊗ Gentoo and Chinstrap ✕ Adélie and Gentoo ⊞ Adélie, Chinstrap and Gentoo

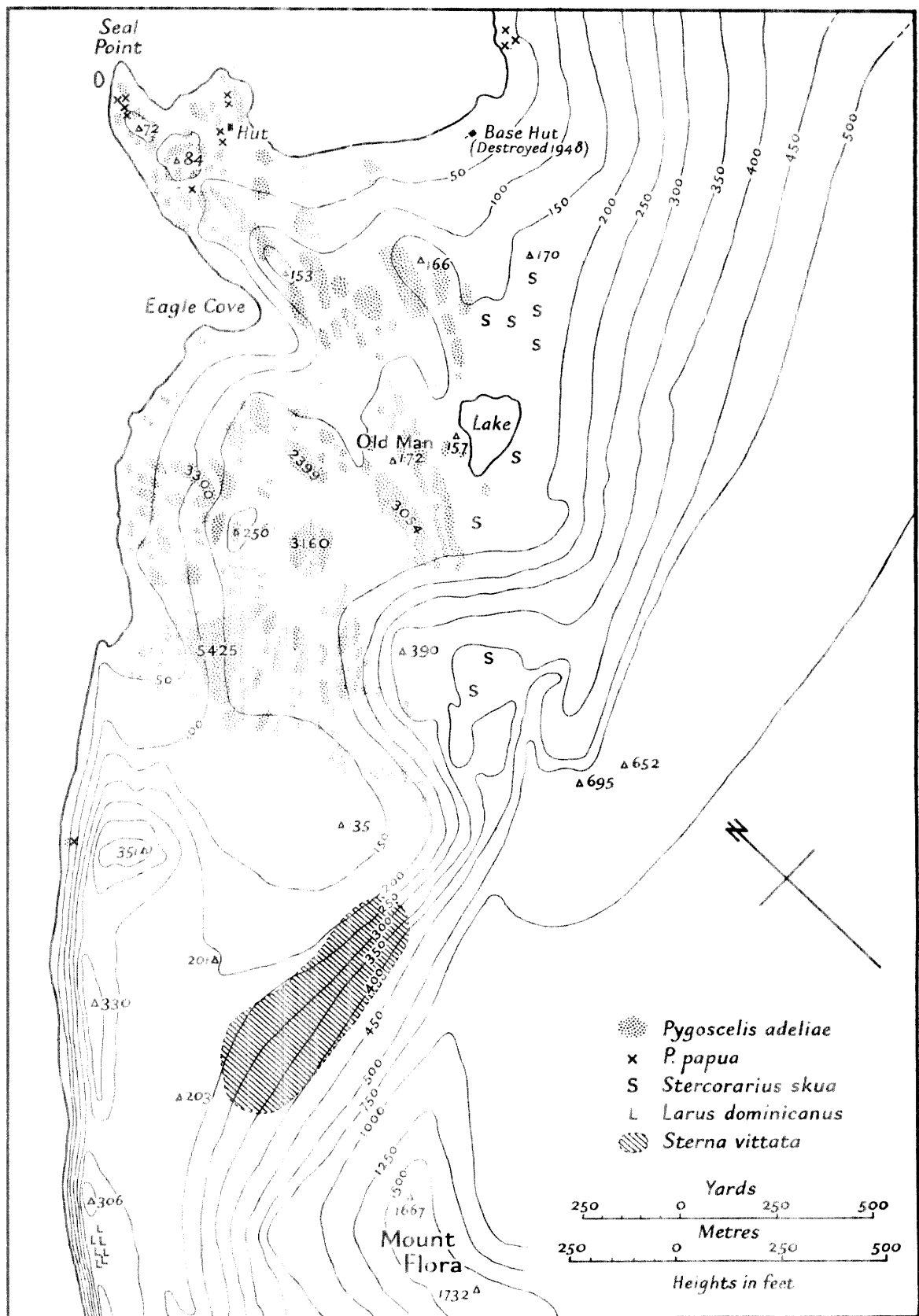
MAP 1. Breeding Distribution of the Pygoscelid Penguins

Note: only the better known breeding areas of the Adélie have been marked in around the Antarctic continent.



MAP II. The Hope Bay rookery —after Andersson (1905).

Note: The Skua is now classified as *Catharacta skua*.



MAP III. The Hope Bay rookery as surveyed by D. James and N. B. Marshall in December 1945, over forty years later.

Note: "Old Man" is not an accepted name. The Skua is now classified as *Catharacta skua*.

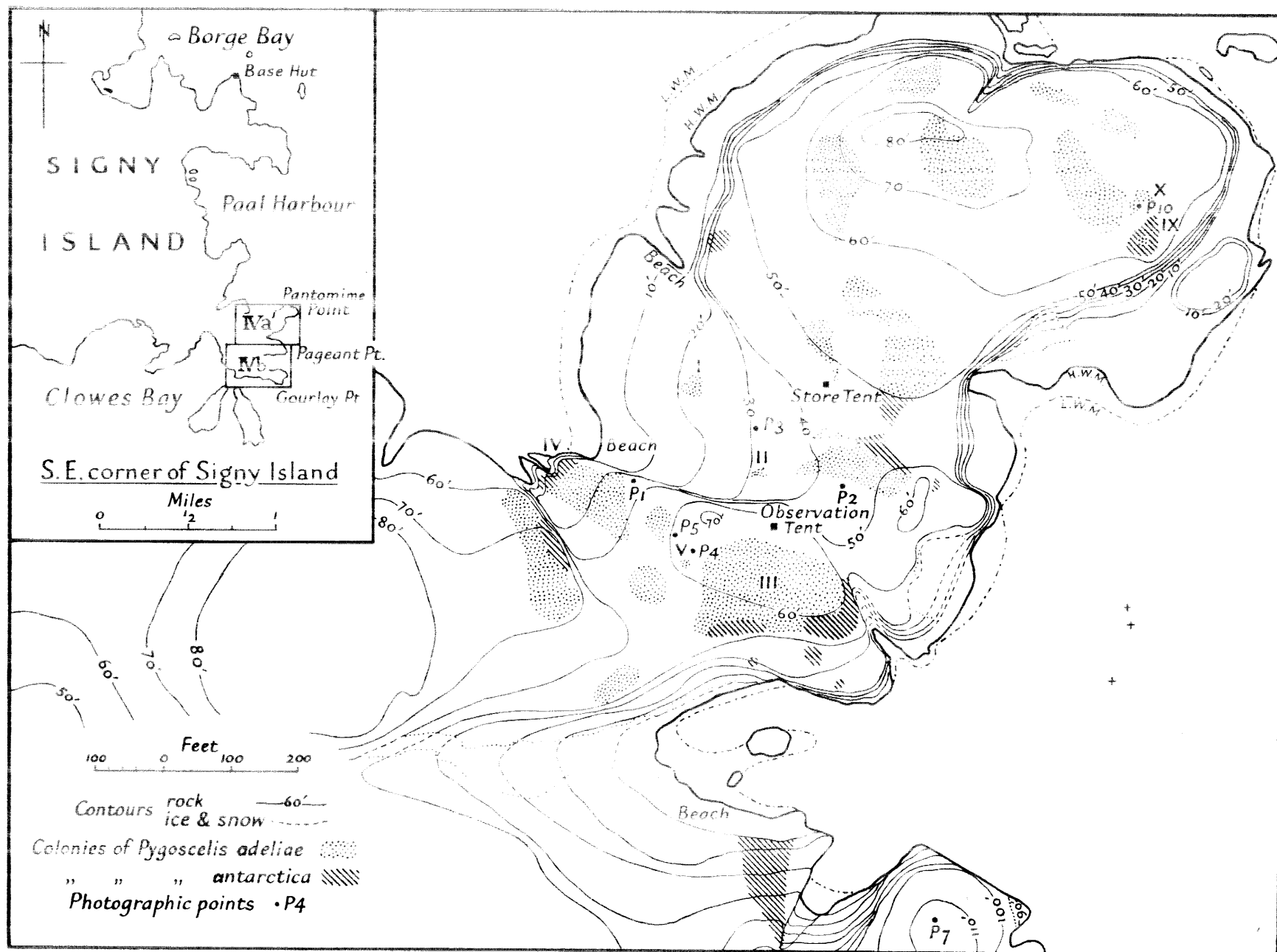
This study on the Pygoscelid Penguins was undertaken while the author was serving as medical officer and biologist with the Falkland Islands Dependencies Survey (F.I.D.S.) from 1947 to 1951. During this period over two years were spent at two F.I.D.S. Bases, Hope Bay and Signy Island, and a further fifteen months on board the expedition's ship R.R.S. *John Biscoe*, in Antarctic waters and between the Falkland Islands and Britain. The rookeries studied at Hope Bay, Graham Land, in 1948-9, consisted of about 100,000 Adélies and several hundred Gentoos (Map III). Ten pairs of Adélies had been ringed in this rookery two seasons before (see Andrew & Roberts, 1952) and it was possible to observe most of these for their third season as marked birds. In early November, 1948, one month after the Adélies had returned, the Base hut at Hope Bay was destroyed by fire during a blizzard. All field-notes and dissection-notes for October and photographic equipment (see p. 94) were lost. The abnormally heavy pack ice that season prevented the *John Biscoe* from reaching Hope Bay until her ninth attempt on February 4th, when all personnel were evacuated and the Base temporarily closed down. Unforeseen circumstances therefore made the first season's studies difficult and the original plan to spend two consecutive seasons at Hope Bay impossible. However, the period of waiting for the ship's arrival from November to February was devoted entirely to an intensive study of the Adélie Penguin.

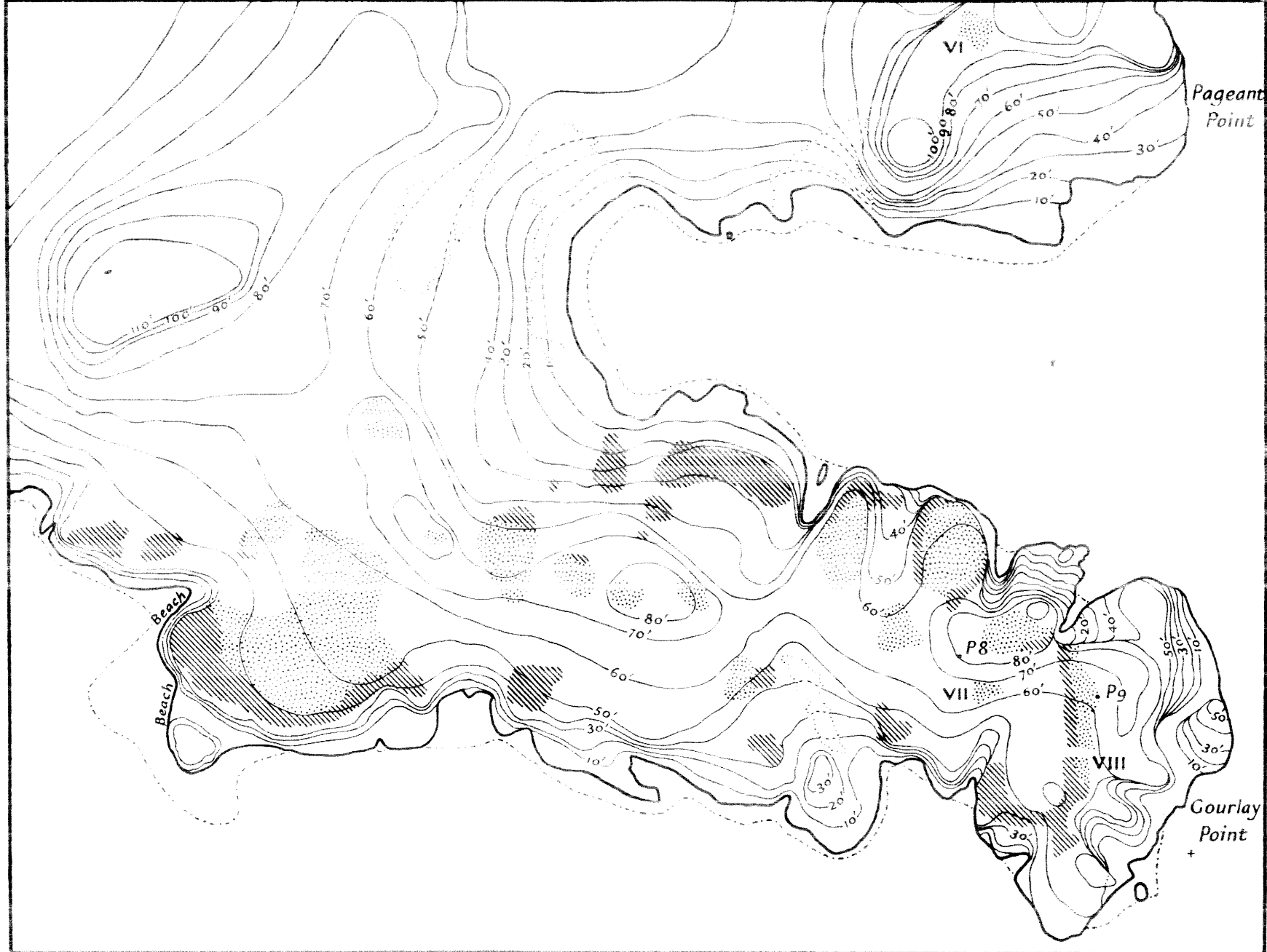
Permission was given by the Governor of the Falkland Islands to return to Britain to re-equip, and to carry out the second year's study, 1950-1, at Signy Island in the South Orkneys. At Gourlay Peninsula, Signy (Map IV), the rookery numbered about 20,000 Adélies and almost as many Chinstraps, and it was there that the ciné-film *Life History of the Adélie Penguin* (see Film Bibliography) was taken. As at Hope Bay, a number of penguins, this time Chinstraps, had been ringed two seasons before, and many were observed for their third season as marked birds.

Observation and laboratory tents (Plate 1a and b) were used at both rookeries throughout the breeding seasons. The former with sleeping-bag, food, heating and duplicate biological equipment were placed within a few yards of some of the ringed and painted birds. From these tents continuous observations could be made throughout day and night, and they also provided shelter during bad weather. Birds were dissected in the laboratory tents and stored until they could be sledged back to Base for dog-food, for if left outside without adequate cover they were devoured by Skuas within a few hours.

It was realised that the ideal way to study the birds was to live among them. Though the observation tents provided full facilities for this, medical and other duties at Base often demanded a compromise, but daily or twice daily visits to the rookery were maintained at Hope Bay from the beginning of October, 1948, until the Base was evacuated in February. At Signy Island, where travelling in bad weather to the rookery 2½ miles away sometimes took two hours, every opportunity was taken to spend a few consecutive days at the observation tent; contact was then kept with Base by radio. Otherwise, visits were made daily from October 13th, 1950, until the peak of egg-laying had passed, and then every other day, or at least every three days, until the first week in April, 1951. The sea ice remained firm until November 7th, but thereafter an overland route had to be taken. A Nansen sledge with plastic runners pulled by five dogs was the best means of transport when there was plenty of snow, but later, when patches of rock were exposed, it was necessary to use a Greenland sledge (Plate 1c) which had metal runners. Dogs were used as much as possible; the exercise kept them fit, and they collected food at the rookery from dissected birds. Occasionally, when the sea was calm enough, a small dinghy with outboard motor could be used at Signy Island for transporting heavy and delicate equipment, such as the sound recorder and ciné-camera, from Base to the observation tent.

By maintaining a number of permanently occupied Bases since 1944, F.I.D.S. has provided opportunities for continuity of work which until recently have been unique in the history of Antarctic exploration (Wordie, 1946 and Fuchs, 1951 & 1953). However, the routine chores of cooking, cleaning the hut and feeding the sledge-dogs, have to be shared by all members of a F.I.D.S. Base, and field work is therefore planned accordingly. Moreover, the expedition ship visits the Bases at the peak of the breeding season which means that there is a danger of a break in the continuity of observations while stores are off-loaded and sorted. Every effort was made to overcome these difficulties, and the writer is much indebted to his companions at Hope Bay and Signy Island for the many ways in which they helped to relieve him of duties at Base during these periods.





MAP IVa and b. The Gourlay Peninsula penguin rookery as surveyed by J. J. Cheal, 1951.

Notes: The snow and ice coverage were diminishing during the period of the survey, and the map does not show the amount of coverage at any one time. The areas on Pantomime Point were plotted on January 19th, 1951, those around Pageant Point on February 5th and the remainder on March 11th. The coastline shown is the high tide mark, low tide being indicated by a pecked line. Some of the more important Adélie colonies are marked in on the map in Roman numerals.

PART I. METHODS OF STUDY

A. MARKING PENGUINS

1. *The importance of Marking Birds*

THE word "marking" here covers any artificial method used for distinguishing individual birds. Marking may be temporary (e.g. painting) or semi-permanent (e.g. metal rings with reference numbers). The importance of studying marked birds cannot be emphasised too much, as the indisputable evidence so gained can help to solve many long-standing ornithological problems. Work on the Song-Sparrow (Nice, 1937) and the Robin (Burkitt, 1924-6, and Lack, 1943) provided ornithologists with examples that have since become classic, yet how few have followed their methods. Richdale (1951) who has studied marked Yellow-eyed Penguins, *Megadyptes antipodes*, for ten* consecutive seasons, in addition to Petrels and Albatrosses, strongly emphasises the need for studying marked birds. My own experience with Pygoscelid Penguins, originally inspired by the methods used by Lack (1943) and Lockley (1942), supports these views wholeheartedly. I would emphasise further three special points which apply particularly to long-lived birds:

i. The importance of mastering methods and technique from the beginning of the study. As the worker discovers more about the bird and its habits, he will find some way of overcoming the difficulties he encounters. For example, wild geese can be driven to tops of hills when moulting, or caught by rocket-nets in winter (Scott, 1952, p. 20); Spotted Flycatchers can be baited with cobwebs (Campbell, quoted by Lockley & Russell, 1953, p. 106); and Tawny Owls can be observed at night by using a red light (H. N. Southern, personal communication). There is probably no species of bird, no matter how shy or difficult to study, that cannot be marked and recaptured in some way without undue disturbance.

ii. The importance of studying a large sample so that allowance can be made for individual variation (p. 25).

iii. The importance of devoting much of the work to birds of known age, i.e. those that have been ringed as youngsters, especially as age groups play an important part in behaviour (p. 25).

Pygoscelid Penguins of known age could not be studied during the course of my work at Hope Bay and Signy Island, as insufficient young had been ringed in previous years. In both study areas, the few Adélies and Chinstraps ringed two seasons earlier (1946-7 and 1948-9) as breeding birds were recaptured and observed through a third season as marked birds. In 1951, several hundred young Adélies and Chinstraps were ringed at Signy Island (Sladen, MSa), and since 1953 the regular ringing and web-marking of young each year at certain F.I.D.S. bases has been encouraged so that a population of penguins of known age is being made available for future work (Sladen, MSb).

A single period of study for the Antarctic worker is limited to two consecutive years, so at the start of this work in 1948 as many methods as possible for catching and marking the Pygoscelid Penguins were tried on a large sample of birds. Penguins under close observation were marked with numbered aluminium rings, and identification from a distance facilitated by use of paint marks and coloured temporary rings.

2. *Paint Marks*

Levick (1915, p. 61) marked the breast plumage of some of his Adélie Penguins with red paint, renewing it as it faded. Bagshawe (1938, p. 186) working on Gentoo and Chinstrap Penguins, used Indian ink applied with a brush on a long bamboo, but this was not easy for the ink froze rapidly despite elaborate precautions. Roberts (1940, p. 201) marked his Gentoos by painting different combinations of colour on their breasts. Sapin-Jaloustre (1951, p. 66 and personal communication) painted large letters on the backs of Adélies. Richdale (1951, p. 47-54) relied entirely on tarsus-rings and web-marking.

The quick drying matt-cellulose paint† used in 1948-51, was specially prepared for aircraft identification

* Now 18 years (personal communication).

† Supplied by I.C.I. Paints Division, Slough, Bucks.

marks at low temperatures. The first attempts at painting Adélies at Hope Bay in 1948 were not as successful as was expected because various patterns on their breasts and backs were too often obliterated by guano during a thaw, or by male tread marks on the backs of females during copulation. Even partial obliteration made them unreliable. It was then discovered that the outer surface of the flippers, where the feathers were dense, short and rarely dirty, was the best place to paint. Two-figure reference numbers about $1\frac{1}{2}$ inches high painted here (Plate IIa) could be read after the birds had been at sea for ten to fourteen days, and then repainted if necessary. Yellow proved to be the most conspicuous and durable colour, but it would flake off unless applied to a dry surface.

Crude daubs covering about half a flipper were put on 1224 non-ringed birds for various investigations. In many cases these lasted throughout the breeding season despite many visits to sea.

3. Rings

Gain (1913, p. 478 and 1914, p. 38) was the first to ring penguins. In January 1909, he put fifty violet celluloid rings on the legs of adult Adélies and seventy-five yellow rings on young. In the following breeding

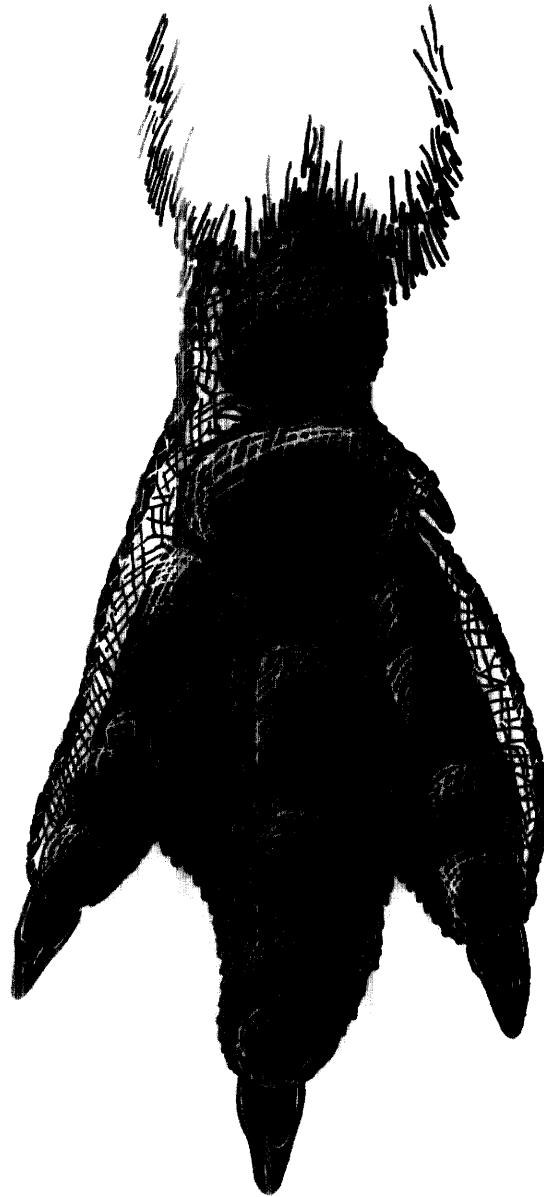


FIGURE 1. The lower portion of the leg (covered by feathers), the tarsus, and the foot of an Adélie Penguin viewed from lower (ventral) surface.

season, eleven adults were observed in November at the rock where they were originally ringed and some were again seen by whalers in November and December 1910. None of the young were recovered.

There are three places where penguins can be ringed:

- a. Round the tarsus. Much of the penguin's weight is taken on this short thick bone (Figure 1), and the undersurface frequently touches the ground.
- b. Round the leg covered with short feathers, just above the tarsus (Figure 1).
- c. Round the flipper where it joins the trunk (Plate II).

i. Temporary Coloured Rings

Celluloid flatband rings were supplied in six colours, 10 mm. wide and 22 mm. diameter. They were not a success when placed round the tarsus or leg. On the tarsus they often caused injury, and on the leg they were difficult to see. Sometimes they proved useful on flippers, where they were conspicuous and caused no injury, but they were often lost at sea, though the Chinstraps retained them better than the Adélies. Coloured celluloid rings were therefore used only on flippers and only in the following cases: for fasting adults at the beginning of the season (chiefly Adélies) or during the moult; as a quick method for marking a bird when the weather did not permit painting or when metal rings were not available, and for the larger chicks.

Painted aluminium overlap rings were coloured with numbers or various combinations of cellulose paints and a key was kept in the field note-book. They were placed round the flipper (Plate IIa) in the hope that they would be more durable than the celluloid rings or paint marks, but they were not a success. Most of them were still in position at the end of the season, but the colours soon wore off at sea. Some of these sample overlap rings survived for two years.

ii. Semi-permanent Aluminium Rings

In October 1944, a number of strips of aluminium alloy sheet, $4 \times \frac{1}{2}$ inch, with a set of number punches were sent to three F.I.D.S. bases for marking penguins. They were to be bent in a circle and fastened with a clip (Figure 2).

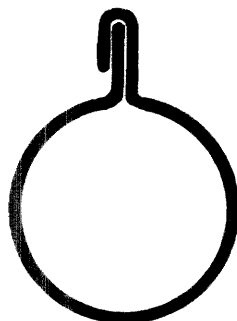


FIGURE 2. Aluminium ring bent in a circle and fastened with a clip.

The first batch of these was used on fifty young Gentoo Penguins in February 1945 at Port Lockroy, Graham Land (Lockley, MS). These appear to have been the first penguins marked with metal rings in the Antarctic. They bore a reference number but no address. Five years later I recaptured one of these birds at the same Gentoo colony. The ring, which had been placed on the feathered leg, was in good condition and the number "47" read fairly easily. Between November 1946 and January 1948, 477 Adélies were ringed, first at Hope Bay (Andrew & Roberts, 1952) and later at Red Rock Ridge, Marguerite Bay (Stonehouse, MS). Two hundred of the Red Rock Ridge Adélies were ringed with Monel metal strips supplied by the Ronne Antarctic Research Expedition. Observations were made on both these colonies in subsequent seasons (pages 49 and 71).

At Hope Bay in 1948, I used $12 \times \frac{1}{2}$ inch strips of aluminium alloy which were cut and hand-stamped with five-figure reference numbers and the words INFORM F.I.D.S. COLONIAL OFFICE, LONDON in letters

$\frac{1}{8}$ inch high. At Signy Island in 1950, pre-cut and stamped strips $4\frac{1}{2} \times \frac{1}{2}$ inch were used, the numbers and letters being the same size as before.

Tarsus-rings with clips (Figure 2) were tried first as they had been used successfully on the Yellow-eyed Penguin, *Megadyptes antipodes* (Richdale, 1948, p. 107 and personal communications). Two difficulties soon became apparent. The inscriptions became abraded on the rocks, and in spite of the greatest care in fitting the rings, some birds were seen limping after several days. Closer examination revealed abrasions on the tarsal tuberosities as a result of chafing and weight-bearing. The rings were therefore transferred to the leg. Richdale (1951a, p. 49) stresses the importance of choosing the correct width for tarsus rings; if too wide they cut into the tarsus, if too narrow the rings are weakened and their life shortened. Richdale was able to check his rings and renewed them at 2-4 year intervals. Even if the F.I.D.S. rings had been slightly narrower, abrasion on the rocks would still have occurred. Tarsus-rings on Pygoscelid Penguins breeding in the Antarctic are therefore unsuitable, though this may not be so with the Falkland Island Gentoos which breed on heathland.

Leg-rings did not cause injury if put on carefully. The ring with a clip was fitted to move freely up and down the lower part of the leg among the feathers, yet never loose enough to allow it to descend over the ankle joint to the tarsus. Most of the F.I.D.S. rings used in 1945 and 1946 were placed round the leg and later recoveries showed that they were not damaged on the rocks. Two leg rings (Nos. 1011 and 1019) out of a total of twenty placed on Adélies in 1946 by Dr. J. D. Andrew, were recovered in seemingly good condition on these birds six years later (see Tables XII and XIII). However, they had the disadvantage of being nearly always hidden by the feathers, the birds having to be caught before they could be shown to be with or without a ring. When a large number of birds was concerned, a task such as this was too great, besides being disturbing to the birds. Moreover, birds ringed as nestlings and returning to a different colony would be completely lost in a crowd of many thousands of unringed penguins.

Flipper-rings (Sladen, 1952) carefully used may ultimately prove superior in every respect. Marked birds could be picked out immediately and ring reference numbers read through binoculars without disturbance. Coloured celluloid flipper-rings were used during the 1948-9 season, but it was not until June 1949 that metal flipper-rings were tried. These proved successful on a party of Gentoos sent back to the London Zoological Society. In December 1949 the first wild birds were marked by this method in the Falkland Islands. Two years later, one of these, a breeding Gentoo, was recovered in the same colony with the ring still in good condition. Four different methods for fixing these rings were tried (Figure 3). Method 4 (Figure 3), with the clip folded on the inside (medial aspect) of the flipper, soon proved to be the most satisfactory and most of the 579 metal flipper-rings used were put on in this way. Many were closely observed throughout the breeding season, and showed no signs of wear. Only slight rubbing of the short tough feathers on the thin anterior edge of the flipper was observed. Method 3 (Figure 3), with the clip pointing downwards, was abandoned as soon as it was discovered that the clip damaged the feathers in the axilla.

The longest survival of a flipper-ring so far recorded is three years* on an adult Gentoo which the writer ringed at Port Lockroy in January 1950. The ring was still in good condition when recovered. Perhaps more significant is the recovery of eight Chinstraps ringed as nestlings in February 1951 and found with rings in good condition two years later near the place of their birth. Expéditions Polaires Françaises experimented with this method in 1951 (Sapin-Jaloustre & Bourlière, 1951, p. 66) during their study of the Adélie Penguin in Adélie Land, and they also appear to have had favourable results.†

The permanency of F.I.D.S. offers facilities for continuity of observation and in 1953 the writer designed a new ring for use by that organisation. The original design has been improved by larger-sized numbers $\frac{1}{4}$ inch high, which in moderately good light can be seen through X8 binoculars from about sixty feet. The rings bear a new inscription, INFORMED.S. BRITISH MUSEUM NAT. HIST. LONDON. They are 99% pure aluminium, 18 S.W.G. and of soft temper. The edges have been treated to ensure smoothness and the inscription stamped with a heavy press to give adequate depth of imprint. Strips pack better than shaped

* Now seven years. (See Sladen, W. J. L. & Tickell, W. L. N. 1958, Antarctic bird-banding by the Falkland Islands Dependencies Survey, 1945-57, *Bird-Banding*, 29, 1-26).

† Since this manuscript was submitted for publication, the Australian National Antarctic Research Expeditions have reported on their trials of flipper-rings on Rockhopper and Macaroni Penguins in 1953 at Heard Island (Downes & Gwynn, 1955). They encountered some difficulties. Penguin ringing up to the time of going to press is well reviewed by Austin, (Austin, O. I. 1957, *Bird-Banding*, 28, 1-26) and further discussed by Sladen and Tickell (1958), *Bird-Banding*, 29, 1-26.

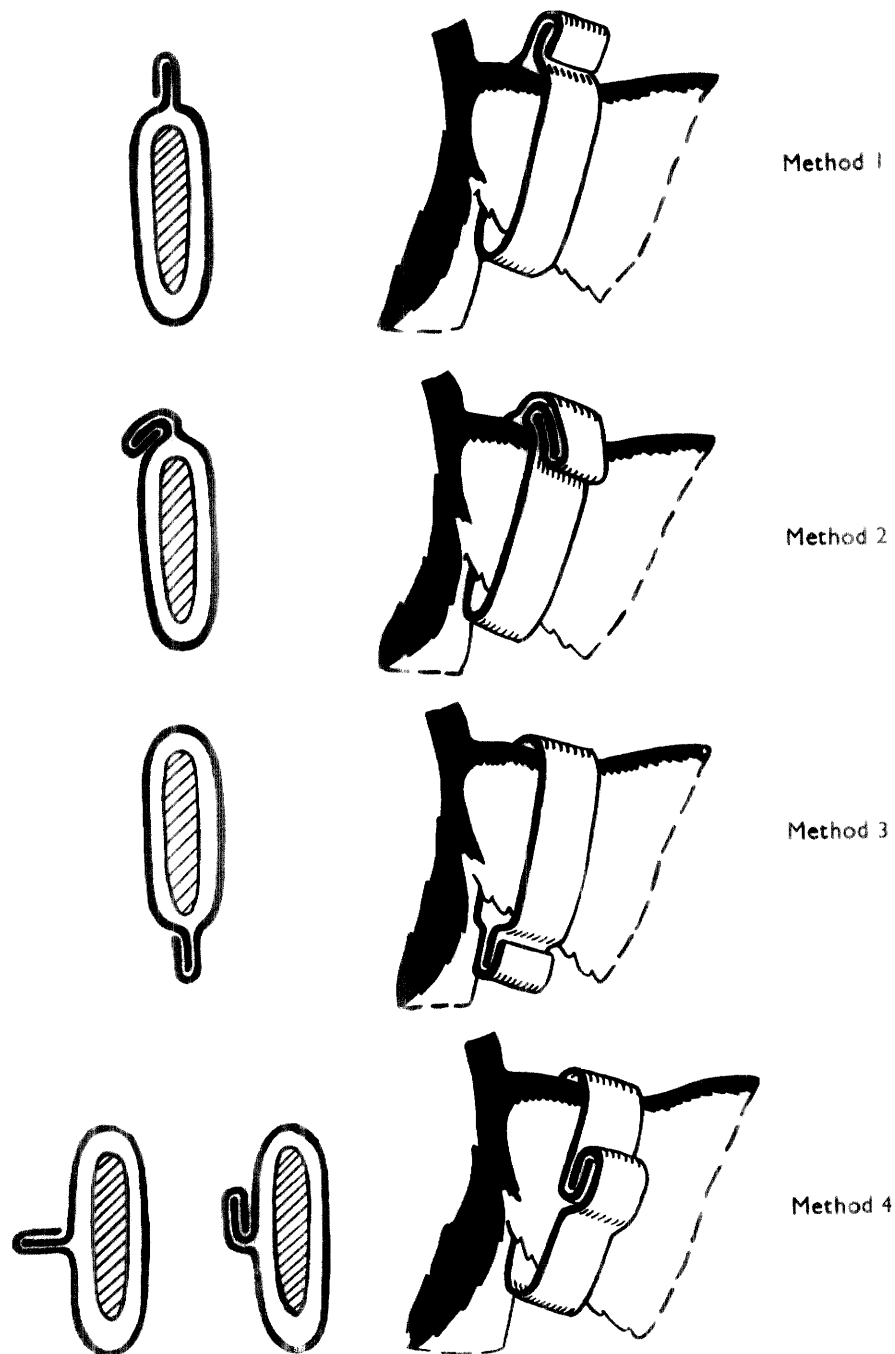


FIGURE 3. Methods tried for semi-permanent aluminium flipper-rings on the Pygoscelid Penguins. Method 4 proved to be the most satisfactory. Method 3 should *never* be used.

rings and are sent in bundles of 100, divided into groups of ten, and in numerical order. The first shaping (Figure 4), which is also the same for leg-rings, is best done with pliers. The size of clip can be varied a little according to the species and sex. The joint must be a good one, but great care must be taken to prevent distortion when it is finished off, by gently inserting the blade of a thin blunt-nosed plier between the flipper and the ring. When the ring is finally in position on the left flipper as described in method 4 (Figure 3), the number can be read the right way up when the bird is standing and the flipper at rest by its side (Figure 5). The lettering INFORM F.I.D.S., etc., will be behind the number, thus safeguarded from abrasion when swimming.

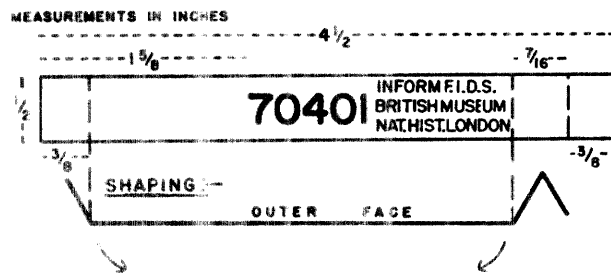


FIGURE 4. Addressed aluminum strip and the first shaping for the flipper-ring.

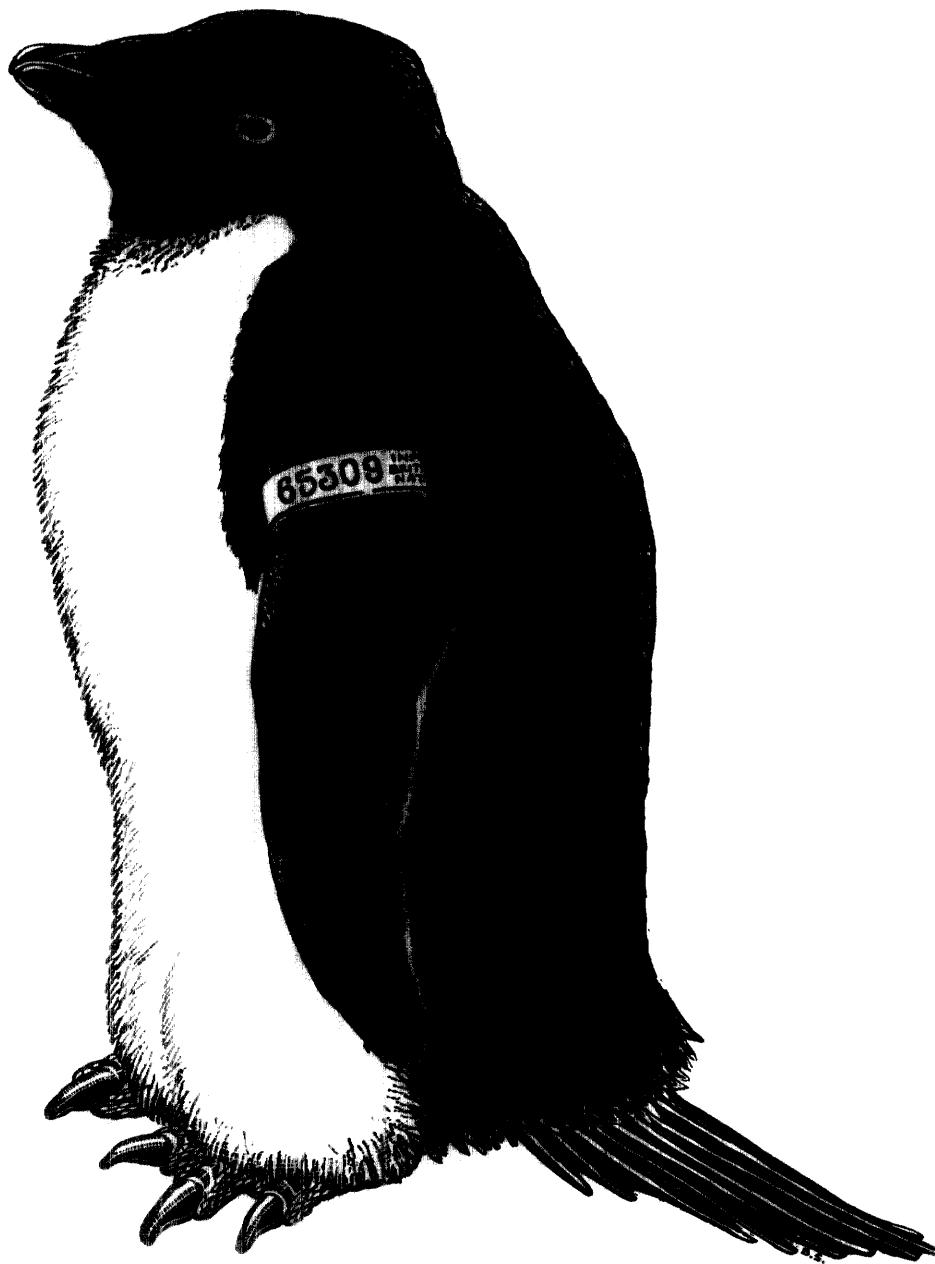


FIGURE 5. Flipper-ring in position on an Adélie Penguin. The reference numbers are 1/4 inch high and easily read through binoculars.

The penguin must have full power of its flippers to escape from its enemies in the water, and any diminution of efficiency might reduce its chances of survival. The metal must be bent smoothly and allowance made for the moult when the flipper almost doubles its thickness. If too tight, the bird may be seriously affected, because an important swimming muscle and tendon pass close to the posterior bend of the ring. If too loose, it may slip off or impede the flipper joints (Plate IIc). Putting on flipper-rings is not a simple process and requires practice, skill and patience.

Recoveries in successive seasons should be interpreted with caution until comparison has been made with the longer established leg-rings. Until this has been thoroughly tested, flipper-rings should not be used universally. It is still necessary to test the relative reliability of flipper-rings and leg rings, and this could be carried out by marking forty to fifty breeding birds with leg-rings only, and the same number of breeding birds with flipper-rings as well as leg-rings. The two groups should be in the same colony, each group being selected to contain the same number of peripheral and centrally placed nests (Figure 6).

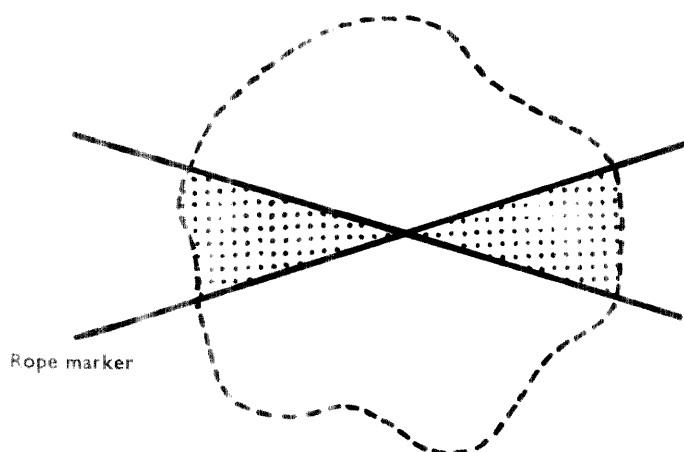


FIGURE 6. Method of dividing a colony with rope marker to test flipper versus leg-rings.

4. Other Methods of Marking Penguins

Web-marking was not used, but work on the Yellow-eyed Penguin (Richdale, 1951a, p. 51) indicates that this is an excellent and simple method. With the Pygoscelid Penguins it should be tried with care at first, as it is possible that their feet are more vascularised than the New Zealand species.

Web-marking is especially suitable for nestlings. The use of a different combination of marks for each season would enable a population of known age to be built up for future study (Sladen, MSb). When recovered again after their migrations these birds should be marked with metal rings.

String for young chicks. Paint was not reliable on down, especially during a thaw when chicks became matted with guano, nor did it last for long under such conditions when painted on the feet and bills. Moreover, coloured celluloid flipper-rings (p. 14) could not be used on chicks until they were about two weeks old. Until then, string was tied loosely round the flippers in place of the rings. They were watched and often handled from day to day, so there was no danger from injury as a result of growth.

4. Other Methods of Marking Penguins

The first consideration must be for the birds, particular care being taken to avoid carelessness that might result in future suffering. It is also essential to disturb the birds as little as possible both when marking them and during subsequent observations. Penguins are not, as one might imagine, easy birds to catch and mark. They are pugnacious and often resist with the utmost vigour, inflicting powerful blows with their flippers and bills. Species differ in their behaviour: Adélies, contrary to Murphy's (1936, p. 408) statement, are boldest, Gentoos shyest and Chinstraps intermediate. Individuals vary greatly in different situations and at different periods in the season. They are shyest at the beginning when attachment to their territories is not reinforced by eggs or young, boldest when defending eggs or young chicks. During incubation, they desert more readily towards the end of a fasting period than at the beginning.

In the Antarctic, one is also confronted with additional difficulties due to the constantly changing and frequently adverse weather.

Time of season and methods of catching. The best way to catch a large number of adults or nestlings is for several people to drive them into a temporary corral of netting, corrugated iron or stones, about three feet high, and about fifteen yards from the colony. With breeding adults this method should be used only before the eggs are laid. On a subsequent visit during egg-laying, the birds can be recaptured one by one at their nests and the ring numbers and other details recorded for specific pairs. Corrals should be removed after use, because they may encourage snow drifts and thus affect the nest-sites. Nestlings should not be ringed until nearly free from down and then only if well nourished. Rings are wasted on weaklings as these birds are likely to be killed by Skuas or Leopard Seals (p. 69).

Disturbance. A penguin should not be ringed at its nest, but rather carried fifteen yards away. This will allow the other birds to settle down, and, equally important, provide enough distance for an initial dash of the ringed bird after release. A bird so treated will pull itself together and finally walk up to its nest as though nothing had happened.

Methods of holding Pygoscelid Penguins. Small penguins should not be held by the body as struggling may result in internal injuries, especially with females at the time of egg-laying. To catch them, they should be grasped by the neck, and they should be carried upside down by the legs, not by the tarsi. When transferring the bird from upright to upside down, the legs should be grasped firmly by one hand and swung up while the other hand continues holding the neck. This avoids strain on the ankle joint. When ringing or painting, the ringer should stand upright and place the head of the penguin gently between his knees with the bird's back facing forwards. In such a position the bird rarely struggles and the flippers and legs are easily accessible even when doing the job single-handed.

Danger to eggs and young from predators. It must be remembered that eggs and even young chicks, left unguarded in a nest while the parent is being ringed, may be destroyed by Skuas and Sheathbills (p. 66). Nest contents should therefore be placed in the pocket, or a suitable container, and replaced just before the bird is released.

Table I summarises the number of penguins marked during the period of study. The discrepancy between totals of semi-permanent rings used and numbers of birds ringed is due to the fact that some of the birds had two kinds of rings. Most of the breeding birds under close observation also had numbers painted on their flippers.

B. MARKING COLONIES AND NEST-SITES

F.I.D.S. provides opportunities for continuity of study, but personnel continually change. In these circumstances the marking of colonies and nest-sites is an essential adjunct to ringing. The markings need to be as durable as possible and to be accurately recorded, so that someone entirely new to the area can find them in later seasons.

Bagshawe (1938, p. 186) marked numbers in enamel paint on stones and placed them by nests. Many were obliterated by guano. Wooden pegs used by Stonehouse (MS) to mark ten nests occupied by ringed Adélies were unsatisfactory as all but two had been removed by wind or nest-building birds when visited eleven months later.

The following methods were used at Hope Bay in November 1946 for marking the nests of ten pairs of ringed Adélies (Andrew & Roberts, 1952). Arrows were painted on prominent rocks nearby, indicating the position of the nests. Paint crosses were also made on, or beside, the nest itself. These were renewed each year because they were abraded by snow and drift and often obliterated by guano. Each nest and its distinctive features were photographed, and the actual position indicated again by a prominent marker (e.g. a glove) in the photograph. A plan of all the nests was drawn up giving compass bearings and distances from a central rock pillar close by, together with a descriptive note of each nest and its surroundings.

Most of Andrew's methods were used during 1948-51, with the following additions resulting from the first year's experience at Hope Bay. A large-scale map (see p. 22) was made showing individual colonies. Colonies of interest for follow-up work were marked on the map in Roman numbers (Map IV), and were identified in the field by numbers painted on one side of one or more of the most conspicuous rocks

(see Plate IIIa and b). Reference numbers of individual nests were also painted on the sides of rocks adjoining the nests. The choice of a vertical, and preferably leeward, surface, was important as it minimised obliteration by guano and penguin feet, and afforded protection to the numbers from abrasion by drift. Plate IIIb shows the paint mark of Colony VI at Hope Bay after four years. It was still as good as new. An improvement on this method would be to chip out numbers on the rock before painting them.

Photographs (p. 94) can be used to fix the positions of quite a number of nests in a comparatively featureless colony.

C. DISSECTION AND SKINNING

1. *Importance of Dissection for Sexing Penguins*

Distinguishing the sexes of birds, especially colonial birds, that show no external dimorphism remains a difficult problem. With existing techniques, dissection is the only infallible method of determining sex, and is therefore essential during the initial stages of a life history study in a place such as the Antarctic where field work cannot be carried out by one person for more than two or three consecutive years. Other methods of sexing Adélie Penguins are given on page 23.

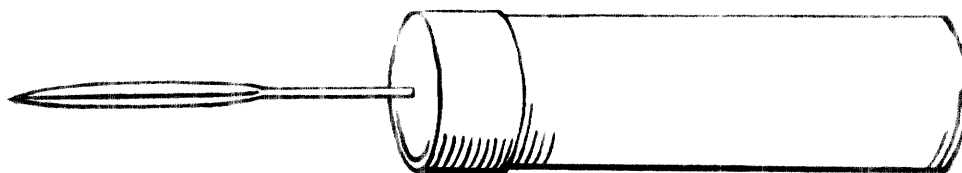


FIGURE 7. Awl used for humane method of killing penguins. The wooden handle is the correct shape for bending the leg-rings.

2. *Data Collected from Dissections*

Fortunately ethics did not have to be considered as penguins formed an essential part of the sledge-dog's diet and provided the best supply of fresh meat for the expedition personnel. The killing was properly controlled so that there was no danger of seriously depleting the population of over 100,000 birds at Hope Bay, or of nearly half that number at Signy. As penguins had to be killed, the work resolved itself into the problem of how to get the maximum amount of biological data from them. At Hope Bay almost every penguin killed was dissected before being fed to the dogs, and at Signy approximately 80% were dissected. All birds collected were sexed and/or weighed. Some were skinned for museum specimens (p. 92). A large proportion were carefully dissected and the following records kept: cloacal temperature; measurements of soft parts, tails, etc.; weight of intestines, liver, heart, and stomach contents; thickness of blubber; a series of gonad measurements; notes on colour and state of plumage, soft parts, iris, incubation area, etc. Finally, various parts of the anatomy, especially gonads, thyroids, internal organs, stomach stones, tarsi and feet, and skulls, were preserved for future macroscopic and microscopic study. Most of the material for microscopic study was preserved in Bouin's solution.

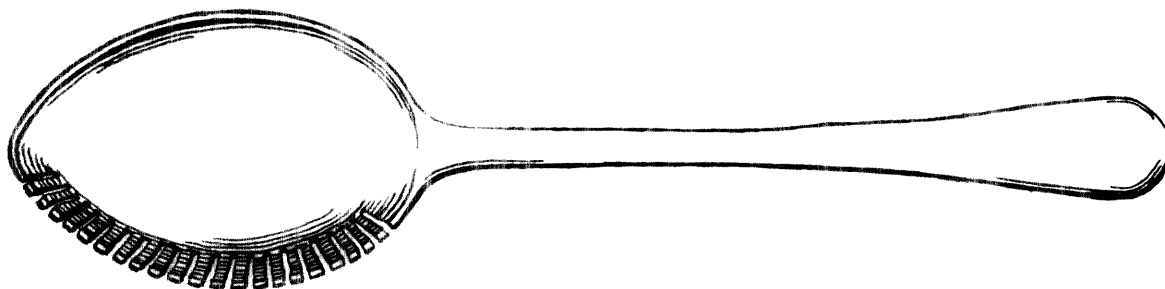


FIGURE 8. Scraping spoon for removing blubber from a penguin skin.

The most humane method of killing was to destroy the brain by a quick thrust and twist of an awl (Figure 7) through the foramen magnum when the head was flexed on the neck. The circumference of the awl handle was the correct size for shaping leg-rings (p. 15), and a rubber bung shielded the point in the pocket. Methods of skinning and preserving are given in the Appendix B (p. 92).

D. PHOTOGRAPHY

Special attention was paid to photographic equipment and technique before leaving the country in 1947, but the fire at Hope Bay in November 1948 destroyed all but one miniature camera, together with all motion and still film taken of the Adélie and Gentoo. One of the chief reasons for returning to the Antarctic in 1949 was, therefore, to repeat this photographic work. At Signy, a detailed record of the life history and breeding behaviour of the Adélie was made in colour. The most characteristic behaviour patterns of the Chinstrap were also filmed, but work on the Gentoo could not be repeated.

The Pygoscelid Penguins proved good subjects for photography, though bad weather, low temperatures and the delay in processing colour film presented a number of technical difficulties.

1. *Ciné-photography*

Ciné-film provides a permanent record of movements and behaviour sequences of large numbers of individuals which can be examined repeatedly at leisure on an animated viewer, and though it can never replace field observations, it can provide valuable confirmation on controversial points. Moreover, a slow panoramic view of a colony taken at regular intervals throughout the breeding season, in successive years, from a fixed photographic point could provide permanent data on seasonal and yearly variations in population, more effectively than a series of still photographs. Populations can be estimated fairly accurately from such a film when examined through an animated viewer.

Furthermore, the technical methods of catching, holding, painting and ringing penguins (described on p. 19) are more easily understood when seen in a film than when read in a scientific report.

For the above reasons the writer feels that motion pictures are an invaluable part of field work, and should be considered as important as still photography and drawings for illustrating published work. Some of the limitations still to be overcome in using the ciné-camera in the Antarctic are given in Appendix C (p. 93).

2. *Still Photography*

Still photography, though less valuable than cine-photography, has certain important advantages. For example, less skill and less elaborate apparatus are required to produce satisfactory results. Moreover, as monochrome and some colour films can be processed immediately after exposure, it is possible to keep a constant check on technique and apparatus.

The still camera's most important role in the present study was to illustrate and support direct observation of the fluctuations of population in a number of marked colonies (Plates III and IV), certain aspects of behaviour, the crèche system, the habitat of the birds and methods of study. For a description of equipment and methods, see Appendix C.

The population of a penguin community fluctuates considerably throughout the breeding season (Figure 9). To a lesser extent it also varies in different environments. For example, it takes longer for the population to build up to its maximum at the beginning of the season in a snow-covered colony than in a snow-free colony (p. 42). Photographs can provide confirmation for direct observations made on small colonies, and knowing the density of population of smaller areas, it is possible to make a rough estimate of larger areas from photographs (the number of nests per unit area being approximately constant). If repeated from year to year such photographs could report total population changes.

Sapin-Jaloustre and Cendron (1953) using similar methods in Adélie Land, claim, perhaps rather optimistically, that accurate counts were made from enlargements of their pictures which were taken in 1/50th of the time required in the field for direct counting. Nevertheless, they stress that such methods should be combined with direct observation.

E. THE USE OF MAPS

Large-scale maps were used, as much as possible, to summarise information of the size and distribution of breeding populations and the habitat preferences of the various species. Maps of the latter showed that Adélie penguins have a preference for the flat and relatively high ground and the Chinstrap penguins for the steeper slopes when breeding side by side (Map IV, surveyed by J. Cheal, 1951). Where the Adélie penguins predominate (Map III, surveyed by James & Marshall, 1945) no particular preference was found. Gentoo colonies are small and scattered (Map III). Map II, after Anderson (1905) shows the distribution of Adélie penguins and Gentoos at Hope Bay in 1901.

PART II. THE ADÉLIE PENGUIN

A. METHODS OF SEXING ADÉLIE PENGUINS

As the sexes of Adélies are indistinguishable externally, dissection (see p. 20) is the only infallible means of distinguishing them.

Roberts (1940, p. 201), the first worker to emphasise the importance of dissection for confirming the sexes of penguins, painted those whose behaviour he was studying, and later killed them for examination. He states that behaviour gave no certain indication of sex, so that many of the earlier observations on the behaviour of penguins are of little value because the sex of the individuals described was open to doubt.

In contrast, Richdale (1951) ringed all his birds, and followed many of them for ten consecutive seasons, without killing any. He claims that he identified the sex of all his closely observed breeding birds. When summarising sex differences (op. cit., p. 107), he states that the only certain way of sexing the Yellow-eyed Penguin, other than by dissection, is to examine the vent of both birds of a mated pair during the span of egg deposition. "This test was subsequently checked by noting definite sexual behaviour patterns. Final confirmation came when a bird, accidentally killed, was dissected, and because Yellow-eyed Penguins change their mates frequently it was possible to trace accurately the sex of every bird that had lived in that particular colony in the research period" (op. cit., p. 3). He also gives eleven subsidiary points which make "fairly reliable tentative guides", especially if a number of them can be assessed together for the bird in question. These are mainly concerned with the pre-egg and incubation period. Richdale's confidence in sexing his birds must be founded, not only on the study of marked birds for a number of consecutive seasons, but also on an intimate knowledge of their ways and behaviour, an intimacy which could come only as a result of living among them. It would otherwise be difficult to understand his references to "young females" and "young males" (op. cit., p. 208) after making it clear that it is only breeding birds that can be sexed, other than by dissection, with any certainty.

The writer's conclusions given below, which are based on dissection together with observation of marked birds, strongly support other less drastic methods. They are given in order of importance.

When seen copulating. This is probably the most certain way of identifying the sexes in the field. All copulating pairs dissected early in the season proved to be the male above and female below, and no example was found of the reversed attitude in coition such as is described by Roberts (1940, p. 208) and Falla (1937, p. 77). This is discussed further on pages 41 and 63.

Incubation routine. The male remained alone to incubate the eggs as soon as the clutch was complete, while the female departed to sea to feed. This normal routine, in which the sex of males was confirmed by fifty-three dissections, could, however, be upset by human or dog interference, and, for other reasons, was not infallible (p. 54).

The ecstatic display. From arrival at the breeding area up to the time of chick-hatching, the ecstatic display was restricted to the male. After the chicks had hatched, the display was observed in both sexes. Evidence for this is given in Table VII, and discussed on page 32.

The female cloaca. Immediately after egg-laying the cloaca was congested (often a dull purple) and dilated, but it soon reassumed its normal external appearance. Blood stains were rare. Richdale (1951, pp. 88 and 107) considers this to be the only certain way of sexing the Yellow-eyed Penguin other than by dissection.

Dominance of the Male. On the whole the male was more aggressive in defence (p. 37). When a pair were together and were disturbed, the male usually took over from the female if she happened to be standing in the nest. About twenty examples of this behaviour were recorded in marked birds whose sexes were later confirmed either by dissection or incubation routine, the male always taking over from the female and never the female from the male.

Weight. If a pair were weighed before egg-laying, the male was nearly always heavier than his mate. Weight was unreliable as a guide at any other time of the breeding season (p. 54).

Appearance and size. The female was usually smaller and sleeker, but a comparison of a large number of measurements from dissected birds showed that there was a considerable overlap. It is, therefore, unwise to attach much importance to these differences even when comparing a pair at their nest.

Tread marks. The reliability of this method used by Levick (1915, p. 58) was limited as there was always danger of confusion between a female with tread marks on her back and dirty males who had been fighting. Moreover, tread marks were seen only during a thaw, and thus were uncommon early in the season before egg-laying. It was, however, a valuable confirmation of sex, especially if one only of a pair had conspicuous tread marks, looked smaller, and was shyer.

Palpation of egg in the uterus. The egg could be felt in the lower abdomen just before laying. This method was abandoned as soon as dissection showed that the shell could be damaged in the early stages of formation by anything but the gentlest handling.

It appears, therefore, that the only certain way of sexing Adélies other than by killing them, is to mark breeding birds before egg-laying and then continue observing them during the early part of the breeding season. Casuals and non-breeders cannot be sexed unless marked and found breeding in another season. The only simple and practical solution to this problem would appear to be the development of a technique for examining the cloaca, either by eversion, or internal examination with an instrument, similar to the technique used for ducks and geese (Elder, 1946; Hanson, 1953).

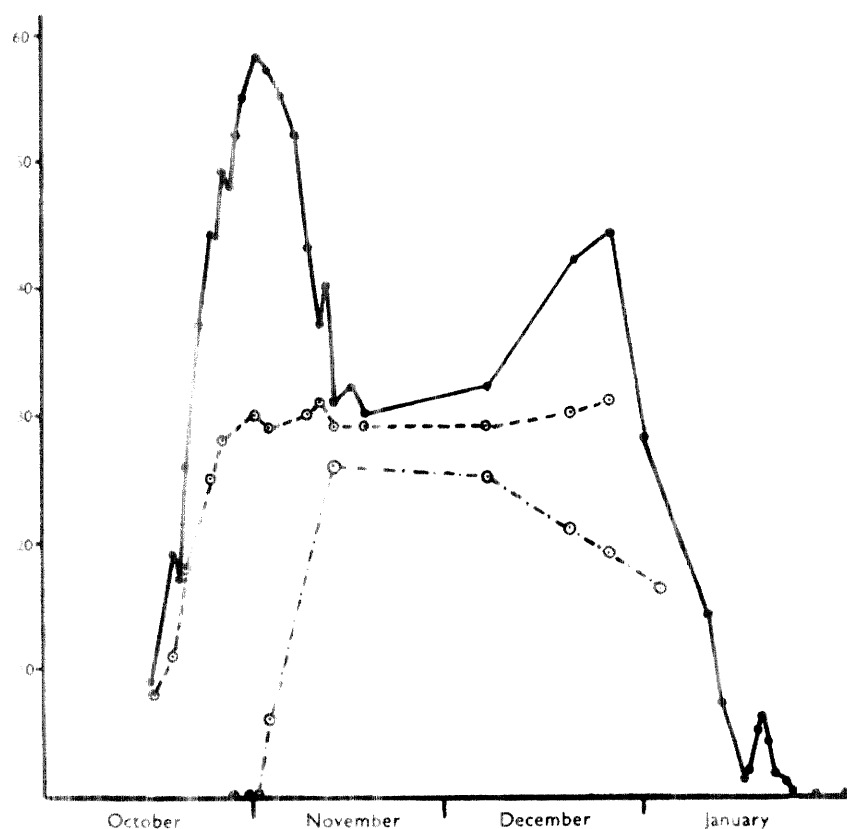


FIGURE 9. Population and nests of Colony V at Signy Island, 1950-51.

Notes: —●— = total number of birds in adult plumage
 - - -○- - - = number of nests or scoops occupied
 . . .○. . . = number of nests containing eggs or chicks

B. AGE GROUPS

It soon became clear that the social structure of an Adélie Penguin community could not be understood by the study of just a few marked and dissected birds. The larger the sample, however, the more variations in behaviour became apparent and the more difficult it was to establish a simple and clear story. At Signy, for example, adults started to return after the winter during the first week in October, although the population did not reach its maximum until one month later (Figure 9). The first eggs were laid on October 29th, yet on November 19th fresh eggs were still being found. Some birds went about their business with an assured manner, others loitered on the periphery of the colonies, or wandered far away from the breeding areas. As I became more familiar with the birds, it appeared that these variations, and other differences in behaviour and breeding efficiency, were due to three important and often interrelated factors. These were, variation among individuals, differences in "intensity" of behaviour, and differences in age and breeding experience.

Individual variation is a well-known factor to all those who have studied a sufficiently large sample. The word "intensity" is also well known to students of animal behaviour. For example, incomplete acts of copulation are described as being at a low intensity, and complete acts at a high intensity. It can be argued that "intensity" is largely dependent on what is perhaps loosely referred to as "breeding condition". Exteroceptive factors, such as snow coverage of nest-sites, presence or absence of sea ice, and weather, combine with proprioceptive factors, such as gonadal development and secretion of hormones, to influence this breeding condition (Roberts, 1940). Other factors, however, such as dominance, morale and health are in my opinion equally important, though they tend to be ignored because it is at present impossible to estimate their importance in the field. Differences in age and breeding experience I believe to be even more important; they are given here in some detail because they do not appear to have received much attention so far in researches into the life histories and behaviour of birds, no doubt because studies of marked birds of known age (e.g. Richdale, 1951) are still almost non-existent.

It was not possible to study Adélies of accurately known age at Hope Bay or Signy (see p. 12), so that the age groups given below are provisional. Evidence has, however, been provided not only from field observations and nest histories of marked birds, but also from a large number of dissections. Moreover, it is hoped that follow-up work on the young Adélies now being marked (see p. 18) each year in the Falkland Islands Dependencies will check their validity.

1. *Suggested Classification of Age Groups*

- i. *Established (experienced) breeders* three to five years old and over; mostly four years old and over.
- ii. *Unestablished (inexperienced) breeders* two to four years; mostly three years old.
- iii. *Non-breeders ("Wanderers") in adult plumage* two to three years old; mostly two years old.
- iv. *Non-breeders ("Wanderers") in immature plumage (Yearlings)*; from leaving the rookery until they moult into adult plumage when about fifteen months old.
- v. *Nestlings (Chicks)*; up to the time when they leave the rookery, nearly two months after hatching.

2. *Breeders*

Table II outlines the differences between the *established* and *unestablished breeders*. These will be discussed under the appropriate sections to which there are page references.

The unestablished breeders are illustrated in Plate V. Plate Va and b, taken on November 4th, show a poorly built nest on the periphery of a small colony. My attention was drawn by the fact that a pair of Sheathbills was taking an interest in the couple at the nest. The female Adélie was lying in the nest, but not on the egg, having scratched it away with some of the stones when settling into a comfortable position for lying down. After the photos were taken, the egg was examined and found to have a dent in it. This had probably been made by the Sheathbills before my arrival. Plate Vc and d, taken on November 6th, show a newly laid egg in a shallow scoop on melting snow (a thaw stream is actually trickling through it) with only two or three stones to represent a nest. This pair appeared to be without the impulse to protect the egg and Plate Vd shows a Sheathbill approaching it and about to break it open, the two neighbours to the left and right actually protesting more than the owner! Such episodes were frequent, usually among birds

on the periphery of the colonies, and it was noticeable how acute the Sheathbills and Skuas were in perceiving the difference between what appeared to be the experienced and inexperienced breeders.

Age groups, intensity of behaviour and individual variation are not the only factors responsible for the diversity of behaviour seen in an Adélie community. Yet another division must be made among the breeders: the *successful* and *unsuccessful breeders*. Breeding routine was maintained so long as there was an egg or chick in the nest, but if these were lost, the bird on duty would desert and move off to sea to break its fast. Most of the unsuccessful breeders were, however, back at their former nest-sites between the time of egg-hatching and early crèche formation (i.e. the re-occupation period; p. 57). The second peak in the population during December (Figure 9) partly represents this additional influx of unsuccessful birds and partly represents the non-breeding "wanderers" (see below).

3. Non-breeders or "Wanderers"

i. In Adult Plumage

The successful breeders, whether established or unestablished, were concerned solely with establishing territory, building nests, incubating eggs and rearing their chicks. Another group of Adélies, though in adult plumage, behaved differently. Individual birds were seen wandering round the periphery of the colonies closely scrutinising their surroundings. If they approached too near an occupied nest, they were pecked away vigorously. Sometimes one would walk through a colony as though in quest of something; it might even settle down in a space just out of pecking range, or stand in an empty nest scoop, or come out and wander round the periphery again. These birds were, however, essentially unattached, unattached to nest-sites, unattached to any particular colony, or even rookery. Lone birds temporarily occupying nest-hollows were males and were frequently seen in the ecstatic display (p. 32).

When grouped together in small parties they wandered further afield reaching the most unlikely places, leaving their foot and flipper marks in the snow as evidence of their restless movements. At Hope Bay, they were sometimes seen inspecting exposed rocky outcrops 1000 feet above sea level, far away from the rookery. Unlike the breeding population, they would return to the sea again during the first fasting period (see p. 52), should open water be near enough.

Wanderers were most in evidence during the two periods when the Adélie population was at its maximum: at the start of egg-laying, and during the re-occupation period (Figure 9). During the re-occupation period, however, they were almost impossible to distinguish externally from the unsuccessful breeders which were returning to re-occupy their territories. Dissections here proved of value (see below), while additional confirmation was provided from the recovery, back at their former nest-sites, of marked birds which had been unsuccessful in breeding.

ii. In Immature Plumage (Yearlings)

The young of the previous season were recognisable by their white throats (Plate Ve). This immature plumage was moulted into adult plumage in February when they were about fifteen months old. When the nestlings leave the rookery at the end of the season, they swim to the pack ice and remain there until they are two, or possibly three years old. There are, therefore, very few records of immature-plumaged birds seen on land. The abnormal summer of 1948-9 was probably responsible for the comparatively large numbers observed at Hope Bay. These observations, together with those of Gourlay rookery, summarised in Table III, permit three fairly distinct groups to be distinguished.

Birds seen between October 21st and 27th. These were the only yearlings seen at Signy Island. They came in with the main influx of breeding birds and wanderers before egg-laying. The *Scotia* naturalists' record of one "white chin" seen on October 14th, 1903, at Laurie Island, South Orkneys (Wilton et al, 1908, p. 50) would fall into this group. An immature male collected on the same day, no doubt the same bird, weighed 7 lb. 13 oz. (3.55 kgm.) and had nothing but a few stones in its stomach (Ross MS, p. 51-52). The average weight of 109 males in adult plumage at Signy between October 14th and 27th, 1950, was 5.00 kgm.; the average thickness of blubber of thirty-four of these was 6 mm. This is in striking contrast to the two male yearlings collected during the same period in 1903 and 1950, which weighed 3.55 kgm. and 3.60 kgm. respectively, and had practically no blubber. The fact that the yearlings were not in the necessary physiological condition for a fast, and did not stay, indicates that these birds were stragglers with the main influx of birds in adult plumage from the pack ice. No yearlings were seen at Hope Bay in 1948 until December 17th.

Birds seen between December 17th and January 13th. These dates roughly coincided with the re-occupation period (Figure 9). The birds were most often seen with the parties of wanderers, though sometimes they might occupy territory on the periphery of a colony for a day. One, actually seen carrying a stone, was occupying a hollow containing a few recently collected stones. Table IV shows that their weight averaged rather less than a sample of seventy-seven adult-plumaged birds of both sexes collected at Hope Bay between December 17th and January 4th, January 4th being the last date on which a yearling was weighed in this group.

Birds seen between January 21st and February 14th. Table IV demonstrates a complete reversal in physiological condition as compared with the last group. The yearlings were much heavier than the adults, and had blubber at least 10 mm. thick (Table III) in contrast to 3 mm. or less in the adult-plumaged birds. These yearlings coming ashore to moult, were often seen among nestlings in the colonies. In addition to these records, the Southern Cross Expedition collected one yearling at Cape Adare on January 18th, 1900 (Sharpe, 1902, p. 115-6), and Falla (1937, p. 84) saw one or two moulting among large numbers of moulting adults on the MacRobertson Land coast on February 13th, 1931. Wilson (1907, p. 57) states that there were no immature-plumaged birds among the large numbers of moulting adults when he landed at Cape Adare on February 17th, 1904. There can be no doubt that the moult of the immature-plumaged Adélies starts before that of the adult-plumaged birds seen at the rookery. This is discussed on page 65.

Two more interesting facts about these yearlings are worth mentioning. Firstly, ten of the tails of fourteen birds examined were found to be damaged, some even reduced to frayed stumps. This damage was as common in yearlings collected in October and December as in January just before the moult. A damaged tail was a rare sight in an adult, even though they were repeatedly buffeted by high seas (p. 46) when landing with food for their chicks. Secondly, intestinal parasites, usually small cestodes, were quite common in the yearlings dissected (see Table III) often causing a localised dilation about 2 cm. long in the small intestine, but they were extremely rare in adult-plumaged birds. Could it be that the older birds acquire an immunity? Or could it be that the young are less conservative in their choice of food and digest infested material which would not be eaten by older birds that feed almost exclusively on *Euphausia*?

4. Further Evidence in Support of the Age Groups.

That birds behave differently according to their age groups is further supported by the following evidence from field observations:

i. To avoid undue disturbance to neighbouring birds, Adélies were carried fifteen yards away from their nests for examination and marking (p. 19). Before the eggs were laid, that is, when the population was at its densest, these temporarily vacated sites were often occupied immediately by other birds, either from the periphery or from a neighbouring nest. These usurpers would flee when the original owners were released and returned.

ii. More striking was the effect of removing a large number of birds from one section of Colony XII. These, required for dog food, were taken in two batches; the first of 50 birds on October 27th, 1950, and the second of 90 on October 30th. The colony, revisited on 28th, looked nearly the same as it had done before the 50 were removed; the gaps had been filled by others. This again happened after the second batch of 90 had been taken from the same place on October 30th, though the new occupants were a little more spaced out than the rest of Colony XII. Moreover, on the same day there was an unusual and striking increase in ecstatic displays (p. 32) seen in this particular section. Now, the time for this investigation had been chosen when most of the population (see Figure 9), and certainly what were supposed to be the established breeders, had arrived and were paired and occupying well-built nests. On October 27th, two days before the first eggs were found at the rookery, some arrivals were still walking into the colony from the sea ice and fights were frequent, but on the 30th arrivals were fewer. A small shifting population of birds was wandering round the periphery of the colonies, and a number of lone, clean, well-nourished and obviously freshly arrived males had, within the last few days, taken up territory on the fringes where the winter snow had now mostly thawed away. It was these, the wanderers and other fairly recently arrived birds, which I believe filled the gaps in Colony XII; birds which would otherwise have taken up poor territory on the periphery of other colonies, or which might not even have had the opportunity of breeding at all.

A bird, marked on October 27th in Colony III, provided some confirmation for this, because on October 31st it was found at a good nest-site towards the centre of Colony XII. It had shifted 70 yards from Colony III where it had previously been alone at a poor nest for at least three days after arrival. It now had a partner. The incubation routine, and the fact that its partner was seen with tread marks on November 2nd, proved this bird to be a male. On November 12th and 13th he was alone incubating one egg, but breeding was unsuccessful. This bird too, was probably an unestablished breeder which shifted from his first nest-site to a better situation.

iii. Nest 55 history, with marked birds, tells much the same story. On October 26th, female *B* was on the periphery of the colony and seen in mutual display with an unmarked bird. On October 27th, *B* was still keeping company with an unmarked male, *D*, which was then ringed. *D* then weighed 5.95 kgm. and was almost certainly a new arrival on 26th. On 28th neither *B* nor *D* could be found in Colony III, nor was the female *B* seen again. A day later, however, *D* was observed in the middle of Colony XI, 100 yards away from Colony III. He did not appear to be attached to any

territory as he ran off readily, and was later seen* dodging among the nesting birds and running the gauntlet of many pecks. He settled down on the periphery then wandered round again, settling down in another place. There could be no doubt that this bird was trying to establish himself somewhere. On November 4th he was still in Colony XI and, by that time, at a good nest-site with an unmarked partner by his side, and this, Nest 55, was his site from then on. The first egg was found on the 10th, the second on the 14th, and his mate must have left him for the sea soon after. Only one chick was found on December 27th, and this was lost before it was a fortnight old. The pair were therefore unsuccessful. On January 25th, he was seen re-occupying his former nest-site 55 and was collected for dissection.

Some interesting points of difference arise from Table VI, which contrasts the behaviour and dissections of two female Adélies newly arrived from the sea ice:

iv. Female *A* arrived at a time when the colonies were less than one-third full and Adélies were coming in as a steady stream all day long. *B*, arriving eight days later, came when colonies were almost filled to capacity. *B*'s weight and blubber thickness demonstrate that it had smaller reserves for a fast than *A*. A similar example has been given (p. 26) of the difference in nourishment of immature-plumaged birds and adults seen between October 14th and 27th. Interpretation of the behaviour of *A* is very dependent on the acceptance or rejection of the principle of individual recognition. This is discussed later (p. 70) but it is assumed for the present, that the birds do recognise each other, and that *A* was therefore "greeting" either her former mate or a previous partner. It does not matter which, the important fact being that the loud mutual display (see p. 34) which they performed, was neither aggressive nor an appeasement ceremony, but a "greeting" ceremony, an appreciation of individual recognition. This interpretation is incompatible with the "trial and error" theory of sex recognition (see p. 63, Sex Recognition) especially as the gonads of *A* were far less well developed than those of *B*, though *B*'s behaviour was one of indecision and inferiority and *A*'s one of purpose and confidence.

Individual variation and intensity of behaviour cannot be solely responsible for the behaviour of the Adélies described in examples *i*, *ii*, and *iii* above, when contrasted with the behaviour of the breeding birds ringed by Andrew at Hope Bay in 1946 which were still at the same nest-sites and paired with the same birds two seasons later (see p. 70). Nor can it be responsible for the contrast in behaviour of the two females described in example *iv*, the one of which wandered aimlessly through three colonies, while the other, also fresh from the sea ice, ran straight up to a nest and joined in loud mutual display with a male already in occupation.

Lastly, some further evidence for differences in the behaviour of the various age groups comes from Tables VIII and IX, showing the readiness with which supposedly established breeders were able to secure new partners if their present ones were removed. It was not possible to carry out the same investigation with supposedly unestablished breeders or "wanderers" as they ran away and sought territory elsewhere, their behaviour thus again contrasting with that of the established breeders.

5. State of the Gonads

There was as much variation in the appearance of Adélies' internal organs, and particularly the gonads, as in their behaviour. For example, four out of five ovaries from immature-plumaged Adélies examined between December 17th and February 14th (Table III) appeared uniformly homogeneous, there being no ovules visible on macroscopic examination. One collected on December 18th, however, showed many regular-sized ovules from 0.5 to 0.75 mm. in diameter in a homogeneous matrix. No correlation was found between the behaviour of these yearlings and the appearance of their gonads. Of the yearlings seen between December 17th and January 13th, most were observed with parties of wanderers, a few were seen on the periphery of colonies, and one was actually nest-building. What would this nest holder do when it returned the following year? Would it breed at the age of two years during its first year in adult plumage?

Some adult-plumaged wanderers which were dissected during the breeding season showed immature gonads, thus providing conclusive evidence that some at any rate did not breed until they were three years old. Most adult-plumaged birds showed mature gonads, but this did not prove that they were going to breed, or had bred in previous seasons. Attention has already been drawn (p. 26) to the difficulty in distinguishing externally the non-breeders in adult plumage from the unsuccessful breeders. It was, therefore, important to ascertain whether dissections showed any difference between breeding and non-breeding birds.

Before egg-laying the ovaries of breeding birds were much enlarged, individual ovules being as much as 38 mm. in diameter, and the oviducts were vascular and tortuous (Figure 12c). After the eggs had been laid there was a rapid diminution in size, but for about six weeks it was possible to observe the flattened, disc-shaped, ruptured follicles among the regressing ovules (Figure 12d). These ruptured follicles were not present in the ovaries of non-breeding wanderers, even in those which in other respects resembled those of

* Here was a good example of the value of a flipper ring and of a large yellow number painted on his right flipper. The bird was discovered with ease in Colony XI, which at that time was not regularly visited, and was followed through binoculars without being disturbed. A leg or tarsus ring would not have been noticed.

the mature adult. Moreover, as already stated, a few wanderers showed definite signs of immaturity, the ovaries appearing homogeneous (or with minute ovules scattered in a homogeneous matrix) and the oviducts flattened, semi-translucent and without kinks.

Undeveloped testes were difficult to demonstrate on macroscopic appearance alone, as the shape and colour showed much individual variation. However, flattened testes, which were also either narrow or slightly S-shaped with pointed upper and lower poles (Figure 12e and f) appeared to denote immaturity, whereas raised testes with rounded upper and lower poles were signs of maturity (Figure 12g and h).

The most reliable external character was the incubation area. Successful breeders showed a conspicuous and often dull purple denuded patch over 2 cm. wide in the lower abdomen from the time of egg-laying until the chicks were about two weeks old, whereas in the non-breeding wanderers it was poorly formed and largely covered with down. However, the unsuccessful breeders showed poorly developed incubation areas also when they returned during the re-occupation period.

The non-breeding wanderer population appeared to vary considerably from place to place, and no doubt, from year to year. Wanderers were not only more frequent at Hope Bay than at Signy, but more birds in adult plumage showed definite signs (Table V) of immaturity. Table V and Figure 12 attempt to clarify this further. Dissected birds can be divided into three groups:

- Group A in which one or more of the signs of immaturity shows beyond doubt that the bird cannot breed.
- Group B in which signs of maturity can be demonstrated, but do not by themselves supply sufficient evidence of actual breeding.
- Group C in which definite signs of breeding can be demonstrated. These signs are restricted to a comparatively short period in the breeding season.

It is hoped that microscopic examination of the reproductive systems collected during this work, will provide further evidence in support of the age grouping adopted in this study.

6. Summary

Established (experienced) Breeders coming direct back to their former nest-sites, independently of their former mates, may soon find a partner with which to keep company until their true mates return. As we shall see later (p. 63), this habit of "keeping company" has survival value, for, should the original mate not return, or return very late, the pair-bond is likely to be established between the two partners. The established male will stay in his site, but the established female may keep company with a male in another nest, though returning to her former nest later.

Unestablished (inexperienced) breeders must first find a nest-site, the availability of which will vary from year to year according to adult mortality. At best (and it appears to be the males that establish *new* territory) they will find a vacant site within a colony, but may be expelled if the rightful owners, arriving late, find them in occupation. At worst, they will establish territory at poor sites on the periphery of colonies, but may change to better situations should the opportunity occur. Their first-year breeding is likely to be unsuccessful, the eggs or young chicks falling a ready prey to Skuas or Sheathbills, or succumbing to severe weather.

Unsuccessful breeders are either established or unestablished birds which, having lost all their eggs or chicks, move off to sea to break their fast, usually returning during the re-occupation period. Unless marked, or dissected, they are difficult to distinguish from the non-breeding wanderers. During the re-occupation period, behaviour among these unsuccessful breeders and the non-breeding wanderers is similar to that seen among all age groups in October before the eggs are laid.

Non-breeding wanderers in adult plumage may be difficult to distinguish as a group if birds of known age are not being studied. Their age will overlap with the unestablished breeders since some two-year-olds may be able to breed, although it is likely that the majority do not breed until they reach the age of three years. As has already been pointed out (Sladen, 1953), these non-breeders provide an important reserve population, their wandering habits serving two important functions for the survival of the species. Firstly, they will quickly take the opportunity to fill any gap in the colonies and may, during the re-occupation period, establish territory in anticipation of the following season. Secondly, by their wanderings to out-of-the-way

places they become familiar with new grounds, and when the usual breeding areas are filled may thus extend the breeding range of the species.

It must be emphasised that these age groups cannot be fully substantiated in the Adélie until birds of known age are studied. In contemplating future work along these lines, it would be necessary to mark large numbers of nestlings consistently each year for a number of years to offset variations among individuals of the same age group.

C DISPLAYS, POSTURES AND NOISES

Work on behaviour was supplemented by ciné-film, which has proved of great value in that it has allowed subsequent, more leisurely scrutiny.

1. Classification

- The Ecstatic Display
- The "Bill to Axilla" Display
- Bowing
- The Mutual Display
- Aggressive Postures
 - Threat—Attack—Fighting—"Pecking"
- Postures and Noises which suggest Nervousness
- Copulation
- Nest-building
- Other Postures and Movements
 - Stretching, Yawning, Head-shaking, Shaking and Swallowing, Preening, Walking, Tobogganing, Before departure to sea, In the water, Landing from the sea, Sleeping, Defaecation, Incubation, Feeding chicks
 - Nest-relief Ceremony
 - Displacement Activities.

2. The Ecstatic Display

There has been some confusion over the name of this display. Wilson's sketch (1907, p. 56) with the caption "the ecstatic attitude of the Adélie Penguin" appears to be the first English description, and this is later quoted by Levick (1915, p. 82-83). Levick's (1914, p. 47) failure to distinguish the ecstatic from another display, now called the mutual display, is responsible for Richdale's (1941, p. 269) uncertainty. Richdale (1951, p. 31) discusses this in his latest work, but does not alter his terminology in spite of the lead given by Roberts (1940, p. 219). Wilson's original name should, however, be accepted, this view being upheld by Falla (1937, p. 77) and by the French term "la position extatique" (Sapin-Jaloustre and Bourlière, 1952, p. 41).

The display may be described as follows: With a few slow preliminary movements of the head to one side, the bird slowly stretches its head and bill upwards, and with jerky rhythmic beats of the flippers and with an apparent air of extreme profundity, thrusts out its chest and emits, at first softly then louder and more distinctly, a *ku-ku-ku-ku-ku*, not unlike the slow roll of a drum. This leads straight into a *kug-gu-gu-gu-gu-ga-aaaa* as the climax is reached, with the neck and bill stretched to fullest height towards the sky, the eyes rolled down and backwards, the occipital crest raised, and the flippers still beating jerkily (Plate VIa and b). The bird slowly relaxes to its normal standing position, or may go straight into the "bill to axilla" display (p. 33). The second sound varies, perhaps the nearest likeness being to a husky hen "cawing" after laying an egg. Levick (1915, p. 83) compares it with the crowing of a cock or the braying of asses. The bill, kept closed for the first sound, is only slightly opened at the climax.

Sometimes the climax sound was prolonged, and on reaching its highest note, fell waveringly with what appeared to be an "imploring" finish, and slight rotation of the head to one side. This long-drawn version of the ecstatic display is, I believe, important and in need of further investigation. It was first recorded on

November 8th, ten days after the first eggs had been laid, and appeared to be confined to lone males at empty nests which had up to then been unsuccessful in acquiring a partner.

Attention has been drawn by most writers to the infectiousness of the display and the fact that both sexes take part (e.g. Levick, 1915, p. 83; Roberts, 1940, p. 219), but Gain (1914, p. 20-21) and Murray (1909, p. 249) describe it as a display of the male Adélie. However, though often infectious, especially early in the season, it is definitely not taken up by all the birds in a colony. Table VII sums up 101 observations extracted from field and dissection notes, of birds of known sex seen in the ecstatic display at Hope Bay and Gourlay rookeries; it shows that the display was seen much more frequently in lone males at empty nests than among males or females over chicks. Table VII also shows that for the early part of the season and up to the time of chick-hatching, the ecstatic display was seen in the male Adélie only, never in the female. When performed by lone males, the display and sound appeared to be the most important means of attracting females to the nest. Typical is the observation made on November 19th, 1950, of a male Adélie whose sex was confirmed by dissection later in the season.

Four days earlier, this bird had been ringed (No. 64090) after being seen in ecstatic display alone at a nest-site with no stones in it. From his subsequent behaviour it was clear that he was a non-breeding "wanderer". At 0100 hrs. he probably had a partner, but they both ran away when disturbed. At 0800 hrs. he was back at his site and seen in ecstatic display which was followed by the "bill to axilla" display. Another ringed male incubating two eggs alone at an adjoining nest was also displaying but did not keep it up for long, whereas 64090 and three other lone birds at empty nest-sites on the periphery continued persistently. A few minutes later, 64090 was joining in quiet mutual display with a "female" (the sex was not ultimately confirmed by dissection) that had come to his nest-site. He followed this act by bowing (p. 33). The "female" remained standing and then responded to another quiet mutual display. Five minutes were enough for "her". Turning about, and with an air of apparent indifference, "she" walked off out of sight. The appearance of 64090 betrayed no sign of emotion. He hunched his head on his shoulders and closed his eyes, and when he next opened them he slowly stretched himself once more into the ecstatic display. At 1900 hrs. he again had a partner and both were standing with eyes closed by the stone-free nest-site. Fifteen minutes later both moved off, and he was afterwards seen wandering among the incubating birds. He certainly did not appear to be attached to his territory, at that time, though he was seen again about three weeks later with a partner at the same site which showed signs of a little nest-building activity.

Perhaps more striking, and again typical of the attraction the ecstatic display has for a female, was the observation made on December 29th, 1948—this time during the re-occupation period. Three birds *A*, *B*, and *C* were involved.

A and *B*, later collected for dissection, were first observed together at a newly-built empty nest. *A* was a well-nourished female whose ovaries showed two ruptured follicles. She had therefore bred, but being unsuccessful had no doubt recently returned to the colony after the usual spell at sea. Her behaviour suggested that she was an unestablished breeder. *B*, a well-nourished male, was either a "wanderer" or an unsuccessful breeder. *B* was bending over his nest, his dirty breast indicating that he had been lying in it. *A* was standing by his side. An ecstatic display from a lone bird, *C*, a few nests away brought *A* running up to *C* and there was probably a quiet mutual display in response. But when *B* stretched into the ecstatic display, *A* ran back to his nest. Three times she was attracted to *C*'s nest and twice back to *B*'s by the respective birds going into ecstatic display, and then she walked off to another colony ten yards away where she was next seen with another bird at a nest. Finally, an ecstatic display from *B* brought her back to the original nest, after which both were collected for dissection.

Further information can be gleaned from four Gourlay rookery nest histories. All the birds were marked and, because they were near the observation tent, were all observed with the same frequency.

Nest 4. This pair were probably together at the nest as early as October 18th, and though they lost their two chicks later in the season, the nest routine was maintained as though they were both experienced breeders. Neither bird was seen in ecstatic display.

Nest 29. This pair appeared to be established breeders. The ecstatic display was only seen once during the period of observation between October 17th and January 6th. This was on December 17th when the male was alone with the chicks which were beginning to lose weight. His mate had been away for at least four days, an unusually long time when feeding chicks.

Nest 5. The male and female were not paired until as late as October 26th and were probably unestablished breeders. For eight days before this, the male had been keeping company with another ringed female who disappeared soon afterwards. During this period he was seen in ecstatic display on three different days. His partner was never seen in ecstatic display but responded to his displays with a quiet mutual display. On October 26th when he and his new mate were first seen together, she was responding to his ecstatic display with a quiet mutual display. Twice on November 21st he was seen in ecstatic display over his two eggs. This was one day before he was relieved from his first fast. While changing his incubation position, after one of these ecstatic displays he went into the loud mutual display over his two eggs. The loud mutual displays of a pair performing the nest-relief ceremony nearby were probably the cause.

Nest 6. The male and female had a nest history which was atypical in a number of respects, and it seemed likely that the male bird, at least, was an unestablished breeder. On October 20th, the male, having been alone at his poorly built nest-site for two days, was frequently seen in ecstatic display. On the following day he was keeping company with the

lone female, which had joined him from *Nest* 8 a few feet away. On October 22nd, she was giving the usual quiet mutual display in response to his ecstatic display. No ecstatic displays were seen between October 26th and November 12th when the pair were together at the nest, but when alone incubating his two eggs on November 19th during the first fast, the male was again seen in the display. His mate was seen in the "bill to axilla" display when alone incubating two eggs at the end of her second fast on December 8th, thirty-six hours before being relieved. She was seen again in the same display and ecstatic display when alone over the surviving chick on December 23rd, two days before it was found dead, and at least four days after her mate had last been seen at the nest.

These few illustrations, which are typical of many, strongly suggest that the display is more frequent among the unestablished (inexperienced) and "wanderer" males, particularly when establishing themselves, than among the established breeders. This conclusion can be further strengthened by the fact that in a total of 225 observations, from November 1948 to January 1949, made on the twelve Adélies originally ringed breeding in 1946 (i.e. they must have been established breeders in 1948), in none was the ecstatic display seen. Moreover, half of these observations were on birds whose incubation routine proved them to be males. It is however important to realise that the negative results from these established breeders, and from examples such as *Nest* 4 above, do not indicate that the birds never went into ecstatic display. They mean, of course, that the display was not seen when the nests were under observation. No doubt they did display, but the point to emphasise is that the displays are far less frequent in established birds than in younger birds. This can be correlated with Table VIII which provides evidence that the experienced male will soon secure another partner even though there may be a number of lone males around.

Three unusual observations may be added. Firstly, a male (dissected) was seen in ecstatic display, on November 19th, on a snow slope and not at a nest-site. Secondly, on January 20th, very late in the season, a female was seen in display away from the nesting area. Lastly, on February 6th, a chick, still mostly covered by down, showed the typical ecstatic display immediately following another typical demonstration of the "bill to axilla" display when on the edge of a colony.

The possible association of this display with "nervous strain" must also be considered. Three possible examples of this can be found in the nest histories above: in the male of *Nest* 29 on December 17th, in the male of *Nest* 5 on November 21st, and in the female of *Nest* 6 on December 23rd. Another example, already quoted in Table VII, concerned a female (No. 62185) which was seen in ecstatic display on two successive days, January 5th and 6th, while alone and still incubating two addled eggs. Three days later, she finally deserted. Moreover, attention has already been drawn to the prolonged "imploring" variation in the climax of the ecstatic which was heard in lone males after nearly all the rest of the community were paired and laying eggs (p. 30). There are, however, a number of unexplained cases where females and males, whose nest-routine was apparently continuing satisfactorily, were seen in display alone over chicks.

To summarise, the most important function of the display appeared to be in pair-formation, where it was confined to the male and most commonly seen in the unpaired bird occupying a nest-site. A female could be attracted by it from some distance, and the usual response when arriving at the nest was a bow (p. 33). A male and female at the same nest were never seen in ecstatic display together; but if the male went into ecstatic display and the female responded, she did so only with a quiet mutual display. Age and breeding experience appeared to be important factors. The established breeders were rarely seen in ecstatic display whereas in the non-breeding "wanderers", unestablished breeders and unestablished unsuccessful breeders the display was more frequently and more persistently repeated. The occurrence of the display in females as well as males after the time when the eggs should have hatched is difficult to explain on the basis of pair-formation alone, but the fact that it is often associated with nervous strain (i.e. at a time when things were not going well with the incubating bird or the chicks) suggests new lines of investigation and analysis. It must also be noted that the ecstatic display probably serves two functions at once, that of attracting a bird of the opposite sex and that of repelling a bird of the same sex. Lastly, we have a few examples, which though isolated cannot be ignored, of birds seen in the display away from territory, and also of one nestling in display while still partly covered in down. The name "ecstatic" is unfortunate, for it certainly does not appear to be "induced under various circumstances by a feeling of satisfaction" as suggested by Levick (1915, p. 83).

The above applies to the Adélie only. The significance of the ecstatic display in the closely related Chinstrap Penguin appears to be a little different, for it was not necessarily confined to the male before the eggs hatched. Also, the ecstatic display in the Adélie and Chinstrap has much in common with the "full trumpet" of the Yellow-eyed Penguin. It should also be noted that Richdale (1951, pp. 23 and 211) attaches much more importance to its "social value" than to its "pair-formation value".

3. The "Bill to Axilla" Display

In the first description of it, this display is referred to as a subsidiary to the ecstatic display (Sladen, 1953, p. 955). It is certainly closely related to the ecstatic but, because it is so distinct, it is now being described separately. It appears to have passed unnoticed by previous workers on the Adélie.

In this display the bird leans forward at an angle of about 45°, sometimes less, and, while the flippers continue beating rhythmically backwards and forwards as in the ecstatic, it rocks its head from side to side with bill directed either to the left or right axilla (where the flipper joins the trunk). A characteristic soft *gurr-gurr-gurr-gurr-gurr* or *gwrr-gwrr-gwrr-gwrr-gwrr* accompanies these movements, one *gurr* for each rock of the head.

Though less common than the ecstatic, the "bill to axilla" display was regularly seen, its most frequent occurrence being among lone males at empty nest-sites. It usually followed immediately after the ecstatic (Plate VIb). Thus, a bird relaxing from the climax of the ecstatic would bring its body down to an angle of 45° and go straight into the "bill to axilla" display. It was also seen immediately before the ecstatic, or frequently just by itself. Unlike the ecstatic, it was not seen away from the nesting areas, but this might have been due to the paucity of observations. It also differed from the ecstatic in having been seen on two occasions performed by females during their first and second fasts. One of these has already been mentioned in *Nest 6* history (p. 32), when the female of the pair was seen in the "bill to axilla" display over two eggs on December 8th near the end of her second fast. The other, on October 30th, was an abnormal situation created by the death of the male of a pair occupying a well-made nest before egg-laying. The lone female, *Nest 33* (see Table IX), was seen in the "bill to axilla" display eight hours later. There are a few records of females in this display over chicks, for example from *Nest 6* on December 23rd, two days before the chick was found dead. Another interesting but isolated record was the nest with the newly hatched chick in which both male and female (dissections H731/1-2; see notes of Table VII) were seen in the "bill to axilla" display and the female also in the ecstatic display.

While it seems likely that it serves some function in pair formation, no instance can be found of the display by itself actually attracting a female from a distance, although such attraction is a common feature of the ecstatic. The "bill to axilla" display closely resembles the attitude of threat (p. 37), and in comparison with the closely-related ecstatic may contain a greater element of repulsion to the same sex and less attraction for the opposite sex. One of the examples above also suggests that "nervous strain" may promote the "bill to axilla" display.

4. Bowing

Opinions differ as to the significance of bowing in the Adélie. Roberts (1940, p. 218) considers it a characteristic display in the Pygoscelid Penguins, and especially in the Gentoo. Richdale (1951, p. 28-30), while admitting that no penguins he has studied display in this manner, considers it has significance only in the Emperor, King and Gentoo, and concludes that undue emphasis has been placed on bowing as "one of the more intense love-habits". In their most recent paper on the displays of the Adélie, the French workers (Sapin-Jaloustre & Bourlière, 1952, p. 47) side with Richdale. Richdale is a little confusing in his use of the word "attitude" (op. cit.). In our present state of knowledge, it may be convenient to class bowing as a posture (attitude) and a display.

There are a number of situations in which penguins assume the bowing posture and these, as Richdale points out, must be due to their anatomical structure. To reach nest material from the ground, to examine an empty nest, or an egg, or to tuck an egg underneath; these and other simple actions result in this *posture* of bowing. The bowing seen in the nest-relief ceremony (Plate VIIIb and d, and p. 47) would, for example, come into this category.

As a *display*, bowing was seen in two regularly repeated situations. The first, immediately before and after copulation (see p. 40), may on further investigation prove to be no more than a posture. In the second situation, however, bowing must be classed as a display as the birds moved in a characteristic and very deliberate manner which suggested "ritualisation". It was seen when two birds of the opposite sex met at a nest-site, usually after a female had been attracted to a male in response to his ecstatic display. One example has already been given (p. 31) of a male bowing to a strange female. Another good example of bowing was seen after ringing a male on October 17th, which at first was lying alone in his nest-site, but later was joined by a female which was seen bowing to him. These two birds kept company for over a week,

after which both paired with other birds. Bowing was thus observed at the very beginning when two birds probably met for the first time. Another example of bowing between occupants of *Nests* 6 and 8 is given on page 63. Its function in pair-formation is discussed under that heading (p. 64).

The most characteristic appearance is an arching of the head and neck forwards, with the bill pointing to the ground and the flippers held tightly to the side and slightly forwards. The similarity of this position with that of the threat posture (p. 37) may be important.

5. *The Mutual Display*

Roberts (1940, p. 218) was the first to name this display, calling it the "mutual epigamic display". Richdale called it the "ecstatic", but as already explained (p. 30) this term was originally used by Wilson for an entirely different display. Richdale draws attention to Hurley's photograph (Falla, 1937, figure 54) with its caption "reciprocal display ceremonies continue after egg-laying has commenced", to refute Roberts's statement that it is confined to the pre-laying period. Sapin-Jaloustre and Bourlière (1952, p. 45), call the display "*la parade mutuelle*". It is best, therefore, to continue calling this the "mutual display", although, as we shall see below, it is sometimes performed by a lone bird, and therefore is not always mutual.

It is convenient to divide the description into two phases, the loud mutual display and the quiet mutual display, but these really represent different levels of intensity.

In the *loud mutual display* (Plate VIIIa) the two birds stand facing each other and with bills pointing upwards, necks out-stretched, eyes rolled down and back, occipital crests raised, and flippers held to the side, and they sway their heads and necks, sometimes the whole of their bodies, alternately from side to side. A great deal of noise accompanies these movements, and bills are wide open. This noise varies considerably, but has a similar pattern to the sound heard in the last phase of the ecstatic display, being a raucous *gug-gug-gug-gaaa*, or *gu-gu-gu-gowa* or *ga-ga-ga-gowa*, which is repeated several times and can be heard for half a mile or more on a calm day. Another slightly quieter but more staccato sound, with faster individual phrases, is a *ut-dg-udg-udg-udg* or *dgu-dgu-dgu-dgu*. It is not known whether sexes differ in voice because both male and female usually call loudly together. In most situations the loud display is repeated several times with intervening pauses, and then usually followed by the quiet mutual display.

In the *quiet mutual display* (Plate VIc), the movements and appearance of the birds are similar to those of the loud mutual display, but at a lower intensity. For example, it is difficult to detect body movement, and neck movements are less pronounced. Bills are closed throughout, there often being a soft *skwar* or no sound at all. The quiet mutual display, which is often repeated, may be seen alone or following the loud mutual display.

The appearance of the mutual display varied according to circumstances and the positions of the birds, and the above descriptions were typical when seen during the nest-relief ceremony. The variations observed, including the display seen in nestlings, are given below.

1. *Mutual display seen between two adults at a nest-site.* Between a pair at an empty nest-site (Plate VIc) the mutual display was seen more frequently before egg-laying, and again on a smaller and more variable scale during the re-occupation period, than at any other time of the breeding season. It was seen on most occasions when one of a pair returned to the nest-site after a brief absence, but was especially frequent during nest-building or after one of the pair had been away from the site after eating snow or sheltering in bad weather. The following two observations were made during nest-building (p. 42). One bird lay in the nest while the other brought stones. Sometimes a quiet mutual display was initiated by the stone collector (either male or female) as it dropped the stone in front of its mate. The bird on the nest might, or might not, respond. If it responded, it would remain lying and move its head and neck from side to side in a horizontal plane, alternating movements with the standing bird which, still bending forwards towards its mate after dropping the stone, would also move in a horizontal plane and perhaps utter a soft *squaw*. Both birds took turns to collect stones or stand by the nest, while the other lay or stood in the site, and change-overs were not infrequent. Sometimes these were unaccompanied by any form of display, at other times either the quiet or the loud mutual display was seen.

On October 28th, 1950, a female with conspicuous treadmarks on her back was seen on four occasions eating snow from the edge of a colony. Each time she returned to her nest, the pair joined in loud mutual displays.

Mutual displays between male and female at an empty nest were also common on first arrival at the

rookery after winter, after disturbance, and in "sympathy" with loud mutual displays in neighbouring nests. The reasons for suspecting that this display was made by established breeders when they first met their former mates or partners at the old nest-sites, have already been discussed (p. 34 and Table VI).

The display was seen in varying degrees of intensity after disturbance or when the birds were worried, either as a result of fights (see *iv* below) or interference other than from penguins. The din and apparent confusion that results when a man walks through a penguin colony is not so much the noise of threat and aggressive protests at his feet, but the clamour of the loud mutual displays that close in behind him. Pairs are re-assorting themselves at their respective nests, loud mutual displays give way to quiet, and finally the birds settle to their previous occupation though still eyeing with suspicion the upheaval as it moves across the colony in the wake of the intruder. Similarly, on many occasions after one of a pair had been caught for marking, it would join in loud mutual displays with its partner at the nest as soon as it was liberated. Finally, there were the occasions when for no apparent reason, a pair would suddenly go into quiet or even loud mutual display. In many instances this was probably in "sympathy" with loud mutual displays made by pairs in neighbouring nests.

The display was seen in most of the same situations between a pair at a nest with eggs, during the period of egg-laying, but as soon as both eggs had been laid, and one bird maintained incubation while the other was at sea, the mutual display was only seen during the nest-relief ceremonies. During these ceremonies, however, the display was seen in its most intense and significant forms (p. 47).

When two birds of the opposite sex were keeping company, the mutual display was again seen in most of the situations described above. Data on marked birds keeping company are scanty; comparison with these and established pairs is not possible and there may be undetected differences in behaviour.

In all the situations described above, the mutual display was between two birds of *opposite* sex at a nest-site. I can find no example from my field or dissection notes of two birds of the *same* sex seen in this display at a nest-site, other than during a fight or as a result of disturbance (see *iv* below).

ii. Mutual display seen in one adult only, in response to the ecstatic display. This was commonly observed and is discussed on page 32. As there is nothing mutual about the display in these circumstances the name is not altogether suitable.

iii. Mutual display seen between two adults away from nest-sites. During the night of November 25th, 1950, occasional birds in parties, resting on a snow slope near a breeding colony above the icefoot along the shore leading to the rookery, were heard in loud mutual display. This was a rare occurrence.

There was also one isolated example far away from the breeding colony. On June 24th, 1950, when the winter ice was breaking up as a result of a series of gales, three Adélies landed near our Base hut. All were females (dissected) and two were seen in mutual display, probably loud, but it was not noted whether this display was seen before or after being disturbed.

iv. Mutual display seen between more than two adults between *bouts of fighting* when the loud mutual display was taken up by the intruder and the two birds at the nest. Thus, three would be seen with heads swaying vigorously, stretched to their fullest height and bills wide open. The sound was an accelerated version of the loud mutual display. In a big fight this would also be taken up by the neighbours. Immediately the loser had been expelled, the two remaining birds joined in prolonged mutual display (see p. 38).

The mutual display was also commonly seen *after disturbance* in more than two adults at once, and not necessarily of opposite sexes.

v. Mutual display seen between adults and nestlings. This appears, with one exception, to have passed unnoticed by previous workers. Sapin-Jaloustre and Bourlière (1952, p. 47 and Plate 3), remarking on the "strange behaviour of an adult and an already well-developed nestling" observed and filmed on January 23rd, 1951, are not certain whether it illustrates a preliminary sketch of a mutual display, or an example of abnormal feeding.

To understand the significance of the mutual display it is important to realise that it is seen regularly between parents and nestlings, and has as much meaning then, as at any time earlier in the season. The nest-relief ceremony continues throughout the guard-stage (p. 55). At first, the chick pays little attention to the noise and movement going on around it, but soon appears to associate the mutual display seen at the nest-relief ceremony with a fresh supply of food. Thus, when two parents are waving their heads from side to side and making a great noise, the chick will endeavour to join in. Being shorter, it will stretch upwards.

its movements and its *peep-peep-peep* call at first betraying no change from the normal food-begging attitude (p. 46). Later, however, still stretching to fullest height, its head will start waving in a circular motion. Here we have the earliest signs of the mutual display in the chick which, as it attains the height of its parents, will change to the side-to-side movements so characteristic of the adults (Plate IXc). Perhaps even more interesting is the gradual change of voice from the infantile "peeping" to a tremulous call which, though higher pitched, has the same pattern and form as the adult noise heard in the loud mutual display. By the time the chick is deserted at the nest by its parents and thus compelled to join others in the crèche, the mutual display is well established between the parents and chick. It is continued, though with diminishing intensity, each time a parent comes back with food, until the end of the season when the chick is fully grown. There is therefore nothing strange about the photograph taken by the French workers (op. cit., Plate 3). It represents the normal parent-chick behaviour and can be seen many times a day when parents are returning to feed their chicks.

Mutual display was occasionally seen between nestlings and adults not their parents. Thus, a parent returning to its colony might be seen in loud mutual display with several chicks (especially early in the crèche formation) before finally running off with its own. An adult resting away from the colony, if run into and disturbed by a feeding chase between nestling and parent, might momentarily go into loud mutual display with the chick in the general excitement. The chick soon returns to its parent, or to its nest-site. During the re-occupation period birds, which by their behaviour were almost certainly unsuccessful breeders or non-breeders, were sometimes seen in loud mutual display over chicks, and this was usually followed by jabbing thrusts directed at the chicks. More data are required from marked birds.

vi. Mutual display seen between two nestlings by themselves. This was recorded occasionally, as on February 6th, 1951, when two chicks joined in a brief loud display and "jabbing" when they met again at their nest-site at the end of the usual feeding chase after their parent (see section on individual recognition, p. 74).

vii. Mutual display occasionally seen in lone adults. On October 30th, 1950, the male of a pair together at empty Nest 34 was collected for dissection. The female, after being weighed and marked, returned immediately and made loud mutual displays horizontally over her nest. The display was not seen in a small sample of other lone birds under similar conditions, so it was probably abnormal behaviour.

Frequently a lone incubating bird, if taken away from its nest for weighing or marking, would, on release, run back eagerly and immediately go into loud display over its eggs. Moreover, the display was seen independently of human interference. For example, on November 21st, one day before relief at the end of his first fast and while changing position over his eggs, the male of Nest 5 (see p. 31) was seen in loud display probably induced by the loud displays of a nest-relief ceremony going on in a neighbouring nest. Another example was a male weighing 3.35 kgm. collected on November 25th after being observed in loud display alone over two eggs. In such circumstances, and at Nest 34 quoted above, the birds do not stretch upwards but, leaning forwards over the nest, wave their heads and necks from side to side in a horizontal plane. Most of these observations were made either at the end of a long fast when the incubating birds were expecting relief from their mates, or near hatching-time in early December.

On January 30th there were only a few adults left at the Hope Bay rookery. Some were feeding chicks and were being chased energetically by them. Others, in the minority, were standing alone at empty nests. Three of these lone birds in a small colony appeared much excited when chicks and parents ran by, and responded with loud mutual displays. After the chicks had passed by, all three went into ecstatic display and a little later still, one into the "bill to axilla" display. One then walked off to sea; the other two started nest-building, but had gone half an hour later.

viii. Mutual display seen in lone captive nestlings. Much time was spent studying and rearing captive Adélie nestlings at Hope Bay and Signy. They were taken from the rookery after they had developed the tremulous mutual display call with their parents. On a number of occasions, after they had become familiar with me, some would go into the loud mutual display before being fed. Sometimes they responded to a human imitation of the loud mutual display, and one even responded to the tune of "D'ye ken John Peel" which was regularly whistled before feeding time.

Enough has been said to make it clear that the mutual display was seen in far more situations than was formerly supposed; moreover, contrary to previous literature, it occurred throughout the entire breeding

season and was taken up by nestlings as well as adults. Undue importance should not be placed on isolated examples of what may later prove to be abnormal behaviour or displacement activities (p. 47); the emphasis should rather be on the regular occurrences of the mutual display between pairs before egg-laying, during the nest-relief ceremonies, and later between parents and nestlings when still at the nest, and finally after the nestlings have moved into the crèche.

From 1948 onwards, the display was often referred to in my field notes as the "mutual recognition" display, because it seemed to play an important part in maintaining the pair-bond in adults and the family bond between parents and chicks. Its role in individual recognition will be discussed later (p. 73).

6. Aggressive Postures

The Adélie is the most aggressive of the Pygoscelid Penguins. Individual birds vary greatly according to temperament, sex, the different phases of the breeding season, and their state of nourishment during the fasting periods. Thus, when a man meets a party of Adélies away from the breeding area, some may flee, others walk up nervously, though a few may even attack with bills and flippers with the same fury as is shown in defence of nest-sites. Early in the breeding season it is difficult to walk through a colony without causing general panic; only a few courageous birds stand their ground, the others flee. As the time for laying eggs approaches, the birds are more pugnacious, but again there are marked differences between individuals and sexes. The females, being more timid, will often run away and leave the males to defend (p. 23). Defence of nests is most vigorous when the eggs are hatching or there are small chicks, and is greatly influenced by the adults' state of nourishment. Towards the end of a fasting period care has to be exercised with some birds to prevent them deserting, yet when fresh back from the sea they behave quite differently.

For example, in *Nest 12* at Hope Bay the female during her first fast always ran away from the nest when I approached, leaving the male to defend. She was a little more courageous after the first egg had been laid, but still ran away on November 12th, the last day of her fast. After eleven days at sea she returned to relieve her mate, and had it not been for the ring that identified her it would have been difficult to realise she was the same bird. She appeared in excellent condition, and now defended the nest and contents well without moving from it. Four days later, incubating alone, she was still defending but making nervous head movements (p. 39) as she remained lying on the eggs.

While it is convenient for descriptive purposes to divide the aggressive attitudes of the Adélie into threat, attack, fighting and pecking, a hard and fast division rarely exists in the field. One attitude may lead quickly to another and some may be seen together.

Threat. There are two characteristic threat attitudes, although there are many variations. The first may be performed by a lying, crouching, or standing bird. If standing, it will lower its head as though beginning a bow (p. 34), and with its flippers held to the side or raised, occipital crest usually erected and eyes rolled downwards, will rotate its head so that one side is at right-angles to the object on which its attention is focussed. This attitude is referred to by Roberts (1940, Figure 24) as the "aposematic display". When crouching, the bird at first looks as though it might be going into the "bill to axilla" display (Plate VI d), but the bill does not get as far as the axilla and there is no rocking of the head. The prone bird raises its neck upwards, arches it over to compensate for its lowly position and shows one side of its face in the same way as in the other two positions. It may also move its head quickly to show the other side of its face. It seems that the birds are "showing off" their conspicuous white eyelids, a sight much enhanced by the rolling down of the eye to show the white sclera, but too much importance should not be attached to this position of the eye, for, as we shall see later (p. 74) it was seen in many situations with no connection whatever with aggression. In one form or other and with great variation in intensity, this threat attitude was commonly seen in reaction to an approaching penguin, and might lead to attack or pecking if it did not withdraw.

The second threat attitude is commonly seen when the stranger is taller than the penguin (such as a dog or man), or is flying above it (such as a Skua). Instead of showing one side of the face, the bird points its bill towards the stranger, puffs out its breast feathers, raises its flippers, rolls its eyes downwards and backwards, raises the crest, and utters a threatening *skwaw*. In this position both eyes are conspicuous to the stranger (see Levick, 1914, Figure 1). The bird may back away, keeping its eyes fixed on its antagonist, or there may be a leap forwards and vigorous attack. Parents will ward off threatened attacks from Skuas and the same attitude is soon taken up by the nestlings in self-defence when left alone. It can also be seen before fights with other Adélies or following the first threat attitude described above.

Attack. The threat attitude often leads to attack, the bird then running or leaping at its antagonist and, in most cases, putting it to flight without opposition. If the antagonist is a man, the bird will attack by fixing its bill firmly on trousers or leg and beating its flippers against the shins in rapid succession. The flipper action causes more pain than the bill, though the latter may occasionally draw blood. The threat and attack are accompanied by a torrent of noise which is difficult to describe but which is not unlike an accelerated mixture of the loud mutual and ecstatic displays (a deep grunting scolding *gwa-a-a-a-a-a*, or *gwarr*, or *grrr*). Wilson's (1907, p. 46) comparison with the rattle of a boy's stick along some corrugated iron palings is an excellent one.

Much the same form of attack can be seen when a healthy nestling is defending itself from a Skua, which may be trying to drag it out of the crèche. The nestling lurches forward in the second threat attitude described above, but often with flippers to side, and comes to an abrupt standstill on its toes with head and bill pointing to the Skua, flippers whirring, and uttering a scolding *chirrup*. As the nestling lurches forward, the Skua retreats with raised wings. This ability to attack was rarely seen until the nestlings went into the crèche, but was noticed occasionally while their parents were still guarding them at the nest. For example, the chick at Nest 24 standing with its parent, attacked me with its bill and a *skwawk* when I approached the nest to catch and weigh it. It was then twenty-one days old, but it did not move into the crèche for another eleven days. Attack was also seen occasionally between Adélies and Chinstraps (p. 67).

Fighting. True fights were intraspecific. Plate VIe shows the characteristic stance. With backs arched, breasts thrust well forward, they bump each other with great energy, striking blows with flippers in such rapid succession that it is impossible to follow individual movements. The hollow drumming sound of flipper against breast is heard above the din of harsh *gwa-a-a-a-a's*. All the time vicious-looking thrusts are made at each other with bills. There is constant manoeuvring to get a firm hold with bill on the other bird, thus providing an anchorage for a further volley of flipper blows. Between bouts of fighting, as already mentioned (p. 35), the loud mutual display is commonly seen, not only being taken up by the combatants, but also by birds in neighbouring territories. The climax is reached if one of the birds loses its footing and is floored. The other, fixing its bill firmly in the opponent's nape will give it a real thrashing with the flippers. The loser scrambles away and a chase begins, the birds dodging among the nest-sites in characteristic fashion, looking very elongated and sleek with flippers held back (p. 39), receiving threats and pecks from their neighbours. The battle may be resumed elsewhere or the victor may give up the chase and return to its nest. Here it will usually join in loud mutual display with its partner. Sometimes a fight between two evenly matched birds will suddenly break up, one running away for good. Very occasionally and rather incongruously it is the victor which runs away. Often, however, an apparently beaten bird will return again and again to the fray.

Though fights are frequent among adults, especially before egg-laying and again during the re-occupation period, I was not fortunate enough to see any which involved marked birds. There was, however, strong circumstantial evidence and evidence from dissections to support the following conclusions:

i. Fights, contrary to Roberts's (1940, p. 204) views, were definitely concerned with territory and/or the re-grouping of pairs.

ii. Male would fight male, and female female. It was not usual for opposite sexes to fight and then most instances could be attributed to a unisexual fight into which a bird of the opposite sex had been inadvertently drawn in the general excitement (see p. 67, and Plate XIc-f).

iii. Fighting was far commoner among the younger age groups (i.e. the unestablished breeders or non-breeding wanderers), big fights being rare among established breeders.

Finally, mention must be made of short-lived "fighting" sometimes seen between chicks. For example, on January 14th, 1949, one of two chicks in a nest pitched into its fellow chick with bill and flabby flippers soon after a parent had returned with food. These examples are, however, difficult to distinguish from "playfulness".

Pecking is really a milder form of attack and is most often performed by birds than remain lying or crouching over their nests. The peck is usually directed with outstretched neck at the occupant of an adjoining nest or a passer-by (Plate VIId). It is commonly seen throughout the season, but particularly at times when nest-building and other activities are at their height. Wilson's (1907, p. 46) description of them

"attempting to cut out each other's tongue" is a good one, but it does not appear to be confined to females as he suggests.

Pecking seems to ward off strangers from the occupant's territory and at the same time discourage would-be stealers of stones. Nests are built just far enough apart to prevent clashes, the birds being unable to reach each other unless they lean forward and stretch out.

7. *Postures and Noises which suggest Nervousness*

It seems remarkable that a penguin should show so little outward sign of emotion when, for example, its mate or eggs are suddenly removed, or other birds are lying dead around it. All previous observers are agreed on this. However, little attention has been paid to attitudes which suggest nervousness and could therefore in some degree be attributed to emotion. The following possibilities are worthy of further study; they were seen more frequently in shy birds (i.e. those that ran away readily) than in the more aggressive ones:

Flipper movement. When an Adélie seems worried or puzzled by a strange object, or seems unsure of its surroundings, or of the reception it will receive from nearby birds, it will flick its flippers to and fro in a jerky fashion, often keeping body alert for a hasty retreat. Of very common occurrence, particularly among non-breeders when wandering round the periphery of colonies, it was also seen when the birds encountered men away from the breeding areas.

Forehead feathers. A study of the great variety of facial expressions of the Adélie with the aid of motion and still photographs would be of value in elucidating what to the human eye appear to be trivial movements, but to the birds themselves are no doubt of the greatest importance (see section on individual recognition, p. 73). For example, the rolling down of the eyes and the raising of the occipital crest are seen in many displays and attitudes and are by no means confined to aggressive acts. The occipital crest is raised in association with a number of different positions of the head. The raising of the forehead feathers, together with smoothing of the occipital crest, however, seems to be primarily associated with nervousness, and was seen as frequently among birds at nest-sites (Levick, 1914, Figure 30) as away from them (see Plate VIIIe, the "wanderer" on rock to right of pair in nest-relief ceremony).

Head movements. Jerky and rapid head movements in all directions are often seen in nervous birds, especially late in incubation or after the eggs have hatched when they are uncertain whether to defend the nest or to run away.

The call note "aark" is a noise which in some, but not in all, circumstances, may be associated with nervousness. For example, it is heard in adults before entering the sea (p. 45), and repeated by nestlings with even greater persistence before plunging in for the first time (p. 62), and by frightened birds when chased.

When walking among nest-sites Adélies hold themselves in a very characteristic manner, keeping feathers tight against their bodies, necks elongated, and flippers right back. It seems as though they are trying to reduce their width to the minimum to avoid pecks delivered from neighbouring nests. (See Plate VIIIg, the "wanderer" on rock to right of pair in nest-relief ceremony).

The mutual display. Two birds at a nest, if approached carefully, and thus not suddenly frightened, often join in the quiet mutual display. This reaction was very constant, and after becoming more familiar with the behaviour of marked Adélies it seemed that firstly, the birds, a little nervous, were going through an act of "reassurance" and confirming each other's presence, and secondly, that this reaction was confined to true pairs or birds of opposite sex "keeping company".

Since returning to Britain and having the opportunity of reading some literature on behaviour, I think it probable that the mutual display here is a displacement activity (p. 48), perhaps a result of a conflict between a desire to flee and to attack. Whichever interpretation is favoured, "reassurance" or displacement activity or both together, it is important to realise that it was not seen only as a result of human interference, but over and over again as a result of other minor and major disturbances. For example, in the course of a fight during the occupation period, which constitutes a major disturbance, pairs standing two to three nests away were seen in quiet mutual display at its lowest intensity; these birds were slightly nervous. Nearer the battle, the intensity would be higher, while at adjoining nests, and between bouts among the

fighters, the loud mutual display would be seen at its highest intensity. Mutual displays seen during a fight therefore appear to be closely related to nervousness, though in fighting they are usually of much higher intensity. (See also section on individual recognition, p. 73).

8. Copulation

The act of copulation varied among individuals, the typical pattern being as follows. The female lying or standing in the nest-site, is gently manoeuvred into a suitable lying position by the male, who walking round the nest in a deep bow (p. 33) with flippers to side, finally approaches from the side. Then, beating his flippers slowly with head still bent low, he mounts about half way along her back, his bill vibrating as it comes in contact with the mandible and chin of the now upturned vibrating bill of the female. The most prolonged phase of the act now occurs, the male treading on her back and gradually moving backwards, his tail wagging from side to side against her upturned tail, while mutual vibration of bills against chins and the male's flipper movements continue. The climax comes as the male's feet reach her rump (Figure 10) and there is a fairly hasty lowering of his now protruding cloaca and a brief contact made with the protruding cloaca of the female. Immediately afterwards the male jumps off and walks around to his place by her side with his head bowed, while the female flirts her tail upwards and forwards in jerky movements. After the act, both birds are commonly seen to shake their heads and swallow (p. 44).



FIGURE 10. Copulation; just before contact. The male is treading the female's back.

From my earliest observations in October 1948 and onwards, no instance of the female's bill being placed inside that of the male, as described and illustrated by Roberts (1940, p. 209 and Figure 18), was seen. The French workers are also agreed on this (Sapin-Jaloustre & Bourlière, 1952, p. 51).

Most often the male mounted straight away with very few preliminary movements, but at other times bowing and coercion might be prolonged. An unresponsive female sometimes stood up after the male had mounted, or opposed his efforts to keep her bill pointing upwards during bill vibration. At other times, by keeping her bill pointing upwards, a female would encourage an unresponsive male to continue treading until a brief contact had been made.

Although copulations were most frequent during spells of good weather, the urge between some birds was so strong that it was seen even when weather was at its foulest. On one occasion a bird was attempting copulation when the wind was blowing at over 60 m.p.h. With flippers working faster than usual, the male appeared more intent on keeping balance on his partner's back than anything else, but a brief contact was made.

On November 21st, 1948, the following notes were made on undisturbed birds from the observation tent:

The temperature was 22° F. and it had been snowing and drifting continuously for over twelve hours with a wind blowing up to 30 m.p.h. One of the marked pairs in the small colony just outside the tent was at Nest III, and their first egg had been laid on the previous day. They were exceptionally late breeders, and by their behaviour were almost certainly unestablished. They had been seen copulating once before on November 14th. At 1300 hrs., the male was standing by, so the female must have been lying on the egg, though it was not possible to read her mark, as nothing but the top of her head and bill showed above the snow. At 1545 hrs., the male was seen finishing coitus, but it was not possible to observe whether contact had been made. The female was now well exposed in spite of the continuing blizzard and the fact that the neighbouring birds were becoming more covered. The male must have trampled down the snow around her during the past three hours. For the following ten minutes he appeared to be in a dilemma. Very restless, he was constantly walking off to the periphery of the colony, disturbing the other birds as he passed them, only to walk back again and join with his mate in a quiet mutual display. He was probably looking for stones, but all was a bleak white waste. The female changed places and he settled down on the egg which by then must have been covered with several inches of snow.

Five hours later, with weather even worse and visibility down to a few yards, the male had changed position again and was now attempting copulation once more. Only part of his mate's back was visible and he was doing his best to keep on it, while vibrating his bill, working his flippers and wagging his tail; but to no avail. At each attempt to get a footing on her ice-covered back he slipped off. After the fourth attempt, he continued his copulatory movements and trod the snow at her right side instead of her back. He would, doubtless, have given up long before had it not been for his mate which kept her bill pointing upwards all the time. There could have been no contact as the female's cloaca was well below the snow level. The sexual impulse must be great when these acts are performed under such adverse conditions. The second egg was found two days later. The female departed to sea, leaving her mate to incubate, but on November 28th the nest was empty and deserted.

Bagshawe (1938) distinguishes between attempted (or incomplete) and complete acts of copulation in his Gentoo and Chinstrap Penguins. In the Adélie, because of variation in time taken during the last phase, it was sometimes difficult to be certain whether the act was completed or not. However, both were seen during the occupation period, and also, though less often among birds at empty nests during the re-occupation period. It was not seen in any of the marked birds attending eggs or chicks. My impression was that incomplete acts were more common among birds that, in other respects, behaved as unestablished breeders, and like the ecstatic display (p. 32) were fewer in the established breeders. These views need confirming with marked birds of known age. In support, however, Table X from Bagshawe's data (1938, Tables VII-IX) not only shows that complete acts were seen from the very start, but that they were more frequent than incomplete acts during the first two weeks. Could this fit in with the fact that, like the Adélies (p. 25), the inexperienced Gentoos were coming into breeding condition later, and that many of the early complete acts were performed by experienced birds?

These observations suggest that what Roberts (1940, p. 209) and Falla (1937, p. 77) interpreted as normal acts of "trial and error" behaviour in sex recognition, were isolated examples of abnormal behaviour which could be better explained in terms of homosexuality or inexperience.

Two examples of abnormal copulatory movements should be mentioned. On October 14th, 1950, a number of early occupants at a small rookery had been collected for dissection. One had been left on the snow slope and was lying breast uppermost. A male, who had probably been disturbed from the rookery, wandered down the snow slope, and approached the dead bird in the usual pre-coition manner with head down as though bowing, and then mounted the breast in an attempt to copulate. He came off again as there was no response and was then collected for dissection. The second type of observation concerns a few examples of unmarked adults, almost certainly non-breeding wanderers or perhaps unsuccessful breeders, seen attempting to mount chicks when at the crèche stage. They got no further than putting one

foot on the chick's back, but the preliminary movements were typical; moreover, in such instances there were no signs of aggression.

9. Nest-building

Nest material generally consisted of stones, though bones from the remains of chicks of previous years were occasionally incorporated. Most observers (e.g. Wilson, 1907, p. 46; Gain, 1914, p. 9 and Levick, 1914, p. 59) record that the female sits in the nest and waits for the male to bring stones, the whole process being closely linked with courtship. Rudmose Brown's statement (Clarke, et al., 1913, p. 250) that both sexes take an equal share in nest-building is, however, nearer the truth. By marking the birds as soon as they arrived in 1950, it was possible to prove that both sexes built but that the male usually showed more initiative than his partner. Moreover, both sexes were seen to build nests alone.

The function of the nest and of nest-building appeared to be chiefly to raise the eggs and incubating bird above ground level, thus lessening the danger of flooding during thaws or of being buried by snow during blizzards. The nest hollow was also shaped to fit the bird when lying on the eggs.

During a thaw one nest was found with a stream of ice-cold water pouring through it. The lone incubating male, his eggs half submerged, was reaching forwards, collecting and arranging stones around him. Next day the eggs were above the water level and dry, though the stream still passed on either side of the nest. The eggs eventually hatched.

Nest-building by Adélies, contrary to the behaviour of some other species of bird, did not appear to have any particular function in courtship between a pair, for, as already stated, Adélies of either sex (usually male) were often seen building large nests alone. Moreover, the size of the nests varied considerably with individuals, the situation, the amount of snow on the ground, and the availability of stones. Plate Vc, for example, shows a pair with an egg but no more than a few stones to represent their nest. It is inconceivable that the building of such a paltry nest played a significant part in the formation of the pair-bond, though the possibility that they might have built it conscientiously, only to lose all as a result of pilfering neighbours (see below) must not be excluded. This needs more investigation.

Successful nest-building in a crowded colony was dependent on the partnership of two birds, and during such activities some of the displays associated with pair formation and maintenance of the pair-bond (e.g. the mutual display) were seen.

The fact that two birds occupying a nest-site were of opposite sexes was confirmed on many occasions in marked and dissected birds, provided, of course, that they were not unnaturally mixed up as a result of disturbance. The normal behaviour was for the male and female (this might be a mated pair, or two "keeping company") to alternate their duties, one lying or crouching in the site, periodically arranging stones around it or scraping them from under to improve the shape, while the other walked off to collect stones. The collector, making no effort to arrange the stones, dropped them haphazardly either in front, or at the side, or sometimes even upon its partner, and would often initiate a quiet mutual display (p. 34) which might or might not be reciprocated by the other. The response of the bird occupying the site varied greatly. Sometimes it completely ignored the constant addition of stone after stone, at other times and perhaps only a few minutes later it arranged them as soon as dropped and joined with its partner in quiet mutual display. Such sudden changes cannot be explained solely in terms of gonad development and/or "releasers of behaviour mechanisms". The whole psychological background of the two birds has to be considered, as well as external factors such as weather, degree of disturbance in neighbouring nests, or the possible effect of proximity of the human observer; this constitutes an impossible task.

Weather and snow cover had considerable influence on nest-building, the greatest activity being observed during a thaw when stones were more easily available. Activity was usually later at snowbound colonies than at the others (Plate VIa), though in some situations (Plate VIc) well-made nests were found on snow at least one foot deep.

Stealing of stones was a common practice among Adélies. Bernacchi (Sharpe, 1902, p. 131) writes of Adélies at Cape Adare

"They are shameless thieves. The thief slowly approaches the one he wishes to rob with a most creditable air of non-chalance and disinterestedness, and if, on getting close, the other looks at him suspiciously, he will immediately gaze around almost childlike and bland, and appear to be admiring the scenery. The assumption of innocence is perfect; but no sooner does the other look in a different direction, than he will dart down on one of the pebbles of its nest and scamper away with it in his beak."

Again, Levick (1915, p. 53) writes:

"There was a particular cock who was an inveterate thief. I think that every stone in his nest had been stolen from neighbours. As he slunk about the colony, his guilty conscience made him smooth his feathers close against his skin and this made him look smaller than the other birds."

These quotations are delightful descriptions of incidents repeated time and again during nest-building. It is difficult not to treat such behaviour anthropomorphically. More detailed investigation is necessary before such statements as are quoted above can be condensed into simple scientific terms. Meanwhile, I favour the anthropomorphic interpretation of the early naturalists; however, Levick's "guilty conscience" look has been classified in this paper as a "posture suggesting nervousness" (p. 39), but there is no reason why his interpretation should not be more accurate than mine.

Roberts (1940, p. 213-14) writing about the Gentoo does not agree with these anthropomorphic interpretations, but raises two valuable points which are still in need of further investigation in penguins. He recounts an incident in which a male at Nest C was seen transferring stones from his own nest to another empty nest nearby, and while he was away a neighbouring male at Nest B took advantage of the opportunity to steal from C. When the bird from B arrived at Nest C at the same time as the rightful owner:

"... the bird from B stopped, looked aside, and gave every indication of having no interest in the matter until the owner of the nest had left with a pebble. He then waddled straight in and helped himself with great haste; in marked contrast to the slow selection of the other bird. The important point to notice, is that whichever of the two arrived first, the bird from B waited every time until the bird from C had gone. After about ten minutes of this, the bird from C caught the 'thief' taking a pebble and pecked at him viciously. The bird from B made absolutely no attempt to retaliate, but fled back to his own nest. I suggest that this behaviour was due to the fact that a pecking order had been established, and that such incidents give no proof of conscious purpose or intelligence."

For his second point, Roberts, quoting Lorenz (1938), suggests that this behaviour can also be explained by the fact that birds were far more aggressive when fighting close to their own nests than away from them. Therefore positions in the "peck order" at any one time could be explained according to which bird was nearest to its nest when two birds last met in conflict. There can be no doubt that territory and the "peck order" are important factors, but it is nevertheless difficult to believe that no vestige of conscious purpose or intelligence is shown by birds in this very variable practice. For example, it seems that Sheath-bills show intelligence in paying more attention to the nests occupied by inexperienced breeders than experienced breeders (p. 25), and Skuas by harrying the weakling and stupid and not the healthy chicks (p. 66). These predators probably know their surroundings, and probably also know their prey as individual birds (p. 66). Similarly, it seems likely that penguins knowing each other as individuals, do show some conscious purpose and intelligence in selecting the nests which they think they can most easily plunder, and in this connection it is important to realise that age and breeding experience must play an important part.

Why is stealing such a common feature of an Adélie community? It must surely have some function. I suggest that it ensures a good supply of stones for those nesting towards the centre of large colonies, thus limiting long walks (and the resulting disturbance of neighbours and inconvenience for the collector) to areas outside where stones are still free for all.

Levick's (1915, p. 61) experiment with painted stones, though designed to test the Adélies' preference for different colours, also demonstrates admirably the way in which a pile of stones placed near a nesting area will eventually become distributed widely in all directions.

Time of nest-building. Nest-building was seen throughout the season, because breeding routine events overlapped considerably, but the greatest activity occurred when the population was reaching its first peak before egg-laying, and again during the re-occupation period. The amount of competition for territory at different times of the season had an important effect on the size of nests and behaviour of individual birds.

Nests were often large when there were only a few birds at nest-sites, as at the beginning of the season when most were still at sea, and again towards the end of the re-occupation period when many birds were otherwise engaged feeding chicks. Moreover, these large nests could be kept by lone birds which could walk off to collect stones without risk of losing any during their absence. Towards the end of the season when the chicks were in the crèches, some of the largest nests belonged to lone non-breeders or unsuccessful breeders (Plate Xe).

When the colonies were crowded and competition for stones great, efficient nest-building, as already mentioned, was dependent on the partnership of two birds or on successful stealing.

The importance of nest-building after the nest-relief ceremony (p. 47) does not appear to have received attention before. Richdale (1951, p. 38) suggests that "fiddling with nesting material" in the Yellow-eyed

Penguin immediately after the nest-relief ceremony during incubation is a displacement activity. I do not think this is so with the Adélie, where nest-building appears to serve a definite function. Incubating birds are alone for considerable periods and they cannot leave the eggs or young chicks for fear of predation from Sheathbills or Skuas, or destruction during bad weather. The stones gradually diminish as it is impossible to defend the nest the whole time from pilfering nest builders. After the change-over, the relieved bird therefore collects a good supply of stones which are later arranged by the incubating bird. This duty is carried out conscientiously during the incubation period but gradually wanes as the chicks grow larger, and it is finally abandoned when the chicks go into the crèche.

Unusual nest-building. Adélies are occasionally seen picking up small lumps of ice. A typical example was recorded on October 30th, 1950, when a few new arrivals were still coming in and occupying territory.

At 0900 hrs., two newly-arrived and conspicuously clean birds were standing asleep in separate positions on the periphery of Colony III, just in front of the observation tent. Eleven hours later they were both building actively, but all the stones collected were small. The bird on the left was twice seen to pick up a piece of ice. These contributions were however short-lived, as they were being dropped into the small thaw puddle which presumably represented the nest-site. Other aspects of this bird's behaviour suggested that it was a first-time breeder.

Some of the activities of the "inexperienced" pair at Nest III on November 21st, 1948, have already been mentioned (p. 41). At 2215 hrs. the male was again in quest of something and was walking around the colony in the raging blizzard, upsetting the others. His examination of a neighbour's tail, the only visible sign above the snow, terminated abruptly when it moved just as he was about to pick it up. He was, no doubt, in quest of nest material, but none was visible anywhere.

In studying marked birds of known age, it would be interesting to know how much of these unusual activities could be attributed to age and breeding experience.

10. Other Postures and Movements

Stretching, Yawning, Head-shaking and Swallowing, are characteristic and very common attitudes, which are important functionally, and possibly also important in displacement activities (p. 48). They can be seen separately, or following each other, for instance, yawning after stretching, or swallowing after head-shaking.

Stretching was always performed by the relieved bird after the nest-relief ceremony, and usually repeated several times.

Yawning (Plate VI f) might follow after stretching, but was usually seen by itself. This posture, first illustrated by Gain (1914, Plate I, Figure 4) and later by Levick (1914, Figure 3) has also been described by Sapin-Jaloustre and Bourlière (1952, p. 43). Photographs show that the neck may be stretched out (Levick) or not (Gain) but the latter is more usual, the head being extended back and sunk on the neck. It does not appear to elicit any response from neighbouring birds.

Head-shaking, seen in most situations, but especially after copulation, the mutual display, the nest-relief ceremony, feeding chicks, or disturbance, was one of the commonest activities of the Adélie. It was frequently seen in bad weather when it was associated with shaking. Murphy (1936, p. 388) states that the external nostrils of the Adélie are obsolete and closed. My own observations do not support this, for, with the bill closed and a sound resembling a little sneeze, beads of moisture were often blown from them during a head-shake. I have seen this attitude in all twelve species of penguin, both wild and captive, that I have had the opportunity of observing.

Shaking, commencing at the head and spreading down the whole body, had much the same appearance as in a dog. It was most frequently observed during sleet, drift or snow, and after coming out of water.

Swallowing usually followed head-shaking and was a very common activity. Faint rasping sounds could be heard as the papillated tongue slid to and fro in contact with the roof of the mouth.

Preening (Plate VII f), is much the same as in other birds, though with a few modifications due to anatomical differences. It was observed most often in the following situations: *i.* after landing from the sea, when birds usually paused for a brief period on the snow slopes or rocks; *ii.* during a thaw, or in wet sleety weather; *iii.* before going to sea. I have often observed marked birds at nests preening and using their oil glands shortly before they were relieved by their mates.

Walking. The Adélie has its own characteristic way of walking, which being more like the human gait than that of any other species of penguin, has earned for it many anthropomorphic descriptions. Its contrast to the "osteoarthritic" but regal gait of the Emperor, or the jerky, almost bouncy movement of the Chinstrap, is plainly shown in the films now available on these species (see film bibliography). The flippers are held in a number of different positions all of which, no doubt, have significance. Plate VIIa illustrates the most usual position when the birds are not disturbed or worried. In a blizzard or gale the flippers are held tightly pressed against the body, like the normal flipper position in the Emperor. When walking across the sea ice, individuals showed a reluctance to take the lead.

Tobogganing is the most economical method of moving over a smooth and soft snow surface, and is more highly developed in the Adélie than in any other species, with the possible exception of the Emperor. When unhurried, Adélies toboggan at the same speed as when they are walking, and they frequently alternate between the two. The feet propel the bird from behind, the tail sticks out horizontally, and the flippers gently alternate (Plate VIIc). When escaping, they fall on to their breasts, and with both flippers and feet exerted to fullest measure, they move away as fast as a sprinting man. They are at an advantage over man in soft snow.

Departure to Sea. Adélies depart to sea in parties of up to, but rarely more than, about one hundred birds. No matter how vast a crowd may be waiting on the edge, they never go into the sea all together. There is usually a great deal of preliminary excitement, scrutiny of the water below, and nervous jostling on the ice (Plate VIIb) or rock edge. Then one bird takes the plunge, and others follow in quick succession. After a number have gone, there is a hold-back which spreads instantly throughout the ranks on land. The excitement has then to build up again before more take the plunge. This initial plunge into the sea is rarely taken unless the departing birds, having repeatedly exchanged the call-note *aark* with others in the water, actually see incoming birds land. Reluctance to be the first into the water frequently results in skirmishes. A bird in the front rank may resist the encouraging pushes from its neighbours, and breaking free, run round to the rear of the party. No other penguin exhibits such nervousness and caution at the water's edge. Adélies have no doubt developed this behaviour because of the Leopard Seals (p. 69 and Plate XIIc) which frequent their normal habitat among the pack ice.

"*Porpoising*" (Plate VIId) is the normal swimming movement of penguins and is used by no other birds. Swimming for several yards under water with the flippers, the Adélie surfaces, and, barely rising as much as a foot, vanishes underneath again a few feet ahead. It no doubt breathes each time it surfaces, and can travel at 15 m.p.h. or more. When surfacing, the flippers are held to the side and slightly forward as a result of the powerful stroke before coming into view.

Ardley (1936, p. 355) describes in detail the actions of the Adélie, swimming under the surface, as seen from R.R.S. *Discovery II*. The flipper movements are the same as the wing movements of terrestrial birds. Penguins "fly" under the water. Swimming on the surface, the bird appears low in the water with its head and tail sticking upwards; the feet are idle or used for steering, and the flippers propel the bird. This way of swimming is not used much as progress is slow and no doubt fatiguing.

Leadership of penguin parties presents some interesting problems for future workers of comparative ethology. It is generally assumed that leadership of flocks in flight (e.g. geese) is by experienced birds. This does not seem to be so in the Adélie. Attention has already been drawn to their reluctance to take the lead when walking over the ice or plunging into the water. This might also apply to parties in the water (see Donald, quoted by Sharpe, 1902, p. 136).

Landing from the sea. When about to land, birds porpoise towards the icefoot, raise their heads when about twenty yards away, then, vanishing beneath the surface, do not appear again until they suddenly pop out of the water one by one onto the ice (Plate VIIf). Sometimes they land erect, and, balanced by their tails, run forward and pull up sharply. At other times, still landing on their feet, they fall onto their bellies and toboggan along the snow surface in a most enchanting manner.

A spectacular and unusual arrival was observed at Hope Bay on December 18th, 1948. In spite of the low tide, large numbers of Adélies had arrived, and were trying to clear the icefoot. Offshore, the water was in a turmoil as party after party failed to do more than crash themselves against the ice cliff and rebound back into the sea, or, completely missing the ice, splash back feet first. For nearly an hour this continued

without a pause, some swimming around, others diving away and porpoising back again, with all the time a regular succession of attempted leaps. As the tide rose some succeeded in scrambling out. Here was a unique opportunity to assess the limits of the Adélie's jumping abilities. Sharpe (1902, p. 133) quotes three feet as an easy jump, and Wilson (1907, p. 40) agrees. The highest leap observed by Levick (1915, p. 73) was five feet above the surface of the water. From the photograph (Plate VIIe) taken at Hope Bay, it appears that the birds were jumping from three to four times their own length; in other words, at least six and probably seven feet.

When landing onto rock or shingle a different technique is used; the birds, landing flat on their bellies, clamber into the upright posture and walk in. At Signy Island, where the icefoot was quickly removed from the rocks by the ocean swell, this was the usual method of landing. An Adélie parent can be picked up by gigantic waves, hurled three times against a vertical piece of rock, and still land apparently unharmed, even though, as dissections showed, there is no protective layer of blubber beneath the skin at that time of the season. However, Lowe (1933, p. 487) has counted as many as 300 feathers on one square inch of a young Gentoo Penguin's body, and it seems probable that these specialised feathers serve to protect the penguin under such conditions. For when slightly raised (Plate IXb) they present an impressive buffer more than half an inch in depth.

Sleeping. Three different sleeping postures were observed: lying down, standing up with head sunk on the shoulders (this was the most usual attitude), and standing up with bill tucked behind one or the other flipper (the least common, and rarely seen, attitude). Wilson (1907, p. 41) comments on this third attitude as a possible relic of the days when the penguin had fully developed wings.

Excretion is explosive, a streak of cloacal contents being squirted from one to two feet. When resting, chicks tuck their heads beneath their parents leaving their vents pointing outwards (Plate IXb), nest hygiene being thus maintained from an early age.

Incubation. Two different postures were observed, crouching and lying. Plate IXa shows the typical crouching position over a newly laid egg, and Plate IXb over a young chick. Crouching over the newly laid egg will prevent it from freezing, protect it from predators and reduce incubation to a minimum until the second egg has been laid. Plate VIIIk shows a bird lying in the typical incubation position. The parent will also lie over the newly hatched chick.

Frequent observations made at Hope Bay during strong gales (60–70 m.p.h.) and heavy drift revealed that incubating Adélies, unlike those away from the nest, did not always face into the wind. Thus, it was not uncommon to see an incubating bird facing in the opposite direction and the wind blowing its tail at right-angles to its body, the feathers on its back clotted with lumps of ice from the drift.

Feeding chicks: i. the food-begging attitude and the parent's response. When the parent bends over it, the newly hatched chick begs for food by vibrating its bill against the mandible or tip of the parent's bill. As the chick grows and feeding usually becomes associated with the arrival of a parent from the sea, this attitude changes slightly. Food-begging (Plate IXd) follows quickly after the mutual display (Plate IXc) and associated noises (or greeting ceremony, see p. 74). When begging for food, the chick, "peeping" continuously, stretches its neck upwards and vibrates its bill along the parent's mandible, sometimes seeking the gape as if requesting it to be opened. The parent holds itself tensely in a characteristic attitude with head arched over the chick, or relaxes to make a number of jabbing movements with its bill at the chick's head, apparently trying to curb its eagerness and importunity. The parent's response may also confirm individual recognition, the parent being able to recognise its chick (when in the crèche) by its actions as well as by its features and voice (p. 36). Food is regurgitated after a few convulsive movements of the body and neck, and the chick feeds from inside the parent's gape at the back of the throat (Plate IXe). When the chick has swallowed some food, the parent re-swallows the remainder in a characteristic manner. A constant feature of feeding was the amount of clear mucous secretion, presumably salivary, that was produced by the parent bird.

ii. Feeding chases (Plate Xc) are first seen about a week after crèche formation and continue until the chicks are fully grown. After the initial greeting ceremony, and sometimes a hurried feed, the chick is drawn away from the crèche. It follows its parent eagerly, stumbling in the snow or over rocks, and "peeping" continuously for food. The parent stops periodically and, after a few preliminary jabs, feeds the chick.

When all the food has been given, the parent's attempts to escape to sea are opposed by the chick which continues the chase at an increasing speed. The parent stops suddenly and turning on the chick covers it with vicious-looking jabs. This continues until the chick wearies and returns to its colony, leaving the parent to depart alone.

These feeding chases appeared to have several functions. Feeding away from the crèche minimised interference from other hungry chicks, and from adults occupying territory. It gave the chicks confidence when away from the protection of the crèche, and sharpened their alertness to the predators around. It kept the chicks fit and taught them the route their parents took to the sea; possibly it even taught them the direction the parents took when swimming away from the rookery, for when full grown, the Adélie chicks plunge for the first time into the sea quite independently of their parents (p. 62).

11. *The Nest-relief Ceremony*

The nest-relief ceremony incorporated several displays and postures. It was seen between a breeding pair when one of the birds returned from sea, either to take over incubation (Plate VIIIa-1) or to care for and feed its chicks during their first month before the crèche stage. Nest-relief ceremonies were therefore first seen during the latter half of November when the females were returning from their period at sea to relieve the males (p. 52). The typical sequence was described in the field at Hope Bay on November 26th, 1948, the sexes of the birds being confirmed later by dissection.

A female Adélie was tobogganing up the snow slope with a few other returning birds. Beautifully clean, they were dispersing from the party without hesitation in different directions, no doubt bound for their nests. This bird paused for about half a minute on the edge of a colony, her head working in all directions, to take in the scene which, owing to some heavy snow, must have changed considerably since she left her mate about a fortnight earlier. Then, a little hesitantly, and pecked by incubating birds, she walked through the colony towards the nest. The couple showed every indication of recognising each other as soon as she arrived, and immediately joined in the loud mutual display, a very noisy affair, the male crouching in the nest, the female facing him a few inches away. Then there followed a succession of bowing movements initiated by the female, in which heads were bent low, within a few inches of the partly obscured egg, then up again with a repetition of the loud mutual display. After this had been repeated several times, the male stepped off the nest and the female took over, tucking the egg underneath her gently. She settled down quickly, lying on the nest, but rising from time to time to change position. The male stood by, constantly stretching to the fullest height on his toes. During the next fourteen minutes, the female remained lying on the egg, but responded to two quiet mutual displays initiated by her mate, who otherwise stood by her side stretching or dozing. Occasionally, he would walk a few steps away, but quickly returned to her side again. Eventually he started collecting stones. This was the final duty the relieved bird had to perform before it departed to sea to break its fast.

The usual variations in this ceremony, whether male or female returning, were in the time taken between the different stages, the intensity and frequency of the mutual displays, and the conscientiousness and energy put into nest-building. The general pattern was, however, constant. The bird returning from the sea found its own nest and, recognising its mate, immediately joined in the loud mutual display. This, repeated several times with mutual bowing movements, was followed by the change-over, the new arrival settling down on the eggs (or chicks) while the relieved bird stood by and stretched. Before the relieved bird walked off to collect stones, there were more loud mutual displays, but with lessening intensity, and often a few quiet displays. As each stone was dropped in front or at the side of the incubating bird, a quiet mutual display was often seen. When the relieved bird stopped building it departed to sea, leaving its mate alone on the eggs, arranging the stones in a desirable position.

The same ceremony was seen after the eggs had hatched, but with less intensity as the chicks grew larger and, of course, ceased altogether when both parents abandoned their guard at the nest and their chicks went into the crèche. The importance of the mutual display seen in the nest-relief ceremony and the parent-chick relations has already been discussed (p. 36-37).

12. *Displacement Activities*

Richdale (1951, p. 35-42) was the first to describe displacement activities (then called substitute activities) in penguins. He found that the three situations described by Tinbergen (1939) for birds in general, held also for penguins. In the first, the animal is "under the influence of two antagonistic drives, the simultaneous expression of which is a physical impossibility"; the second happens "when an action in a chain is frustrated"; and the third is seen "following upon the exhaustion of the normal reaction to stimuli". Richdale also describes a fourth category which he suggests is not included in Tinbergen's descriptions, as, for

example, when a parent penguin, unable to respond to the pleadings of chicks for food, does something else instead. But could not this come into Tinbergen's second, or even his first, category?

I was not aware of this aspect of animal behaviour when I left the Antarctic in 1951, so what follows concerning the Adélie has been extracted subsequently from field notes, and should be regarded as tentative. The subject of displacement activities in penguins is in need of further investigation.

The association of the *ecstatic* and "*bill to axilla*" displays with nervous strain, and some of the isolated examples quoted on page 32, suggest that these activities may be related to displacement activities.

The mutual display and its possible relation to displacement activities has already been discussed (p. 39).

Postures and noises which suggest nervousness (p. 39), especially flipper movements, variation in the forehead crest and head movements, may be important displacement activities, but in our present state of knowledge I prefer to leave them under this heading of "nervous" attitudes.

Nest-building by the relieved bird after the nest-relief ceremony appears to serve a definite function (p. 43) and cannot be compared with Richdale's (1951, p. 38) "fiddling with nest material" observed under similar conditions. However, an Adélie, when not knowing whether or not to flee or to defend eggs or young, would sometimes rearrange stones around its nest; this was almost certainly a displacement activity. Another possible example, though it is more likely to be an assertion of territorial rights, is the nest-building observed in unsuccessful breeders, non-breeders or even yearlings (p. 27). Examples of unusual nest-building and their possible relation to displacement activities are discussed on page 44.

No doubt, it is in those often inconspicuous but common attitudes such as stretching, yawning, head-shaking and swallowing (p. 44), that most of the Adélies' displacement activities are to be found. Preening, however (unlike Richdale's observations in the Yellow-eyed Penguin), seemed to be largely functional.

D. THE BREEDING SEASON

The Adélie is a migratory species; the breeding season starts in September and October when birds return to the rookeries to occupy their nest-sites, and ends when the young depart to sea in February.

1. Occupation Period

The occupation period may be defined as the period from arrival at the rookery until the last egg has been laid.

Date of arrival. No Adélies were seen during a sledge journey to James Ross Island in September, 1948, but a few had already arrived at the Hope Bay rookery when we returned on September 30th. They had apparently been in occupation for a day or two. On October 2nd, 1950, twelve unidentified penguins were observed crossing the ice in the direction of Coronation Island. From October 5th to 10th we were sledging along the south coast of Coronation Island to the east of Signy Island; a lone Gentoo was seen on the sea ice on the 5th, and the first Adélies were seen on the 8th, when we were camped on the east side of Amphibolite Point. Thirty had already arrived at the rookery there and were scattered thinly over the whole area. On October 9th the number had increased by only two. On the same day, fourteen were counted at another rookery in Shingle Bay. Table XI gives arrival dates from various localities (see discussion on p. 49) according to latitude.

Distance travelled. Mackintosh and Herdman (1940, Plate LXIX) give the apparent mean position of the ice edge for September and October as over 200 miles away from Hope Bay and the South Orkneys. Adélies may have to travel as far as this, if not farther, from their winter quarters (p. 65). The last stage of their journey will take them over long stretches of rough and difficult sea ice. At Signy, for example, the nearest patch of open water was nearly twenty miles away and the estimated distance for their walk from thirty to forty miles. In other parts of the Antarctic they sometimes have to walk as much as sixty miles over the ice.

Occupation of nest-sites. Birds did not travel in the dark. On October 17th penguins first started arriving at about 1100 hrs. The parties soon scattered to various parts of the rookery. It seemed that most birds

were intent on reaching some particular goal. They paused frequently, sometimes from vantage points on the tops of boulders, and with their heads moving in all directions appeared to be searching for familiar landmarks. Some accelerated on approaching a particular colony, and in two instances a bird was seen to make straight for a particular site and, after a brief pause, start to build a nest. A typical example of the difference in behaviour between the established breeder and the unestablished breeder (or non-breeding "wanderer") is given in Table VI. The established breeder walked straight up to a lone male occupying a nest-site, and both immediately joined in repeated loud mutual displays; the unestablished bird wandered around the periphery of three colonies.

Of the twenty-seven birds dissected between October 8th and 10th (i.e. during the first three days of the occupation period), seventeen proved to be males, thus contradicting Levick's contention (1915, p. 59) that the females return first, stake claims to territories, and wait for the males.

Evidence that Adélies, once established, are faithful to their old nest-sites and mates is given in Tables XII and XIII, and further discussed in the section on individual recognition (p. 70).

Colonies were usually situated in places where least snow lay at the beginning of the season. It seemed remarkable, however, that some should occupy sites such as those illustrated in Plates XIa and VIc where snow covered the rocks by a foot or more. A later photograph (Plate XIb) revealed little difference in the surrounding terrain. Levick (1915, p. 62) describes a knoll which, though perfectly accessible over hard ice during the occupation period, was surrounded by deep and dirty thaw water later in the breeding season. Nests were never built there, but a similar knoll connected by a causeway was fully occupied. Murphy (1936, p. 394) thinks that some peculiar instinctive behaviour accounts for this so-called "foresight". Could it not be more simply explained by realising the importance of recognition of the nest-site, of the differences in behaviour of the various age-groups which make up a penguin community, and the fact that they are gregarious by nature? Thus, the experienced breeders coming back and re-occupying their old sites (even though covered by snow) might well set an "example" for the unestablished inexperienced breeders. Equally important, and in need of further investigation in birds of known age, might be the nest-building activities of the non-breeders and unsuccessful breeders during the re-occupation period (p. 57). It is probable that these birds become familiar with their surroundings in readiness for the next Spring.

The sounds heard at the rookery during the occupation period give an indication of the general activities. During the first few days when very little was happening, occasional *aark* call-notes recalled the sounds so often heard among the ice floes at sea. This sound was not uttered at the colony except by adults before they departed for the sea (p. 45), until the end of the season when the full-grown young were gathering on the beaches (p. 62 and Table XVII). The noise of the loud mutual displays gradually increased, being most frequent when most arrivals were coming in. The ecstatic display was first seen and heard on October 9th, and increased in frequency as more birds occupied territories, reaching its greatest intensity before egg-laying.

Eggs. The first eggs were found at Hope Bay on November 1st, when a search over an area containing about 10,000 nests revealed only twenty single eggs. The female of a pair collected at a nest with one egg, showed a dilated and pink external orifice, suggesting that the egg had been laid a few hours previously. On dissection, the egg-shell gland was empty, but the top of the oviduct contained the ovule of the second egg. At Signy, the first eggs were seen on October 29th, one in the middle of each of two colonies.

Table XI compares the recorded dates of arrival and of the first eggs with the latitude of the colony in question. The data may not be absolutely reliable since the recorders of the various expeditions did not always state how thoroughly they examined the rookeries, and first eggs are easily missed, especially in bad weather, because they are often hidden as the bird crouches over them. It may, however, serve as a foundation for future work, particularly with international co-operation. Present information seems to indicate that latitude is less important in determining dates of arrival and egg-laying, than local ice conditions and weather.

The normal clutch was two eggs, but sometimes only one egg was laid. No nest containing three eggs was ever seen. There was no evidence to support earlier reports that penguins stole each others' eggs (they certainly cannot hold them in their bills) and the occasional records of three eggs in a nest were probably due to fighting. An egg, once displaced from a nest, might lie in a "no-man's-land" on the territory boundary from which it would soon be removed by Sheathbills or Skuas. If, however, it went beyond the boundary into another territory, the owner might roll it into its own nest which already contained two eggs.

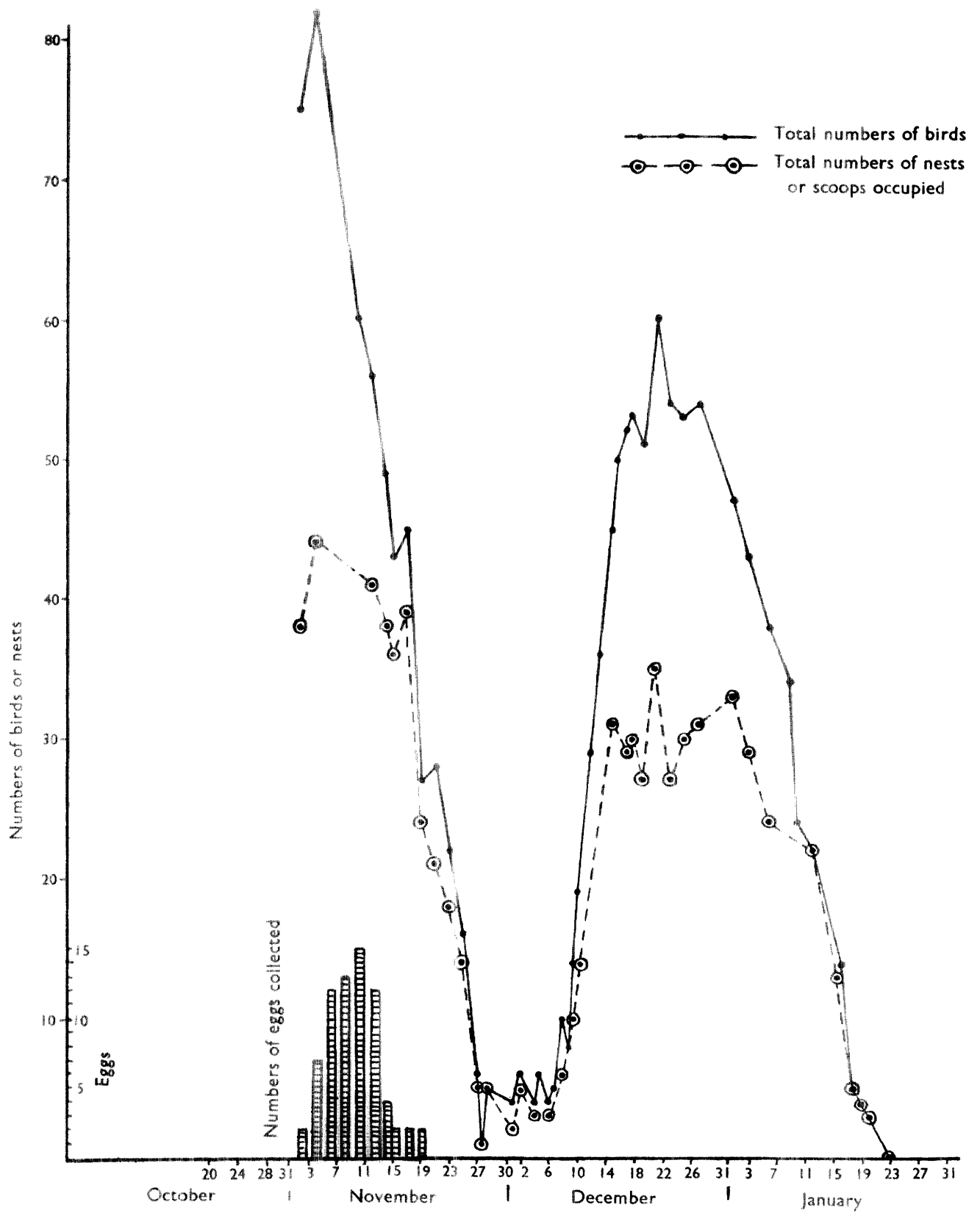


FIGURE 11. Population and nests of Colony IX at Sigriy Island, 1950-51. All the eggs laid were removed within twenty-four hours of being laid. In this experimental colony all breeders were thus made "unsuccessful".

A few birds incubating two eggs were given a third. Some accepted them, others did not, but even those that accepted them did not keep three eggs for long, as they were found with two eggs only a few days later. Gwynne (1953a) records three-egg clutches as a rarity in the Rockhopper Penguin, *Eudyptes chrysocome* (Miller) and the Gentoo Penguin.

Data on the interval between first and second eggs, reliable to the nearest day, from Hope Bay for nine nests including those mentioned in Table XIV, gave an average of 3.7 days, and for sixteen nests at Signy including the ones mentioned in Table XV, an average of 3.0 days. The range at Hope Bay was 3–4 days and at Signy 2–4 days, the average for the twenty-five nests from both areas being 3.2 days. The very bad weather during egg-laying at Hope Bay no doubt accounted for the greater interval there.

The weight and size of Adélie eggs varied a great deal. Marshall (MS) collected thirty-five eggs on the day of first laying (November 4th) at Hope Bay in 1946, and these averaged 70×55 mm. On November 5th, twenty-eight eggs averaged 69×54 mm., and on November 13th, forty-two eggs again averaged 70×55 mm.

The weights of the first seven eggs collected at the same rookery on November 1st, 1948 were 118, 120, 120, 125, 129, 130 and 138 gms. (average 126 gms.). Tables XIV and XV give some weights and dimensions of eggs collected from marked nests at Hope Bay and Signy.

Some species of penguins (e.g. the Rockhopper, *Eudyptes chrysocome*, and Gentoo) will lay again if their eggs are removed as soon as laid. To settle this controversial point in the case of Adélies, experimental colonies were selected and all the eggs removed from them within twenty-four hours of being laid. The fullest data were obtained at Colony IX at Signy which had about forty breeding pairs (see Figure 11). During the period of egg-laying, November 2nd to 19th, seventy-three eggs were collected. On an average, therefore, each female laid two eggs (some were, no doubt, taken by Sheathbills and Skuas) which is the normal clutch-size. This was confirmed by four marked pairs in this colony: two laid two eggs each, one only one egg, and the fourth (Nest 45) laid a third egg three days after I had removed the second egg (Table XV). At Hope Bay, where seven pairs were studied in marked nests (Table XIV), three laid two eggs only, two one egg only, and two a third egg. The Adélie's breeding routine is such that the female returns to sea to feed as soon as the full clutch has been laid (p. 52), but she will occasionally, though only occasionally, lay a third egg if the other two are removed as soon as laid before she goes off.

During the re-occupation period (p. 57) thousands of birds which had lost eggs earlier in the season were closely watched at both rookeries, but in no nests were second clutches found.

2. Incubation Period

Previous published records suggest that the incubation period varies from thirty to thirty-seven days, but the early workers did not define what they meant by the incubation period. At Hope Bay and Signy Island it was observed that the two eggs of a clutch rarely hatched on the same day, so the practice of measuring the period from the laying of the last egg to hatching of the first chick (Moreau, 1946) has not been used. The incubation period, recorded to the nearest day from nests in which the eggs were marked, is here given separately for the first and second eggs of the clutch, from the day of laying until the chick was completely out of the egg. The chick took from twenty-four to forty-eight hours to emerge from the shell after first chipping.

First eggs. At Hope Bay, reliable data were available for four nests only, one egg taking 36 days to hatch, two taking 37 and one 38 days. At Signy, seven eggs took 35 days, and two took 36 and 37 days.

Second eggs. Three at Hope Bay took 35, 35 and 36 days and four at Signy took 33, 33, 34 and 35 days, while another four nests at Signy with doubtful dates also gave an average of 34 days.

The average period for both rookeries combined can therefore be summarised thus:

For thirteen first eggs	36 days
For seven second eggs	34 days
For eleven second eggs (including some doubtful dates)	34 days

The longer incubation periods at Hope Bay were, in my opinion, due to the bad weather during the incubation period, and not to differences in latitude or hours of daylight.

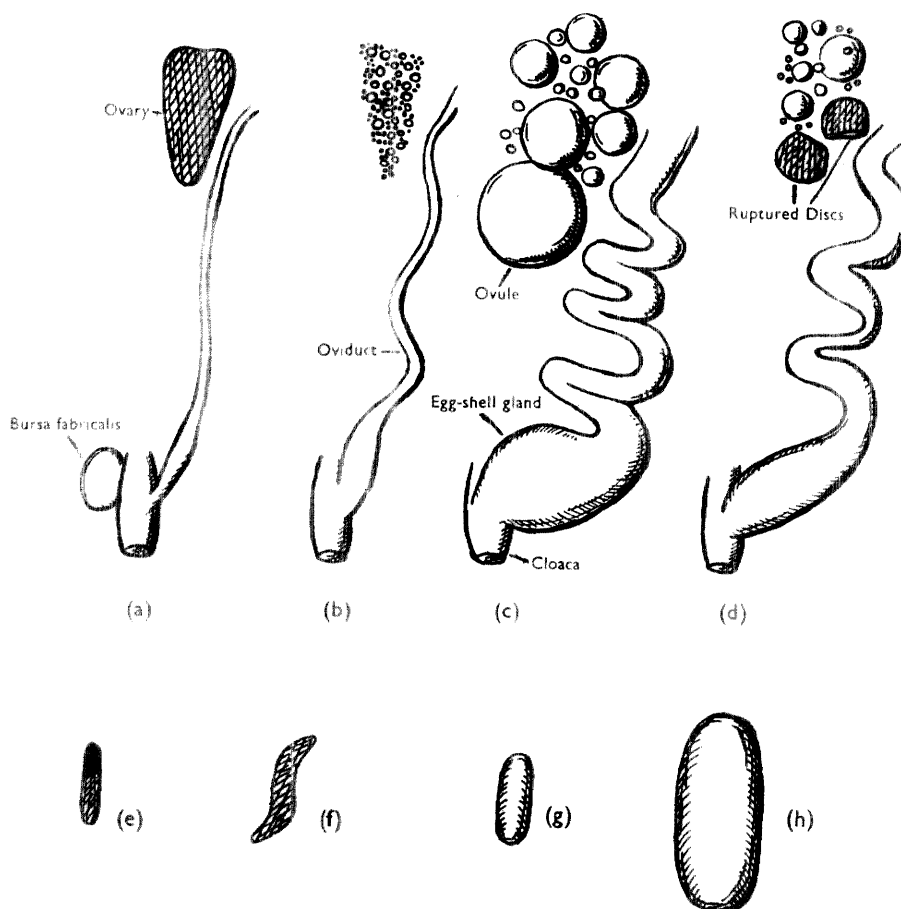


FIGURE 12. Mature and immature reproductive organs of the Adélie.

Notes: (a)–(d) female. (e)–(h) male, left testis. (a) nestling and immature plumage. (b) and (g) winter, adult plumage. (c) and (h) mature adult, before egg-laying. (d) breeding female, after laying two eggs. (e) nestling. (f) undeveloped testis.

3. The Fasting Periods

Fasting periods, two for each member of the pair, started at the beginning of the period of occupation and continued until the end of the incubation period. The existence of fasting periods was recorded by most earlier expeditions, though prior to the present study no one had measured their length. Four reliable ways of perceiving that Adélies were truly fasting were: *i.* the continual presence of bile-stained (green) excreta around the nests, in contrast to the pink excreta around the nests of any birds that had been feeding; *ii.* a steady loss in weight (Figures 13 and 14); *iii.* contracted and bile-stained stomachs, sometimes containing stones and/or fluid, also contracted intestines and reduction in mesenteric, mediastinal and skin fat (ascertained in many hundreds of dissections), and *iv.* absence of tracks on the sea ice going away from the rookery, this latter being reliable only under certain conditions and before the “wanderers” returned (p. 26).

Once they had arrived at the rookery at the beginning of the season, breeding Adélies remained at their nest-sites for about $2\frac{1}{2}$ to $3\frac{1}{2}$ weeks without food. There were occasions when one of a pair left the nest-site temporarily, for example, to collect nest material, eat snow, or as was often observed in females during bad weather at Hope Bay, to shelter behind a rock on the edge of the colony. It was most unusual for them to return to sea, but an exception from Nest 6 history is given below. As soon as nests had been built and eggs laid, the females (not the males, as wrongly stated by Levick, 1915, p. 67) walked off to sea to feed, thus ending their first fast. The males, remaining alone to incubate the eggs, continued their first fast for another 2 or $2\frac{1}{2}$ weeks until their mates returned from the sea. Another and shorter period, the second fast, was completed by each sex, by which time the eggs were hatched or hatching. The longest first fasts recorded were 42 days for a male (Nest 40 at Signy. See Table XVI and Plate VIII) and 23 days for a

female. Table XVI gives the fasting periods from some of the marked pairs at Hope Bay and Signy. Data for the first fasts from Hope Bay are incomplete because of the loss of all October field notes (p. 9). Data from Signy are also not quite complete as we were away sledging on Coronation Island when the first Adélies were seen. Birds were not marked until October 17th, 10 days after the first arrivals had been observed on the Coronation Island rookeries. The average lengths of the first fast for seven males and seven females marked on October 17th or 18th were at least 40 and 21 days respectively, possibly a few days longer. Hence the male that returns early has sufficient body reserves for a fast of at least six weeks, and the female for one of over three weeks. To this period can be added at least two or three more days for the birds' long journey across the sea ice from their winter quarters. Stomachs of newly-arrived birds were empty and bile-stained. Figure 15 represents these averages diagrammatically. The male's first fast of at least six weeks is remarkable and known to be exceeded by only one other species of bird, the male Emperor Penguin, which fasts for 90 days (Prévost, 1953). The male Emperor is, however, about five times heavier than the Adélie before its fast.

Pink excreta were occasionally seen around a nest occupied by a male incubating alone soon after the eggs had been laid. Out of a sample of fifty-three dissections of males found alone during their first fast after their mates had left them, only two had partly digested food in their stomachs, whereas the stomachs of all the others were empty and stained with bile. This latter was puzzling until the behaviour of the male of Nest 6 at Signy was recorded. When seen at the nest with his mate and their first egg on November 11th at 1530 hrs., he had been fasting for twenty-five days. The egg was laid on the 10th. When next visited at 1830 hrs., on the 12th, the female was alone on the egg. Three and a half hours later the male was back and crouching over the egg, his mate bringing stones to build up the nest. He had just returned from the sea, for his plumage was wet and quite clean and he was excreting pink *Euphausia* remains. His weight was 4.1 kgm. Both birds were together at 0100 hrs., on 13th, but at 0900 hrs. the male was alone incubating two eggs. On 14th his weight had dropped appreciably (see Figure 14) to 3.8 kgm., but his excreta were still pink. On 15th, when his weight was 3.8 kgm., the excreta were stained with bile. It had thus taken three days for all traces of food to pass through the intestines.

This brief and unusual break in the normal fasting routine appeared to coincide with the presence of pack ice within sight of the rookery.

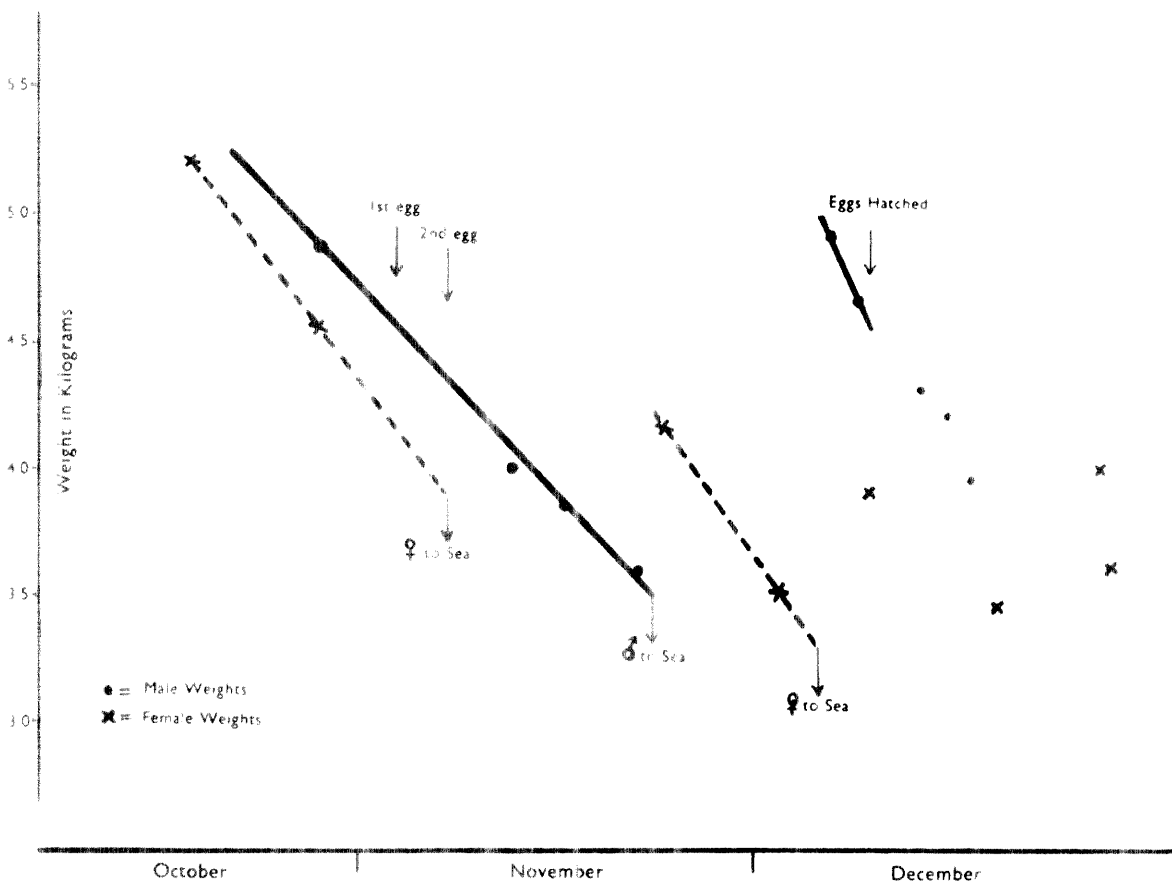


FIGURE 13. Weights of a pair of marked Adélies during the first and second fasting periods.

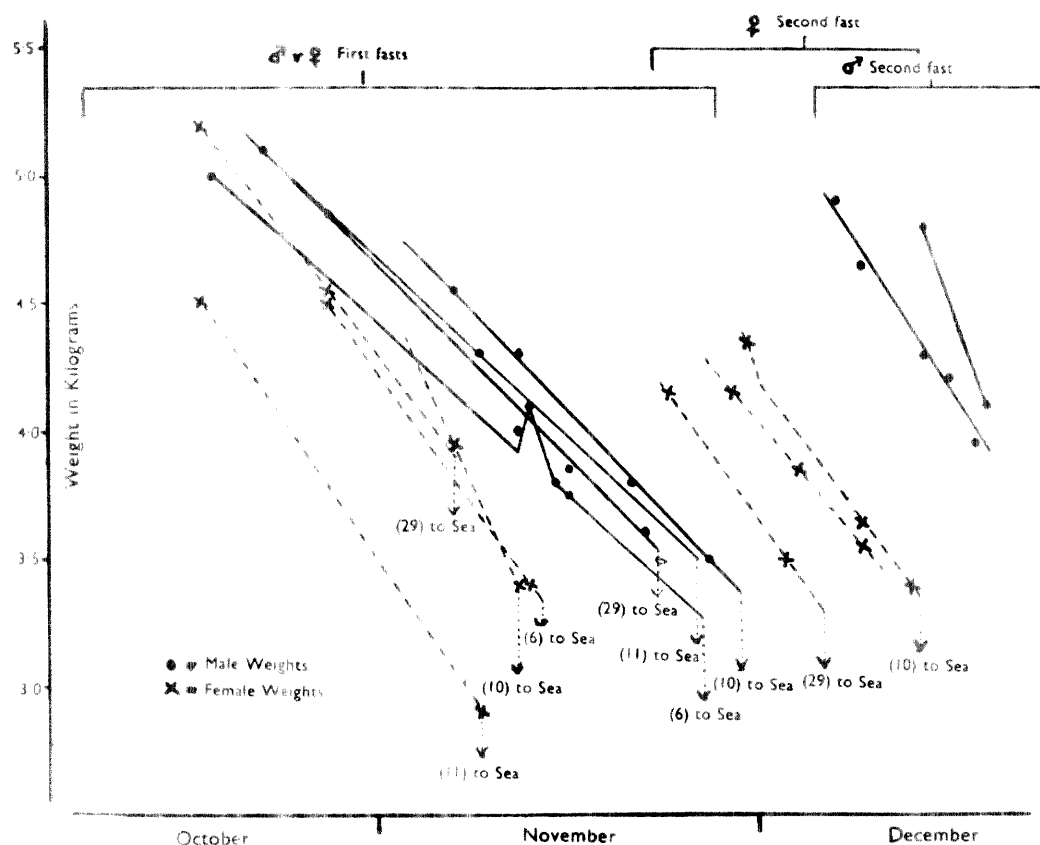


FIGURE 14. Loss of weight of four marked Adélie pairs during their first and second fasting periods. The nest numbers are given in brackets (e.g. (6) = Nest 6).

Of fifty-four birds incubating alone, dissected soon after egg-laying, fifty-three were male and one female (D954/5). This rare exception shows that the incubation routine is not an infallible way of sexing unmarked Adélies (see p. 23). Female D954/5, dissected on November 16th at Hope Bay, was very thin, weighing only 2.8 kgm. Her stomach was stained green with bile and the ovary showed two recently ruptured follicles proving that she had laid eggs. It was confirmed by experiment on others that this bird had almost certainly lost its mate through interference by dogs. If the male was taken away before the female had gone to sea, she would continue incubating for a few days, but her body reserves would become so low that she would have to desert in order to feed (see Table IX, Nest 35 on November 13th; p. 83). Birds unmolested by dogs or men would have to face this particular catastrophe extremely rarely, for adult mortality normally occurs at sea and not on land.

Figure 14 illustrates the following interesting points concerning fluctuations in the weights of four marked pairs of fasting birds:

i. During the first fast the males lost weight more gradually than the females. Estimated from the eight curves of first fasts, the average weight of females at the end of their first fast (i.e. as soon as eggs had been laid) was 3.4 kgm.; the average weight of males at the time when their mates left them during their first fast was 4.2 kgm., and at the end of their first fast 3.4 kgm. Hence, the males at the end of their first fast, came down to the same weight as the females at the end of theirs.

ii. In the second fast, both males and females lost weight at approximately the same rate as the females did in their first fast. The males, however, gained more weight between fasts and were, therefore, heavier than females at the beginning and end of their respective second fasts. The females were heavier than their mates at the end of the males' first fast, when the females returned well-fed from the sea to take over incubation.

Random weights of unmarked birds therefore, have limited value and may even lead to confusion, especially during the latter half of November.

From the evidence, it can be concluded* that the Adélie could not breed successfully unless the male remained behind to incubate the eggs as soon as they were laid.

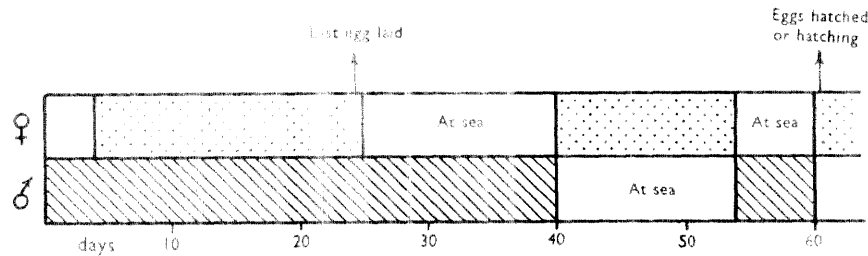


FIGURE 15. Diagrammatic nest-history up to hatching of eggs made from the averages of seven males and seven females ringed at Signy Island on October 17th and 18th, 1950. Male fasting periods at nest (shaded); female (dotted). (Note: the first birds observed back at the rookery were seen on October 8th, so the first fasting periods are likely to be even longer than stated.)

4. Care and Growth of Young

Stages of development. summarised in Table XVII, are divided into three main periods: the guard stage, the crèche stage (see p. 59), and the dispersal of the crèches and departure of the young (see p. 62).

In the guard stage (Richdale's term), one of the parents guarded the chicks and fed them while the other went to sea to collect more food. This lasted for about a month, the approximate weekly changes being as follows: During the first week the chicks were covered completely by the parent, which lay over them as though incubating eggs; in the second week the parent crouched over the chicks, which were mostly covered, their rear portions sticking out (Plates VI d and IX b) thus maintaining nest hygiene; in the third week the chicks were strong enough to stand, though they were still keeping close to their parents (Plate X a); in the fourth week chicks started to explore the area around the nest (Plate X b) and exercise their flippers. This fourth week was a crucial stage in the chicks' life. Parents were paying less attention to them; the nest-relief ceremonies were briefer and collection of nest material by the relieved bird was not being carried out with the former thoroughness. Nests therefore became neglected, and stones were eagerly removed by the unsuccessful breeders and non-breeders which had arrived back in the colonies (see p. 57).

Parental routine. Dissections showed that birds returning for the first and second fasts usually had bile-stained stomachs (i.e. they had not fed for about three days), whereas at the time of hatching, the stomachs of incoming parents contained semi-digested food. The behaviour of the parents is thus adapted to the presence of chicks which hatched during their absence at sea. How this adaptation is brought about is an interesting problem for further investigation.

During the guard stage, the usual interval between feeding of chicks was two days, though it varied from one to five days. Feeding and guarding were shared by both sexes, the males possibly taking slightly more responsibility than the females. Thus, out of a total of 297† records of marked birds seen with young at twenty-one nests, 156 were males and 141 females.

During the crèche stage, visits with food became less frequent and were easily missed as parents rarely stayed long at the rookery after feeding their chicks, and, as we shall see later (p. 61), there were no "guardians" of the crèches. Again, both sexes shared in feeding the chicks up to their final departure.

Weights. There were three phases in the growth curve of the chicks (Figures 17 and 18). In the first, lasting one to three days, there might be no gain in weight at all; in the second, there was a rapid and steady increase which continued to about the time of crèche formation; and in the third phase, fluctuation in

* Sapin-Jaloustre's observations (Sapin-Jaloustre & Bourlière, 1951) in Adélie Land in 1950, do not entirely support this conclusion. They state that immediately after the second egg was laid, one of the couple left for the sea. In seven cases it was the female, in two cases the male. Presumably these were marked birds but they do not state how they sexed their marked birds.

† There were many more observations, but for this analysis records within the same 12-hour period have been considered as one observation only.

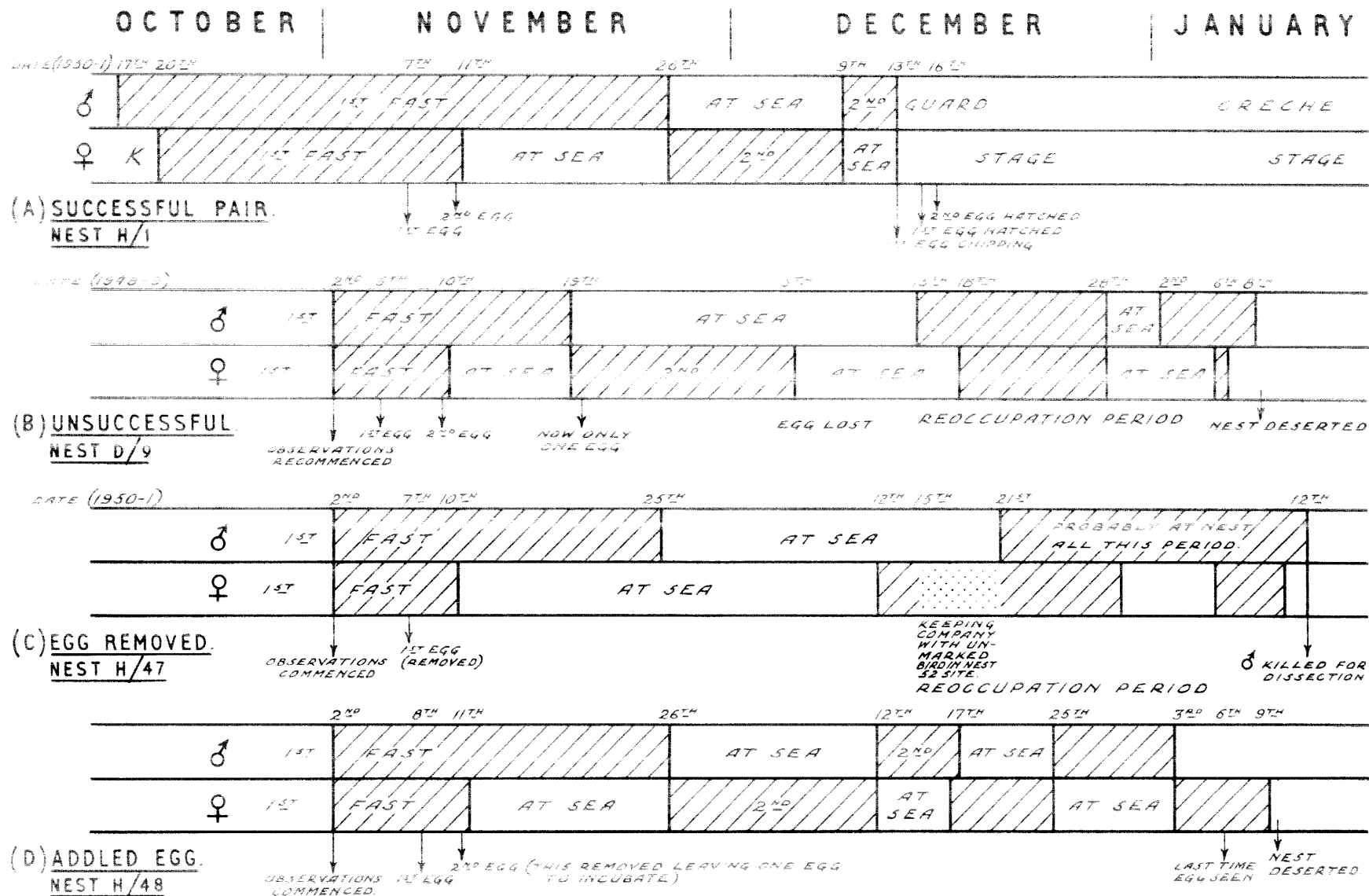


FIGURE 16. Fasting Periods up to egg-hatching represented diagrammatically of: (A) a successful pair, (B) an unsuccessful pair, (C) a pair whose egg (the only one laid) was removed within twenty-four hours of being laid, and (D) a pair which continued incubating an added egg.

Notes: All birds were marked and observed at their nest-sites.

(A) The male kept company (= K) with another female before its mate returned on October 20th.

(B) The birds of Nest D/9 were first ringed when breeding in November 1946, and returned to the same nest-site in 1947-8, and 1948-9. They lost their eggs as a result of bad weather during the 1948-9 season at Hope Bay, when loss of eggs was 80-90% (see page 69).

(C) See page 57. During the re-occupation period the female kept company with unmarked birds at two different nest-sites (represented by dots), but returned to her former site when her mate returned (page 72).

(D) If the egg is added, the fasting periods continue until the egg is lost. In this nest the female had four fasts before the nest was finally abandoned on January 9th (see page 57).

weights continued until the chick left the rookery. It seemed that the newly hatched chick could survive for a day or two without food and thus allow for the uncertain date of its parent's return from the sea with the first meal. The fluctuations in weight during the crèche stage were chiefly due to the fact that the young Adélie could accommodate $1\frac{1}{2}$ lbs. or more of food in its stomach.

Plumage and moult. In most of the newly hatched chicks the down was dark sooty grey, slightly darker on the head, but others were silver grey with dark heads, a curious dimorphism which does not appear to be shared by the young of other species of penguins. At Hope Bay, the proportion of silver-greys to sooty-greys was about three to two. No correlation with sex could be found in a small number dissected. The first down was soon replaced by a second down of uniform dark grey.

The first signs of moult into immature (or yearling) plumage were seen during the fifth week (Table XVII). This was a gradual process taking up to four weeks, the parts which first became free from down being those where chafing was greatest, such as the chin, the inside of the flippers, the lower abdomen and thighs. Many fully grown chicks seen along the coast before departure had residual tufts of down clinging to their crowns and the backs of their flippers.

The changes in the voice of chicks from simple "peeps" to "tremulous peeps" before the crèche stage, has been discussed in the section on mutual display (p. 35-36) and will be further discussed in the chapter on individual recognition (p. 70).

5. The Re-occupation Period

Counts of numbers of adults at colonies during the breeding season showed two conspicuous peaks (Figures 9 and 11), the first during the occupation period (p. 48) and the second roughly between hatching and early crèche formation. Successful breeders, unsuccessful breeders and non-breeding "wanderers" all contributed to this second peak.

i. The routine of the *successful breeders* was that of parents returning to feed and guard their chicks during the guard stage. This had little effect in raising the population, because the relieved parent usually left for sea to collect more food soon after the nest-relief ceremony.

ii. The *unsuccessful breeders* contributed to the rise in population more than any other group, hence the name "re-occupation period". Breeding routine was maintained as long as there was an egg or chick in the nest. If disaster overtook these, the bird on duty deserted within twenty-four hours and walked off to sea to feed, but four marked nests in which eggs were removed within twenty-four hours of laying, proved to be exceptions. The females departed as usual, but the males remained alone at the empty nest for from seven to fourteen days before eventually deserting. They thus continued their first fast as if incubating eggs, though none of them remained long enough to meet their mates when they returned from the sea (Figure 16c). The essential difference, however, between successful and unsuccessful breeders was that the former focussed their attention on the egg or chick, the mates leading separate lives after the pre-egg stage except for brief but intense encounters at the nest during the nest-relief ceremonies, whereas the unsuccessful breeders not only returned after feeding but remained together for a further period. Generally speaking, the earlier a pair lost their eggs, the earlier they returned to re-occupy their previous site, and the longer they stayed. Most of them were back between the time of hatching and early crèche formation. Nests were rebuilt with varying efficiency. Some of the largest nests of the season were seen during this period (Plate Xc). The original pair-bond was usually maintained though birds would keep company with others if their mates did not return at the same time (Figure 16c). The male was more faithful to his nest-site than his mate, and often came back first and fasted longer, usually alone, at his pile of stones. Dissections of many of these re-occupying birds revealed a noticeable hypertrophy of the gonads, though never to the same extent as at the beginning of the season. No second clutch was laid, nor would there have been any chance of success so late in the season. Those that had lost chicks, especially young chicks, usually returned after a spell at sea, but for a shorter time than those that had lost eggs.

Addled eggs were soon trampled on or extruded from nests which also contained a chick. If chicks were not hatched, incubation continued for a considerable period after the chicks at other nests had hatched. For example, three marked pairs which did not hatch their eggs continued incubating until December 31st, January 9th (Figure 16d) and January 16th.

iii. *Non-breeding "wanderers"* Ways of distinguishing non-breeding "wanderers" from the unsuccessful breeders have already been discussed (p. 26). The distinction was difficult to make during the re-occupation period, but the infiltration of small numbers of unmarked birds into colonies which contained marked birds, and evidence of non-breeding (Table V and Figure 12) from dissections, indicated that these birds were important participants in the re-occupation period.

The re-occupation period was more noticeable at Hope Bay than at Signy because of the very high mortality of eggs at the former (p. 69). There were many strange situations recorded, confirming beyond doubt that sometimes the rightful owners with chicks were being ousted. One on December 23rd deserves special mention.

A big fight was in progress. A bird lying over one chick in a nest well covered with excreta (i.e. strong evidence that the nest belonged to a parent feeding chicks and not to a fasting unsuccessful breeder), was being attacked by a couple. Another chick, probably from the same nest, was in the midst of the battle. The bird and the chick over which it was lying were eventually ousted from the nest. Struggles and "peeps" from the helpless chicks had no effect on the attackers, and the ousted parent making no effort to come back and defend again, stood on the edge of the colony occasionally closing its eyes and shaking itself. One of the attackers eventually settled in the nest and its partner stood beside it, both ignoring the chicks and their plaintive cries.

Three more examples of this behaviour were recorded, two of these in marked nests. Were these usurpers inexperienced, unsuccessful breeders trying to improve their nest-sites, or aggressive non-breeders staking a claim on territory for next season? Abnormal behaviour such as this illustrated the limits to which territorial fights would go. Many less aggressive acts in situations where competition for sites was less keen,

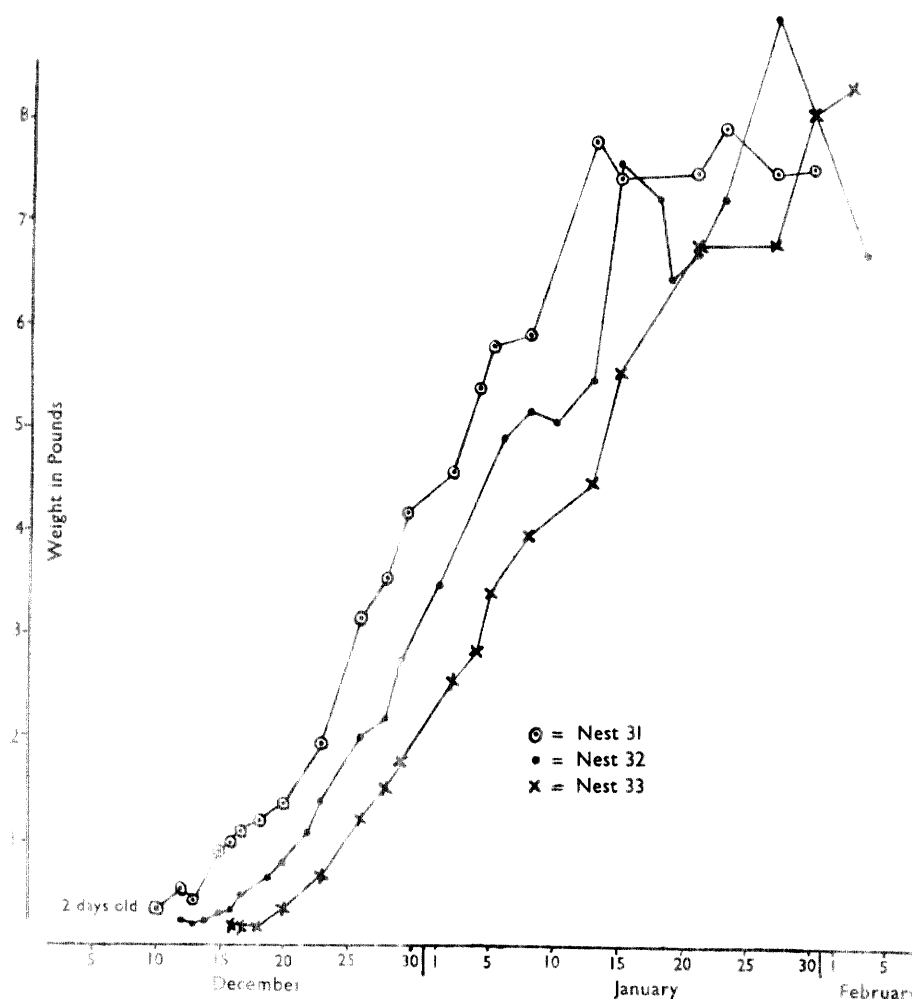


FIGURE 17. Weight curve for three marked Adélie chicks in three nests at Hope Bay, 1948-9.

left me with the impression that this latter part of the season was a very important period for the establishment of future territorial rights and pair-bonds among the unsuccessful, unestablished breeders or non-breeders. It was probably largely because of this that the established unsuccessful breeders also returned from the sea to maintain their territorial rights.

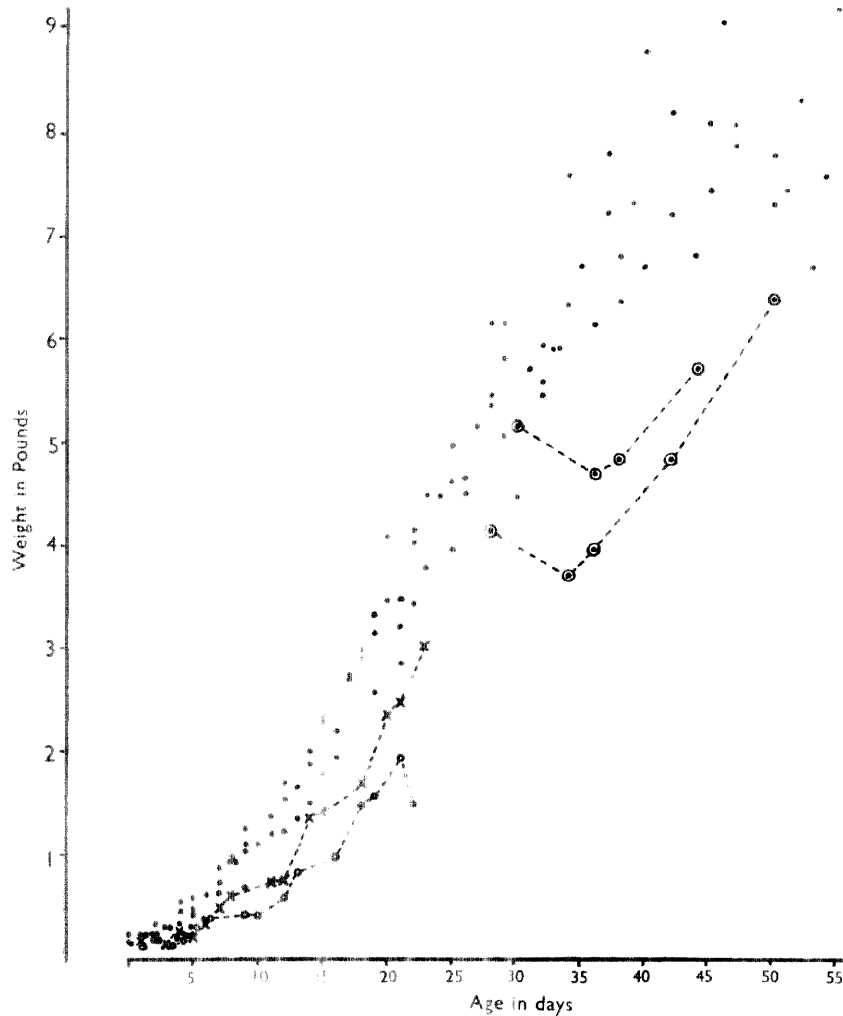


FIGURE 18. Weight curve of marked Adélie chicks according to age. (The dots joined up represent two nests in which there were two chicks.)

6. The Crèche Stage

At the end of the "guard" stage the chicks of certain species of penguin, for example the Emperor, King, Gentoo, Chinstrap and Adélie, form groups or crèches. The Adélie crèches did not form suddenly. The first signs were occasional clusters of three to seven chicks huddled together in an empty nest-site or against a rock. These groups increased in size as more and more parents left their chicks unguarded. The crèches often moved slightly from place to place, and small crèches from outlying colonies fused with larger ones (Plate Xd) until they contained a hundred or more chicks. At Hope Bay, the first signs of crèche formation were seen on January 8th, thirty-one days after the first chicks had hatched. Six chicks in marked nests were 28, 29, 30, 31 and 32 days old when first found left alone by their parents, the average of 30 days confirming the age calculated above from field observations.

At Signy, conditions were more variable. The first chicks were seen alone on December 23rd, only 19 days after the first eggs had hatched, and the average age at which ten chicks at marked nests were left

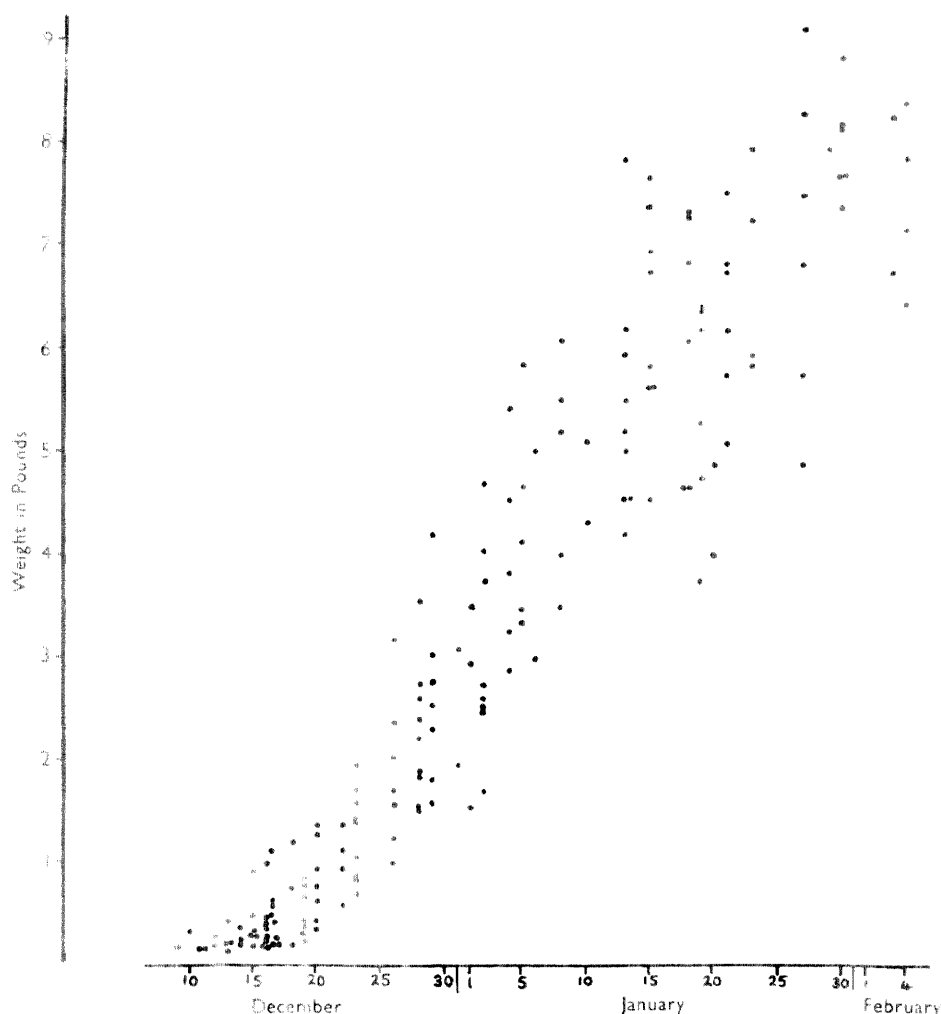


FIGURE 19. Weights of Adélie chicks according to date

alone was 19 days, with a range of 17-28 days. All these marked chicks eventually died (see p. 70), most of them from starvation, so that the Signy data cannot be regarded as typical. Moreover, crèche formation did not become really evident there until the end of the fourth week after hatching. It can therefore be concluded that the average age of the chick when it goes into the crèche is about one month (Table XVII).

i. Evidence that parents feed their own chicks. Richdale (1951) has shown that parent Yellow-eyed Penguins recognise and feed their own chicks. Unlike the Adélie, the nests of Yellow-eyed Penguins are scattered among rough and wooded country and their chicks do not collect together in crèches. Previous literature summarised by Murphy (1936, p. 398) and Roberts (1940, p. 224) suggests that parent Adélies do not recognise their own chicks in the crèche, so that on arrival they have to run the gauntlet of pestering young. The fittest and largest chicks survived; the weaker ones, because their demands for food were not satisfied, falling an easy prey to the Skuas. In their two papers on the Adélie, Sapin-Jaloustre and Bourlière (1951 and 1952) do not contradict this.

In 1948-9, by placing coloured rings round the flippers of chicks of marked parents before they went into the crèches, it was possible to demonstrate that the parents found and fed their own offspring and only exceptionally fed strange chicks. Additional evidence was provided from field observations on unmarked birds and by ciné photography. Table XVIII summarises data collected from the nest histories of marked adults and chicks after these had reached the crèche stage, and shows that out of a total of seventy-one observations, only twice were the parents seen feeding chicks that were not their own. One case was a parent male seen in its nest with three other chicks in addition to its own. This was a fairly common

occurrence in the early days of crèche formation and in no way indicated that the particular parent was unable to recognise its own young. The other case was of a marked parent who, in addition to feeding its own two chicks, gave one feed to a third. This chick, the offspring of a neighbouring nest, was larger than the other two and, being extremely persistent in its begging for food, was eventually given one hasty mouthful in between feeds to the other two. Many instances of strange chicks begging for food from marked parents were observed, but in only this one was a chick successful.

During the first week of the crèche stage, chicks often returned to their nests in anticipation of food even though both parents were away at sea. This, however, varied according to the number of adults (e.g. unsuccessful breeders) re-occupying the territory nearby, the chicks tending to keep in closer groups if adults were few or scattered. Many of the observations in Table XVIII were therefore recorded from nest-sites, though after feeding, the chicks usually returned to the crèche. When the feeding chases started during the chick's sixth week, parent and chick were often seen some distance away from the crèches.

Circumstantial evidence that the chicks are fed only by their own parents comes from the behaviour of the marked, unsuccessful breeders that returned during the re-occupation period. Of 162 records of such birds observed during the crèche stage not one was seen feeding a chick whether marked or unmarked, nor was an unmarked adult of any age group ever seen feeding a marked chick of marked parents. Consequently, if one of their own parents was killed or not seen again, the chicks invariably died. Moreover, and quite contrary to previous views on the survival of the fittest in the crèches, many of the chicks that hatched later in the season showed no trace of emaciation, simply because they were being looked after by their own parents, and therefore did not have to compete for food with the other larger and stronger chicks in the crèche.

Additional evidence, from field observations on unmarked birds shown in the film (Film 1, see Bibliography), adds weight to the above argument. For example, when parents arrived fresh from the sea and walked up to groups of chicks still mostly in down, there was no mad rush towards the adults. The chicks stood their ground, and observed the adults intently. Their reaction was one of expectancy and sharp observation. Adults also came in with an air of determination, looking here and there as they passed through the throng. If a chick did not come straight up, the parent might pause and go into loud mutual display. Once a chick, though hidden from view (it was probably lying asleep), suddenly put its head up on hearing the loud mutual display of a newly arrived adult and rushed towards it. Recognition between parent and chick is discussed later (p. 72).

ii Are there "guardians" of the crèches?

"The young birds . . . are pooled in crèches of from twelve to twenty or more individuals, which are guarded and shepherded by a few old birds, so that the others are free to forage."

Thus, does Murphy (1936, p. 398) sum up early stages of crèche formation. The idea of "guardians" for the crèche has been founded on the views that adults neither behave as mated pairs nor as specific parents after their chicks have gone into the crèche. My observations on the crèche stage and individual recognition between parent and chick, make these views no longer tenable. Moreover, nowhere in the literature is there any mention of the exact status of these "guardians". In the early days of the crèche stage, parents did show some interest in protecting their own chicks (and incidentally any others which happened to be nearby) but there was no evidence whatever for any rota of guard duties. As the chicks grew larger, the parents' visits became fewer, and when they did arrive they rarely stayed long at the rookery after feeding their chicks before departing to sea again for more food. It has already been shown that during the re-occupation period unsuccessful breeders returned to their former nest-sites and occupied them for several days in succession (Figure 16b and c), and that non-breeders also took possession of unoccupied nests. Presumably, it is these birds that previous observers have mistaken for "guardians" of the crèches, a function which they do not perform. Unsuccessful breeders were often seen pecking at chicks, not to persuade them back into a crèche, but to keep them away from their own territory. Plate Xf illustrates this well. Note how the chicks are arranged around the adult just beyond pecking range. Chicks in a crèche tended to crowd around adults of any sort. Thus Plate Xg shows an Adélie crèche in a small Gentoo colony! There were no adult Adélies nearby at all. All eggs in this Gentoo colony were lost in bad weather earlier in the season, so they were either unsuccessful breeders or non-breeders. It must therefore be concluded that there are no "guardians" to the crèches. Each adult Adélie, whether parent, unsuccessful breeder or non-breeder, acts as an individual, and there is no evidence of communal behaviour.

iii. *Factors contributing to crèche formation.* Four factors should be considered: food supplies, temperature, predation and the gregarious nature of penguins.

Food supplies. On the evidence then available, Lack (1947, p. 325) suggested that the crèche system was an unavoidable maladaptation to a variable food supply. Like asynchronous hatching in a hawk brood, it might facilitate the survival of a proportion of the young during food shortage when otherwise many more might starve. He further suggested, quoting Wilson, that this habit might be the only way in which the Emperor Penguin has been able to maintain itself under Antarctic conditions, one chick apparently being more than two parents can raise successfully. Since Adélie (and possibly all other crèche-forming penguins*) parents feed only their own chicks, this theory can no longer be maintained.

Temperature. In the Antarctic species of penguin, the origin of the crèches may possibly be connected with severe cold (Roberts, 1940, p. 224). Stonehouse (1953) implied that this is so for the Emperor, even the adults forming "huddles" at particularly low temperatures. This factor is in need of further investigation in the Adélie, but it did not appear to be important.

Predation (see p. 66 *et seq.*). For three reasons, this appeared to be the most important factor encouraging crèche formation. Firstly, the reaction of chicks at the crèche stage to a low-flying Skua was to bunch together. Secondly, while the reaction of adult Adélies to interference by man or dog was either threat, attack or dispersal, the reaction of chicks was again to bunch together. Photographs of crèches in solid masses should therefore be interpreted with some caution, for the photographer might have unintentionally disturbed the birds, thus causing them to come closer together before taking the picture. Thirdly, as we shall see later, the crèche stage did not last for more than three weeks, the chicks then dispersing back to their nest-sites. Skuas could then be seen walking among the scattered chicks which showed little fear and did not bunch together as they had done earlier. They appeared to have gained sufficient confidence to stand their own ground.

The gregarious nature of penguins, and particularly of the Antarctic species must also be taken into consideration. Penguins, as so aptly described by Richdale, are "fond of company"

7. *Dispersal of the Crèches and Departure*

Towards the end of the crèche stage, chicks showed a preference for lying in their nest-sites, though they readily bunched together when frightened. There was, however, much variation, crèches in some colonies remaining tightly clustered while those in others dispersed. Dispersal gradually became more general, but as the season drew to a close a different behaviour was noted. The chicks collected in small parties on the edge of the colonies, often within sight of the sea, or moved down to the beaches where they stood for long periods watching parents come and go. The call note *aark* which was first heard in the chicks' eighth week now increased and echoed everywhere on the rookery and along the coast. The youthful calls were softer and higher pitched than those of the adults.

According to some observers, the adults lure the young to the water and teach them to swim before departure. Others state that the chicks remain on shore until starvation forces them to take to the sea. Neither of these appeared to be the case at Hope Bay or Signy. Examination of stomach contents of chicks collecting at the water's edge before departure usually showed some food debris. It therefore seems unlikely that they go long without food before they leave. The fluctuations in weight at this stage (Figure 17) were considerable, and were, no doubt, due to the occasional large meals brought to them by their parents.

Field observations showed that the chicks gathered in small parties on the shore when almost free from down, that there were no preliminary swimming "lessons" with adults, and that young departed quite independently of adults (Film 3, see Bibliography) but swam in the same direction. On February 14th no adults were seen at Signy, but out of thirty remaining chicks only one looked really emaciated and some of them were producing pink excreta (*Euphausia* debris). Four days later there were still eight young, but on the 25th they had all gone. The last record for the season was on March 1st when one adult was seen on the rookery.

* Prévost (1955), working on the Emperor Penguin in 1952 has shown, contrary to previous literature, that parents recognised and fed their own chicks

8. *Pair-formation*

Having considered the breeding habits of the Adélie we may now consider pair-formation, but two related subjects, "keeping company" and sex recognition, must be considered first.

"*Keeping Company*". Richdale (1945) was the first to use this term. His most recent definition (1951, p. 6): "To me, this phrase seems to express exactly how two birds of the opposite sex behave towards each other under certain conditions", does not go far enough, particularly as it leaves the "certain conditions" undefined. In this study of the Adélie, the term is used to describe the partnership of two birds of opposite sex at a nest-site, which may or may not lead to the establishment of a mated pair. (For definition of a mated pair, see below.) I believe this habit of "keeping company" has survival value in facilitating the formation of new pair-bonds, should the original mate of an established breeder fail to return, or return very late. It also enables more efficient nest-building and defence of nest material which would otherwise be difficult for a single bird in a crowded colony. The experiments carried out before egg-laying and during the re-occupation period, summarised in Tables VIII and IX showed that supposedly established breeders often acquired new partners within a few hours of one of either sex being removed, in spite of the presence of other single birds (presumably unestablished or non-breeders) nearby.

Sex Recognition. Roberts's (1940) conclusion that recognition of the sexes in the Pygoscelid Penguins, particularly in the Gentoo, results from "trial and error" behaviour early in the season, has already been criticised by Richdale (1951, p. 69). Roberts states that on October 11th he saw two female Gentoos fulfilling the active male role, the position of the two sexes being reversed. It appears, however, that the so-called "active male role" was merely one bird scrambling on the back of the other and standing there without attempting to complete the sexual act. This appears to be the only definite example of the reversed attitude seen among the penguins under his observation. As already suggested (p. 41), I do not think this was an act of normal "trial and error" behaviour, but an example of abnormal behaviour which could be better explained in terms of homosexuality or of "inexperience".

Quoting from previous literature Roberts remarks that very few cases of reversed attitudes in coition have been described in birds. As they chiefly refer to unmarked birds of species which show no sexual dimorphism, and whose sexes were not confirmed by dissection, they should be treated with great caution. Although Huxley (1914), for example, goes to considerable lengths to justify his conclusions on the sexing of his unmarked Great Crested Grebes which he saw in reversed attitude, his final word is by no means conclusive. Roberts's observations before egg-laying were restricted to a short period from October 9th to 12th and he was unable to visit the Gentoo colony again until October 20th, one day before egg-laying. During the earlier visit, the role of the sexes in display had been interchangeable, but on the 20th the males only were seen offering nest material to females, and from this date onwards males mounting females appeared to proceed to successful coition. Bagshawe's (1938) account of the same species, based on daily observations from early Spring, does not present such a simple picture. Moreover, Bagshawe observed complete acts of copulation from the very beginning of the season (see Table X).

No example of a reversed attitude in coition, or of homosexual copulation, was observed in the Adélie even during the early part of the occupation period, nor during the re-occupation period (p. 57). All my field observations and dissections, supplemented by recoveries of marked birds in successive seasons which were still at their original nest-sites and still with their previous mates, provided strong evidence that Adélies knew each others' sex from the time that they first arrived at the rookeries. This was illustrated in a most charming and amusing way by the Adélies of Nests 6 and 8:

A male (6RF) was first seen at Nest 6, and marked, on October 18th. His sex was confirmed later by breeding routine, ecstatic display and copulation (see p. 23). He remained alone at his nest until 21st. At 1400 hrs. on that day, he was nest-building and collecting stones from Nest 8 occupied by a bird (later marked 8RF) which had only just arrived. They occasionally bowed together (p. 34), but no quiet mutual display was seen at first. The normal reaction of one penguin to another stealing its stones is immediate attack, but instead 8RF walked across to Nest 6, two yards away, and collecting a stone from there, took it back and placed it in Nest 8. 6RF collected another stone from Nest 8 and while he was doing this 8RF collected one from Nest 6; and so they continued with absolutely no signs of aggression whatever, until I was quite tired of watching them. It was difficult to say who was winning. A quiet mutual display was first seen when both birds happened to meet together at Nest 8. It seemed that these two had decided to become partners but had not made up their minds in whose territory they would settle. I crawled out of my tent and caught the unmarked bird of Nest 8, for it was most important to mark it and try to confirm its sex from its subsequent behaviour during the season. It was painted and ringed, but ran away afterwards.

Before dark, I was delighted to see 8RF back again and standing by the side of 6RF in Nest 6. Nest 8 was left empty. 6RF and 8RF "kept company" at Nest 6 for the next three days and then, when observed again on October 26th, 6RF

was found, still in Nest 6, with a new partner (25RF) which subsequently proved to be his mate. At the same time 8RF was observed back in Nest 8, the nest in which it had been first seen on October 21st. 8RF was also with a new partner (26RF). 26RF remained with 8RF and they had eggs, 26RF's sex being confirmed later by dissection as a male and thus proving 8RF to be a female.

Here was an example of a male 6RF and a female 8RF which, right from the start, knew each other's sexes, kept company and a few days later separated.

Pair-formation. Before pair-formation can be considered, "mated pair" must be defined. Richdale (1951, p. 6) defines mating as signifying "that two birds have definitely started family life together for the ensuing season, but not necessarily that coition has yet occurred". His remark that "mating" is not synonymous with "coition" fits Adélie behaviour, because many birds keeping company with others early in the season were seen copulating before their mates joined them. But how can family life start without copulation? Richdale's references to mated birds no doubt apply to marked birds which he subsequently followed through to egg-laying, but very few people have had an opportunity of following marked penguins through subsequent seasons. At present it is perhaps wisest to define a "mated pair" as two birds of the opposite sex which for one particular season have consummated their partnership by producing an egg. Thus, an established Adélie, A, returning to its old nest-site, may keep company with another bird, B. It may display, copulate and nest-build with B who, a few days later, may be expelled by another bird, C, of the same sex. A and C may then remain together for the rest of the occupation period until the eggs are laid. A and C can then be considered as mated even though eggs might be lost, and also although A might keep company during the re-occupation period with a different bird in the absence of its mate.

Pair-formation can therefore be defined in the same words as used by Richdale (op. cit., p. 7) but with a slightly different meaning for the word "mate", thus: "Pair-formation is the process by which two birds of opposite sex come together and subsequently mate for at least one season." What is particularly in need of further investigation, on birds of known age, is the important difference in behaviour between experienced, inexperienced and non-breeding birds, at the beginning of the season and during the re-occupation period. Table VI illustrates what I believe to be the typical behaviour of one bird that had already bred and was returning to its former nest-site, and the other which was not yet established.

Richdale (op. cit., p. 86) describes six types of "allied behaviour" recognisable in pair-formation: affinity, "divorce", "flirtation", period of receptivity, "trial and error" theory of sex recognition, and the function of head feathers. The last two he does not support. For the Adélie, it is convenient to discuss four aspects of pair-formation which include most of Richdale's: the chief displays associated with pair-formation, period of receptivity, affinity and keeping company (see above).

The chief displays associated with pair-formation appeared to be the ecstatic and the closely related "bill to axilla" displays, bowing, and the mutual display. The ecstatic was used by the male for attracting the female to the nest (p. 32). The usual response on arrival at the nest was a bow, and there might also be a quiet mutual display. It has been suggested that the bow may be a form of appeasement ceremony. The ecstatic display might serve the function of repelling birds of the same sex as well as attracting birds of the opposite sex. The "bill to axilla" display which so often followed on from the ecstatic might be primarily concerned with repelling (p. 33).

Concerning *the period of receptivity*, Roberts (1940, p. 210) states that display before a female Gentoo with unenlarged ovary fails to produce any response. Richdale (1951, p. 69) refutes this by quoting examples from his field observations and concludes that gonadal development is not a necessary precursor of pair-formation, although during that phase some mated pairs are doubtless formed. My own field observations, correlated with a large number of dissections of all three Pygoscelid Penguins, support Richdale's views. The re-occupation period appeared to be an important time for the establishment of future pair-bonds and territorial rights (see p. 58).

Affinity, a term understood in human relationships but little mentioned in works on birds, has been emphasised by Richdale. One interesting example given by Richdale (1951) concerns a female who had an affinity for a male, although both had other mates. They sometimes kept company and when one of the mates died, bred together.

The Adélie, though more faithful to its territory and possibly partners (p. 70) than the Yellow-eyed Penguin, shows these discerning qualities as well. They not only take in their surroundings, but are highly aware of the temperaments of other birds around them. The affinity of one bird towards another might thus play an important part in pair-formation and in other social relationships in the breeding area.

E. THE WINTER

1. *The Moul*

In February 1948, I saw a few moulting adults at the Argentine Islands off the west coast of Graham Land, but on arrival at Hope Bay on March 1st no birds were seen anywhere. In the following season, a few yearling Adélies moulted at Hope Bay (p. 27 and Table III), but no yearling or adult birds were seen moulting at Signy in 1951.

A study of the literature reveals that the majority of Adélies leave the rookeries at the end of the season and moult among the pack ice. Their numbers on land in any particular place vary from year to year, no doubt according to the prevailing pack ice conditions. Thus, at Cape Adare, the majority had left on February 17th, 1899, and those remaining were still moulting (Hanson, 1902, p. 94). Only occasional penguins were seen on March 7th, and on the 18th the last record for the season was one lone moulting adult. Wilson (1907, p. 57) found "very large numbers" of moulting adults at the same rookery on February 17th four years later, and in 1911 Levick (1914, p. 14) reports "some thousands" of adults remaining to moult after the young had left. As Levick's estimation of numbers of Adélies at Cape Adare (*op. cit.*, p. 35) was some 700,000 birds, it is clear that only a small proportion remained to moult. A study of the moult of Chinstraps at Signy showed that yearlings moulted first, then unsuccessful breeders, and finally the successful breeders. The successful breeders began their moult over a month after the yearlings. Richdale (1951, p. 285) has likewise shown in the Yellow-eyed Penguin that the successful breeders also moult later than the unsuccessful and what he calls "unemployed" birds. The moulting routine in the Adélie is probably the same as that of the Chinstrap, for the only moulting birds at Hope Bay were yearlings seen between January 21st and February 4th, when young were still being fed (see p. 27). The comparatively small numbers of birds seen by the Cape Adare observers were probably unsuccessful breeders, the successful breeders having migrated to the pack ice, just before their young, to feed and fatten before their moult. Worsley's diary (MS) reports that Sir Ernest Shackleton's party saw thousands of Adélies moulting in the pack ice between February 17th and March 26th, 1916, when the expedition was drifting in the Weddell Sea between 50 and 150 miles from the nearest rookeries.

An account of the moult of adult Adélies has been given by Cendron (1953). Thirty birds were marked, three of which were studied for the complete moult. The weights, obtained by temporarily anaesthetising the birds, showed an average loss of 40% during the moult.

2. *Winter Movements*

This is the biggest blank in our knowledge of the Adélie. A mass of information from shore parties, supplemented by those men who have been compelled to drift amidst the Antarctic ice throughout the winter months (for example the *Belgica* and *Endurance* Expeditions), indicates that the winter movements of these birds depend on ice conditions, and that their range is restricted to those areas of loose pack which separate the solid ice to the south from the open water to the north. It is therefore better to regard the Adélie not so much as a migratory species, a fact that cannot be denied, but as a species which winters and feeds in the pack ice, its visits to land outside the breeding season being dependent on the proximity of suitable pack ice. At Hope Bay, for example, none were seen with any certainty during the winter of 1945 (Marshall, MS), whereas during the next winter, Andrew (MS) saw birds in March, their numbers increasing to 500-1000 in mid April, falling off again at the end of the month, but increasing during the first half of May. He saw about 100 again in early June, a few on July 20th to 21st, and none in August. In 1948, none were seen during the winter months. At Signy, in 1950, Adélies were seen in small numbers throughout the winter whenever gales broke up the sea ice and brought open water with pack ice near to the island.

F. MORTALITY AND PREDATORS

Mortality at the rookery during the breeding season was almost entirely confined to eggs and young, except when men and dogs were responsible. Adults have no natural predators on land and survived the rigours of the weather. Successful rearing of chicks depended on a definite breeding routine. If the male departed to sea first after egg-laying, the female ultimately deserted. One of the parents had to be back with food in its stomach within a day or two of hatching, otherwise the chick perished. Proper development

of young was dependent on regular feeding by both parents and recognition of offspring in the crèche, the chick(s) otherwise becoming undernourished and falling easy prey to Skuas. These, and other aspects of the breeding routine, could be upset by environmental conditions as will be shown below. What is in need of further investigation in birds of known age, however, is the effect of individual variation and of breeding experience on egg and chick mortality. For example, it would be interesting to know if partnership between experienced and inexperienced adults would be less successful than between two well established experienced birds.

1. Predators on Land

The Skua (Catharacta skua) (Plate XIIa). This was the most important natural land-predator, and returned from its winter migrations about the same time as the penguins. The Skuas did not lay their eggs, however, until early December, over a month after the first Adélie eggs had been laid. Up to the time when their eggs hatched, the Skuas were chiefly scavengers, though they plundered many penguin eggs. Their nesting areas were usually littered with the remains of egg shells. One piece with pencil marks on it had come from a marked nest about $\frac{1}{2}$ mile away. Ponting, the photographer on Scott's last expedition, took a remarkable series of motion pictures to illustrate the way in which a Skua could grasp an egg in its bill and fly away without breaking it. This same habit was seen at Hope Bay. Also, on several occasions when vast numbers of Adélie eggs were lying abandoned and frozen solid during bad weather (see below), Skuas were observed dropping them from a height on to the rocks below, like a Carrion-crow dropping a snail, or a gull a shell-fish. Skuas were never seen to attack a healthy adult penguin.

The first Skua chicks hatched at Hope Bay on January 16th, when the Adélie chicks were at the crèche stage, and at that time the Skuas' behaviour changed noticeably. Adélie chicks were attacked when separated from the crèche, or, as was often the case, tugged away from it by their legs. An alert chick would stumble back and resist further aggression. Others would allow themselves to be repeatedly dragged out and jabbed at until the muscles of their legs were laid bare and they had no further strength to walk. A few sharp jabs from the Skua would end the chick's life, but sometimes the Skuas appeared to play with their prey like a cat with a mouse. One chick seen at Hope Bay was a gruesome sight as it staggered about "peeping" continuously, almost blind and half scalped, while a Skua slowly walked alongside, jabbing here and tugging there at its blood-stained plumage. Another equally gruesome method of attack was for the Skua to peck continuously at the cloacal region until the unfortunate chick was disembowelled alive.

I was, however, constantly impressed by the fact that the Skuas weeded out weakling chicks (Plate XII b), or those slow to learn the dangers of being isolated from the crèches. The Skuas appeared to be ever watchful and probably knew the individual birds of an area thoroughly. Perhaps we underestimate the watchfulness of birds and the attention they pay to their environment. Probably predators like the Skua select intended prey several days beforehand, and so long as there is an adequate supply of food they will make as little effort as is necessary to secure it. Time and again I have watched the approach of a Skua to an emaciated starving chick and thought it would fall an easy prey, yet if the chick showed a bold front, faced its opponent, showing the typical aggressive displays, even beating back weakly with its flippers, the Skua would raise its wings in "defence" and retreat. Any isolated chick that could do this would be able to get back to the greater safety of the crèche. A few days later, the same bird would be too weak to show any alertness and would thus succumb. The tendency to weed out the weaklings or those which do not defend themselves properly, suggests that predation by the Skua, like that of the *Falconidae* (Rudebeck, 1950 and 1951) is selective. A population of over 100,000 Adélies supported about ten breeding pairs (and some non-breeders) of Skuas at Hope Bay where other sources of food for their young were negligible. The fact that the Skua does not have unlimited supremacy over its prey might well be the most important factor in limiting the Skua populations which are so often associated with a penguin rookery.

The Sheathbill (Chionis alba) (Plate Vb and d). These are scavengers of very catholic diet which nest exclusively among the penguins. Their behaviour and distribution at Hope Bay and Signy suggested that they are more territorial than the Skuas, each pair confining its feeding activities to its own penguin colony or section of colony. Unlike the Skuas, some of the Sheathbills pass the winter in the Antarctic. Their numbers increased in the Spring around our Base where there was abundant food from the dog spans. When the penguins arrived, nearly all the Sheathbills moved off to the rookeries and remained there for the rest of the season.

Sheathbills are skilful robbers of penguins' eggs, and appear to pay special attention to the nests of those individuals whose behaviour suggest that they are inexperienced breeders (see p. 25–26 and Plate V). The shell is perforated quickly and some of the contents sipped out to make it lighter for carrying away to a less crowded place. Marshall (MS) found the first Sheathbill eggs on December 7th in 1945. In 1948 they were first seen on December 13th, so, as with the Skuas, their chicks hatched at the time when food was most plentiful. They were never seen to kill penguin chicks, but the neighbourhood of their nests was littered with the remains of chicks which had either succumbed to the rigours of the climate, died from starvation, or were the remains of those that had been killed by Skuas. On February 3rd, an interesting method was observed by which a Sheathbill secured *Euphausia* from a parent Adélie when feeding its chicks. Walking close to the parent, the Sheathbill sprang into the air and brushed the penguin with its wing just as food was being regurgitated to the chick. This rapid action took the Adélie by surprise with a mouthful of food, and, as its immediate reaction was to jab out at the Sheathbill, it could not help dropping some of the food which the Sheathbill seized from under its bill. The attack was repeated several times but was successful only on the first occasion.

Giant Petrels (*Macronektes giganteus*) were not seen killing adults or chicks and were infrequent visitors to the rookeries. They were scavengers and occasionally seen feeding off carcasses, especially if drifting in the sea.

Dominican Gulls (*Larus dominicanus*) bred in a small colony at Hope Bay (Maps II and III) within $\frac{1}{2}$ mile of the Adélie and Gentoo rookery, but they were not seen interfering with the birds at all. The Skuas probably kept them away. Bagshawe (1938) reports Gulls robbing eggs from the Gentoo and Chinstrap Penguins under his observation.

Human, and especially *sledge-dog*, interference can be a serious menace to penguin populations near an Antarctic Base. Between 1945 and 1947, loose dogs were the main culprits in devastating many thousand Adélie families at the Hope Bay rookery. For the season 1948–9 all dogs were kept chained which made it possible to carry out the present study with only slight fears of very occasional escapes. The marked birds nested in remote or otherwise protected parts of the rookery, and it did not appear that any of them suffered during the season. Penguins are often needed as food for dogs and men. Killing in a large rookery need not be harmful, provided that it is carefully controlled and based on a knowledge of the life history and behaviour. Thus, penguins required for dog-feeding should, if possible, be collected in October at the beginning of the occupation period. Three well nourished Adélies collected at this time were equivalent in weight to five collected later when fasting or feeding chicks, and the carcasses keep indefinitely if stored in an ice cave away from the scavenging Skuas.

Dissections of large batches of Adélies killed indiscriminately in colonies during the occupation period usually showed a greater proportion of males to females. For example, out of fifty killed at Signy on October 27th, thirty-five were males. This disproportion was not necessarily due to an inequality in the sex ratio, but to a difference in behaviour of the two sexes, males usually defending their nests whilst the females ran away. By removing the birds that stand their ground and defend their nests, unnatural predators such as men and dogs may have precisely the opposite effect to natural predators on an Adélie community, unless the killing is controlled.

2. Interference on Land

Inter-specific Competition, though not seen between the Adélies and Gentoos at Hope Bay, was recorded on several occasions between Adélies and Chinstraps at Signy. Here they nested side by side, and Adélies were occasionally ousted from their nests at egg-laying time by Chinstraps which had just returned to breed at the beginning of their occupation period. This resulted in a small mortality of Adélie eggs. Chinstraps occupying the nests of marked unsuccessful Adélies were also expelled by the rightful owners when the Adélies returned during their re-occupation period.

Intra-specific Competition. Perhaps more attention should be paid to the possibility of lowered morale and psychological strain (see p. 69) as contributory factors to adult mortality. Plate XIc–f taken on October 24th, of a fight involving three Adélies whose sexes were afterwards confirmed by dissection, illustrate how this might occur. Two females were engaged in a violent battle and smeared from bill to foot with guano. A slightly cleaner male periodically entered the fray, though never with the same vigour

as the others. Between bouts of fighting all would join in loud mutual displays (see p. 38). Suddenly, and for no apparent reason, one female gave up the fight and ran to a rock on the edge of the colony (Plate XIId) where she paused awhile, then, very slowly walking to the snow slope nearby, she slipped onto her belly and there remained with flippers outstretched in a thoroughly exhausted condition (Plate XIIf). This was no isolated example. Adélies are the most aggressive of all penguins, and similar scenes were common during the latter part of the occupation period and again during the re-occupation period. What was the fate of these birds when they eventually went to sea in a low state of morale? Might they fall an easier prey to the Leopard Seal (p. 69) than alert birds in high morale? Experience with captive penguins has repeatedly given me the impression that a loss of desire to live is an irreversible process. Could not this also be so in the wild?

Elephant Seals (*Mirounga leonina*), which hauled out to moult, occasionally interfered with breeding Adélies by rolling on their nests. Mortality from this cause was very low except on occasions when the seals were panicked by human interference. The seals would then flatten everything in their way.

3. Predators at Sea

Leopard Seal (*Hydrurga leptonyx*). Levick (1915, p. 74) gives the fullest account available of predation by the Leopard Seal, and considers this animal to be the only real enemy of the Adélie in the water. The seals were never far from the Cape Adare rookery and were thought to kill a great number of penguins. One dissected (no date given) had the carcasses of eighteen penguins in its stomach, and the intestines were stuffed with the feathers of many more. He describes the seals as lying in wait beneath the overhanging ledges of the icefoot ready to grasp any unsuspecting bird as it plunged in (Plate XIIc). When a party of Adélies in the water was attacked, they porpoised off scattering in a "mad panic". When one was overtaken by the seal, it abandoned the attempt to get away and swam round and round in a circle of about twelve yards diameter. So long as it could keep this up its ability to turn more quickly than its enemy saved it, but in the end exhaustion overcame the bird and the seal had its prey. Levick also says a hungry seal would swallow Adélies whole, but when well fed they skinned them first. This they did by seizing the bird by the feathers, and shaking from side to side until a large portion of the skin came away. Another grip on the feathers elsewhere and a shake would free more. This was repeated until most of the skin and feathers had been removed. The Leopard Seal probably had a variety of methods of killing and eating its prey.

On February 25th, 1951, our ship R.R.S. *John Biscoe* had anchored in Sandefjord Bay, Coronation Island, and I was one of a small shore party chosen to inspect the F.I.D.S. hut and depot there. On the way back to the ship, our life-boat was pushing slowly through a belt of thick brash ice, just off-shore from a large Chinstrap rookery, when a tail and two penguin feet attracted our attention. They were sticking out of the ice in a most unusual manner. Dominican Gulls were circling above, but they did not land on the object. Suddenly it disappeared under the ice as though something was tugging it from below. I had a ciné-camera in my hands and was able to record what followed. A Leopard Seal's head shot out of the water and flung a part of the carcass away from it. Subsequent analysis of this film (Film 3, see Bibliography) showed a very quick movement of the seal's head, first in extension and then flexion, flinging what appeared to be the skin forwards with great strength. Before the head disappeared beneath the ice, the mouth opened wide to swallow what appeared to be part of the body. The skin floated away, and the Gulls swooped lower. A few seconds later the seal's head came out of the ice again and, with wide open mouth and astonishingly quick action, swallowed the rest.

Levick does not believe penguins pay attention to the Leopard Seal when lying on an ice floe. In this the opinions of other observers differ, for there are one or two records (e.g. Bagshawe) of seals removing penguins from floes.

Hamilton's (1939, p. 260) analysis of the food of Leopard Seals collected by various expeditions, shows that out of thirty-two seals eight had the remains of penguins in their stomachs. There can be no doubt that penguins are an important item of food. The possible seasonal changes in a diet which, among other things, includes squid, seal, fish, crustacea and carrion (i.e. dead penguin, seal and whale), have not been studied. Also the fact that they eat carrion means that the presence of penguin feathers in their stomachs is not proof that they had successfully hunted and killed living penguins. There are only a few records of Leopard Seals actually seen killing penguins. Bagshawe (1938, p. 206) saw one just off-shore kill about six

Gentoos on March 6th. On March 18th, several more were seen caught and torn to pieces. At this time of the season (op. cit., p. 223) young Gentoos were entering the water for the first time. At other times of the year Bagshawe saw occasional penguins killed, but he gives more records of penguins escaping. Thus on one occasion (November 7th), a Gentoo, either falling or diving into the water from an ice floe just in front of a Leopard Seal's nose escaped unharmed. Dr. R. M. Laws (personal communication), who observed these seals in the South Orkneys and South Georgia, has seen them attempting to catch adult penguins, and has come to the conclusion that the penguins were equally fast and better at manoeuvring, and thus stood a very good chance of escape.

On February 5th, 1904, the *Scotia* naturalists found penguin remains in the stomach of a Leopard Seal that had hauled out onto one of the beaches. This date again coincided with the departure of young Adélie Penguins, which is earlier than that of the other Pygoscelid species (Wilton, *et al.*, p. 100 and 101). The only occasion on which I have seen a Leopard Seal killing a penguin was on February 25th (see above) at a time when the very first Chinstrap young were probably entering the water.

By contrast, Worsley (MS), who with Shackleton's party drifted for seventeen consecutive months in the Weddell Sea ice, never once reported Leopard Seals attacking penguins, either Adélie or Emperor, on ice-floes or in the water, though on many occasions the seals were seen on the same day as the penguins. Unfortunately, only two seal dissections were recorded; one seal killed on January 1st had probably been eating Crabeater Seal, and the other killed on March 30th had a stomach distended with fish. Mr. J. M. Wordie (personal communication), who was with the same party, confirms Worsley's observations by writing, "Leopard Seals are aggressive and I have seen them chase a man, but I have never seen them actually catching penguins". In spite of this, the Adélies appeared to be as reluctant to enter the water when among the pack ice as when leaving the rookery (p. 45) because, Worsley writes, "It is very evident that the Adélie's hereditary foes are only in the water, for whenever we chase . . . them, they never take to the water, though they could easily escape by so doing."

From the few records at present available, it appears that the largest numbers of penguins are killed at a time of the season when the young penguins are leaving the rookeries, and at other times comparatively few are taken. A portion of any population will be made up of birds which are inexperienced, aged, ailing, possibly those in low morale (see p. 68), or inherently stupid, and these might be the ones that fall victim. In other words, predation on penguins by the Leopard Seal, like predation by the Skua (p. 66) might well be selective, a healthy alert Adélie being able to ward off an attack or out-manoeuvre a seal, unless caught by surprise.

Killer Whale (Orcinus orca). Observations by Wilson, Levick and others go to show that the Killer Whale does not prey on penguins.

4. Weather and Sea Ice Conditions

At Hope Bay during the re-occupation period and before the crèche stage, accurate counts made of sixteen small colonies totalling 1791 nests showed that the mortality of eggs and young chicks up to then was approximately 82% (Table XIX). This estimate was a conservative one, for in other parts of the rookery not counted accurately, especially in the larger colonies, it appeared to be as high as 90%. This loss was almost entirely of eggs, and resulted from a combination of low temperatures, adverse winds, and excessive snow and drift during November (Table XX). Predation by Skuas and Sheathbills was negligible in comparison. For example, on November 19th, with a gale blowing and the temperature down to 13° F., deserted eggs were lying everywhere, their shells split open and contents frozen. Skuas and Sheathbills had far more than they wanted. The greatest losses were in the colonies where snow lay thickest, and it soon became apparent that the greatest climatic menace to successful breeding was burial of nests and incubating birds under snow for more than a few consecutive days. This was well illustrated in two colonies situated within a hundred yards of each other. Colony III was in a shallow trough between two rocky mounds, fully exposed to the prevailing south-westerly winds but partially sheltered from most other directions. Colony IV surrounded a cairn on the highest and most exposed part of Seal Point (Map III). It was one of the windiest colonies in the rookery. South-westerly gales, which often blew at 60 m.p.h. for days on end, with gusts up to 90 m.p.h. or over, swept down the local glacier and reached their greatest fury as they shrieked up the scree slope from the nearby cove. In spite of its situation, the occupants of Colony IV had a lower mortality (60%) of eggs and young chicks in early January than any other colony counted

(Table XIX). The nests in Colony III, however, remained covered by snow for most of the season. The colony was too sheltered from other directions, and because of the abnormal weather of the 1948–9 season, all eggs were deserted and destroyed. This 100% mortality was typical of many other similarly situated colonies. Plate XII d and e taken during the 1948–9 season show the colony practically obliterated by snow. Plate XII f shows it under what must have been more usual circumstances four years later during the 1952–3 season. At the beginning of November 1948 there were thirty-five pairs. Four years later (Hunt & Coley, MS) thirty-three nests were occupied, and on January 4th, 1953, twenty-seven nests and a total of twenty-nine chicks were counted. The breeding success of Colony III in 1952–3 was therefore greater than the most successful colony counted at the corresponding date in 1949.

Chick mortality from the crèche stage onwards was not large at Hope Bay in 1949, and predation by Skuas probably accounted for most of it. At Signy, 1950–51, there was a lower mortality of eggs and young chicks (about 60% as compared with 80–90% at Hope Bay), but a very high mortality from the crèche stage onwards. Substantial evidence was collected suggesting that the Adélie parent travels to the pack ice to collect food for the chicks. The 1950–51 season was unusually ice-free, and this was very probably the chief cause of the mortality, the parents having to travel so far for food that many deserted, or were unable to bring it back regularly enough to maintain normal chick growth.

G. INDIVIDUAL RECOGNITION

This section includes further evidence from field observations of the part that territory, visual and auditory recognition and the mutual display (Sladen, 1953) play in recognition between one Adélie and another.

1. Territory

The conclusions of Levick (1914, p. 101), and other earlier writers, that birds do not return to the same sites in successive years, cannot be substantiated from data on marked birds. Gain (1914, p. 38) marked fifty Adélies with violet celluloid rings on January 12th, 1909. Early next breeding season eleven of these birds were recaptured at the rock where originally ringed. Some were again recovered by whalers in November and December, 1910 (Gain, 1913, p. 479). Gain's birds, though not ringed until late in the season during the re-occupation period, showed a tendency to return to their former breeding area.

On November 19th, 1946, Andrew (Andrew & Roberts, 1952) ringed ten pairs of Adélies at their nest-sites (see Table XII). The sites, carefully marked and located (see p. 19) were chosen close to some easily recognisable rock feature and, when possible, isolated from neighbouring nests. By November 23rd, most of the nests contained two eggs and the remainder one. The pairing of all twenty birds was therefore definite and productive. The nests, and the area around them, were kept under close observation (Roberts, MS) in October and November, 1947. Of the twenty birds originally ringed, seventeen were recaptured. Six pairs were the same and had returned to their old nest-sites. The four birds of two other pairs (Nests 5 and 6) each had an unmarked mate, one bird of each original pair keeping its old nest-site, whilst the other went to an adjacent site. Of another pair (Nest 1), only one ringed bird was recaptured at its nest-site and it had an unmarked mate. The tenth pair (Nest 4) was not recaptured. Each of the eleven nests had two eggs, two pairs hatching one chick only, the rest hatching two chicks each.

During the following season (Sladen, MS), fourteen were again recaptured. Four pairs were again the same, each returning to its old nest-site and laying eggs. A fifth pair (Nest 8) were seen together at their original site early in the season, but no eggs were laid, and one of the birds was not seen again after November 14th. Four other birds from Nests 5a, 5b, 6a and 6b had, as in 1947, unmarked mates which may or may not have been the same as those of 1947. The remaining six ringed in 1946 were not recaptured. Observations between 1949 and 1951 were not possible as the F.I.D.S. Base at Hope Bay was temporarily closed.

In the 1952–3 season, data collected by Hunt and Coley (summarised in Tables XII and XIII) provided further evidence that Adélies, once established as pairs, are remarkably faithful to their nest-sites and mates. Thus, of the thirteen recaptured birds in Table XIII originally ringed as breeders, two, and probably three, were found in the nest-sites they had been occupying four years back, and one female at the site at

which she had been originally ringed six years back. Moreover, as regards the other six birds found with unmarked mates in 1952, not one of their former marked mates was recaptured; had they been present, it is likely that they would have been with their original mates. Bearing in mind the possibility of human and dog interference from the British and Argentine Bases nearby, and the difficulty in identifying marked birds (all Hope Bay birds had only leg rings), it seems remarkable that the recovery-rate should be so high. These results from Hope Bay for the period 1946 to 1953 are important as, apart from Richdale's work on New Zealand penguins, they represent the first attempt to follow up marked penguins for several years.* There is, however, need for repetition of this investigation on a larger scale. The original nest-sites chosen by Andrew in 1946 were close to some well defined rock features and, where possible, isolated. Would the same results be obtained if a group of birds were ringed in the middle of a large featureless colony? Would such birds come back to exactly the same sites and remain in the same pairs as consistently as Andrew's 1946 birds, or mine of 1948? Circumstantial evidence suggests that the pairs at Andrew's Nests 5 and 6 which separated during the 1947-8 season were, in 1946, not both established breeders.

It would also be interesting to know what factors contribute to make a bird an experienced and successful breeder. For instance, are individual variations in temperament important, and does the success or failure of their first breeding season affect them? An unsuccessful breeding pair may actually spend longer together at their nest than a successful pair (Figure 16a and b). An unsuccessful first year might therefore even provide a better opportunity for establishing the pair-bond in subsequent years than a successful first year. The pair-bond might also be broken if one of the partners kept company with another bird for too long (p. 63) in the absence of its true mate. This could easily happen with an unsuccessful pair which, having lost its eggs, returned later during the re-occupation period. The problems awaiting future research are many.

The Hope Bay results show that birds return to their old territory and maintain their pair-bond in subsequent years. Is this primarily the result of the birds returning to the same territory, or the result of established birds recognising each other as individuals? Previous workers have suggested that it is primarily the nest-site that serves to maintain the pair-bond from year to year (e.g. Roberts, 1940, p. 204 and Richdale, 1951, p. 58). On the other hand, evidence from my field notes suggests that a pair might well remain together in subsequent seasons, provided they were both experienced and established. I suggest then, that if they were breeding in a large featureless colony they would still tend to keep together, though their nest-sites might vary slightly in position from year to year.

Though territory is an important factor in bringing both members of a pair back to known ground, I believe that in penguins the most important factor for maintaining the pair-bond may well be the visual and auditory recognition of the birds as individuals. The following examples, a few of many that could be given, provide evidence in support of this supposition. It should be borne in mind that Adélie nests are normally from one to two feet apart.

i. Between mated adults

The first example concerns an unmarked pair observed on December 11th, 1948, the sexes of which were later confirmed by dissection.

The weather was very bad with continuous wind, drift and snow, and most of the incubating birds in the colony were more than half-covered with snow, only a portion of their backs and heads showing. Rocky features were partially covered and nest-sites completely hidden. A male returning from the sea to relieve its mate at the nest was seen walking through the colony receiving the usual (but rather half-hearted) pecks from neighbours and pausing to get its bearings. Stopping at one nest, he joined in about four loud mutual displays with an incubating bird, after which he received a peck and, moving on, found what appeared to be his real mate incubating eggs in the next nest. Both birds responded very quickly and joined in loud mutual displays.

Breeding success is dependent on two of a pair recognising each other even under such adverse conditions as when nest-sites are obliterated and mates partially covered by snow. These conclusions were later confirmed in marked birds. Also of interest in this example was the apparent mistaken identity which did not become obvious until the two birds concerned had repeated the loud mutual display four times. This suggests that the mutual display may act as a confirmation of recognition (see below) under such circumstances, as no doubt it does between parents and chicks in the crèche (p. 35-36).

* Additional confirmation is claimed by Stonehouse (1953, p. 29) who ringed ten pairs of Adélies in January 1948 at Red Rock Ridge, but, like Gain's birds, they were not ringed until the re-occupation period and could not therefore be guaranteed as true breeding pairs.

The second example was observed at Nest 47 in Colony IX on Signy Island (see Figure 16c), where a pair was first ringed on November 2nd, six days before their only egg was laid:

This egg was removed. The female remained until the 10th, but as no second egg was laid, she moved off to sea leaving her mate alone at an empty nest. He occupied the site alone for fifteen days after she had gone, but on November 27th the nest was found deserted. On December 12th and 13th, the female was back in her own site alone. On 15th, and at 0800 hrs. on 17th, she was found in a different adjacent site keeping company with an unmarked bird. Her old site (Nest 47), at least on 15th, was occupied by a pair of unmarked Adélies. At 1930 hrs. on 17th, she was seen occupying another adjacent nest-site (Nest 52), but after being disturbed by being chased and caught for repainting and weighing, she returned to her old nest-site No. 47. On 19th, she was again at Nest 52, and keeping company with an unmarked bird, her old nest-site being occupied by a lone Chinstrap Penguin (Colony IX was a mixed colony of Adélies and Chinstraps, see p. 67). On 21st, her mate was back in Nest 47 and she was at his side. They were still together on December 23rd, and tread marks on her back indicated that copulation had taken place. They were still together on January 10th but had probably not occupied the nest during the whole of the intervening time. On January 12th, the male's sex was confirmed by dissection.

During the re-occupation period, the female of this nest occupied two different sites and kept company with one, probably two, unmarked birds before her true mate returned. She then shifted back to her original nest-site, the site to which she had first returned after her spell at sea and from which she had no doubt been attracted away by her unmarked consorts.

The third example is from Nest 11 at Hope Bay:

The male was more nervous than other marked males. His mate, also marked, was found with an egg on November 11th, but later on the same day, she had gone, leaving him incubating the single egg alone. As he continued his first fast he became more and more nervous until on November 23rd, after being weighed, he unfortunately refused to return to his egg and walked off to sea. He was not observed again until the re-occupation period, when on December 28th he was found alone in his nest-site. His mate had returned to the site on November 26th, three days after he had deserted, but finding it unoccupied, had gone off again. After December 28th I did not see the male again until January 4th and then, to my surprise, discovered him alone occupying a different nest-site ten feet away from Nest 11. He continued to occupy this new site until January 16th, most of the time alone, but on January 6th his mate was seen at his side. She was not seen again, but it seems unlikely that these two birds would have come together again at a nest-site ten feet away (about seven nests away) unless they were able to recognise each other as individuals. This nervous male had probably changed his site because of my interference.

A fourth example concerned Nest 8 at Hope Bay:

Two marked birds keeping company, occupied the nest-site from December 24th until January 4th and then shifted to a new site seven feet away and remained together for another nine days.

ii. *Between neighbouring breeding adults*

One more example of considerable interest, was of two marked birds of opposite sex which had nested and lost their eggs in adjacent sites in Colony XVII at Hope Bay, and which were found keeping company on December 27th during the re-occupation period in a different colony sixty feet away. The female (VR) had brown tread marks on her back, and both were seen in mutual display at a well built nest towards the centre of their new colony. Colony XVII had been buried under snow for most of the season and on this date was completely abandoned. Surely it was not just chance that drew these two close neighbours together in the absence of their true mates (one of the mates had been killed for dissection, and the other had revisited Colony XVII for one day only on December 12th and had not been seen since) at a site so far away from their original ones. These neighbours must have recognised each other as individuals.

iii. *Between parents and chicks at the crèche stage*

Evidence has already been given (p. 60) for recognition between parents and their chicks when at the crèche stage. A few chicks moulting their second down were marked and transferred to another crèche, still within view of their own colony but a quarter of a mile away. Most were back within twenty-four hours. Even though stronger than the other chicks in the new area, I do not believe they would have been fed by adults other than their own parents, and it is probable that they would have starved had they not been able to find their way back to their own area. The nest-site is, however, less important than visual recognition, because, as has already been indicated (p. 61), parents and chicks recognise each other when the chicks are in a crèche which may be many yards away from their abandoned nest-site. Moreover, the crèches often shift their position from day to day.

2. *Visual and Auditory Recognition*

Field experiments showed that parents adopted chicks from other nests if they were small, but very rarely ones that were large enough to stand up. These experiments need repeating on a larger scale with

marked birds of known age, but the results so far obtained and a close study of the birds and the parent-chick behaviour patterns throughout the two breeding seasons, led me to believe that visual recognition was the most important single factor involved. It was slowly acquired during the early stages of chick growth, and fully developed by the time the chicks went into the crèche. I believe also that the great variation in character, appearance (see p. 39), stance, voice, etc., between one adult and another, and between adults and chicks, contribute much more than any other factors to this recognition.

I will never forget my confusion and bewilderment when first confronted with a crowd of over sixty sledge dogs. In spite of the variety of coat patterns, it seemed at first an impossibility to distinguish one from the other. Yet after a few weeks of handling and close association my initial confusion had been turned into confidence. It was not so much the obvious differences in coat pattern that distinguished them, but an accumulation of small differences which, taken by themselves, would have provided but flimsy evidence for recognition: the way they walked or held their tails, slight differences in facial expression, their reactions to men or other dogs, their voices. These and other differences built up a picture in my mind which a still photograph showing coat pattern could not recapture. Sometimes when examining pictures of similar looking huskies, I have had doubts as to their identity, whereas a glance at them in the flesh would have revealed their identity. The more one gets to know animals by living among them for long periods, the easier it becomes to pick out little differences in character, expression, deportment and voice. It is reasonable to suppose that these powers of observation should be more highly developed in penguins, since their success in breeding must largely depend on them.

3. *The Significance of the Mutual Display*

The "welcome" ceremony described by Richdale (1951, p. 21) in the Yellow-eyed Penguin had much in common with the mutual display seen during the nest-relief ceremony in the Adélie, but with one difference: nowhere in Richdale's account is there any reference to the Yellow-eyed Penguin chick joining in the display. In the Adélie, the mutual display was seen at its highest intensity during the nest-relief ceremonies (p. 47). A good indication of intensity was the number of times that the loud display was repeated. Though there was considerable variation in intensity between different pairs, these ceremonies were more prolonged during the incubation period than during the guard stage. Moreover, the loud mutual display seen between parent and offspring during the crèche stage seemed to decrease in intensity as the season advanced and could be brief and easily missed when the chicks were nearly full grown. It seems significant that it could again become intense if, by chance, both parents met at the colony when back to feed chicks.

Two more important observations should be mentioned. Firstly, a parent and offspring might join in the quiet mutual display (i.e. low intensity) between feeds long after the initial bout of loud displays, which had hailed their first meeting, had died down. Secondly, the mutual display was not necessarily confined to a mated pair, or parent and offspring. It was seen between birds who were keeping company (p. 35), or in the general excitement of a fight (p. 35), or between strange chicks and adults when the chicks were importuning for food. Two typical examples at the end of the season illustrate these observations:

On February 9th, at Signy, an unmarked adult on arriving at a colony fresh from the sea, was seen to go into loud mutual display. The noise attracted several hungry chicks, and also one well nourished down-free chick A. Chick A responded to the adult's loud mutual display with its own higher pitched tremulous loud mutual display (see p. 36). The adult pecked the other chicks away while chick A remained by its side. Later A also helped keep any persistent chicks away by pecking them. From evidence already given from marked birds, there seemed no doubt that this adult was the parent of chick A. If the parent had wanted to feed the other persistent chicks it could have done so, as its offspring A did not appear hungry, and apart from an occasional peck at them showed very little interest. Later A asked for food by tickling the parent's bill and received some immediately. There was no feeding chase on this occasion, and after most of the food had been given to A, the parent started to gather stones and deposit them at a nest-site by which it had been standing for most of the time. Both occasionally joined in the quiet mutual display (i.e. low intensity) and this was usually followed by begging for more food and another feed. Both were later collected for dissection. The adult was a male weighing 4.15 kgm., with 7 oz. semi-digested *Euphausia* left in its stomach. Chick A weighed 3.95 kgm., and had 1 lb. 9 oz. of *Euphausia* and some stones in its stomach.

The other instance was recorded on the same day in a neighbouring colony. A freshly arrived adult walked straight to the middle of the colony, where it remained. A loud mutual display made by this single adult attracted three chicks. Chicks and adult joined in the mutual display, but when a chick begged for food the adult pecked it away. I was watching this bird from my observation tent, so it was undisturbed. At intervals for the next hour, various chicks coming up to this adult would receive a loud mutual display in response, but this was invariably followed by pecking when the chick begged for food. When not being disturbed by chicks the adult stood preening. No nest-building was seen and later it walked away. This unmarked adult was probably a parent which returned to feed its chick but failed to find it, and moved off without feeding the strangers.

There are three possible ways of interpreting the mutual display of the Adélie when seen in its most usual form. It can be regarded as incipient threat and an appeasement ceremony (i.e. basically aggressive), or as a "greeting" ceremony, or as a confirmation, re-enforcement and "reassurance" of individual recognition.

Incipient threat and appeasement ceremony. The view that it is incipient threat and an appeasement ceremony is accepted by Roberts (1940, p. 214) for penguins, and by many other writers for other species of birds. It can be argued that because the loud mutual display is seen between fighting Adélies, it is basically aggressive. Moreover, characteristics of the attitude of threat, such as the raising of the occipital crest and downward rolling of the eyes, are also seen in the mutual display (Plate VIc). But why should the display seen in fighting not be just as conveniently explained either as an act of "reassurance" (p. 39 and see below) or as a displacement activity (p. 48)? The occipital crest is raised in many situations and by no means only in threat or aggression. Similarly, the position of the eyes is not necessarily aggressive, Plate IXb showing them rolled downwards even when the bird is apparently completely relaxed and undisturbed.

It has been suggested that the so-called appeasement ceremony has been evolved in order to overcome the normal reaction of an adult bird to peck at any other which comes within striking distance, and that the penguin occupying the nest will thus tend to react aggressively to its approaching mate. There seem to be no grounds for this belief in the Adélie. Unless the incubating bird is partially hidden by snow (p. 71), the two members of a pair appear to recognise each other from a distance. I have even observed recognition from a distance by a bird approaching its mate from behind. Moreover, even if there were an aggressive element in the loud mutual display seen between mates during the nest-relief ceremony (which I do not believe), how could the same be true in the identical movements between parents and chicks? Why should an appeasement ceremony be necessary after the chick in the crèche has recognised its parent's voice and come running up to it? Why should the quiet mutual display be repeated by the parent and chick at irregular intervals between bouts of feeding?

A greeting ceremony. The following points favour the interpretation of the mutual display as a greeting ceremony.

Firstly, the birds appear to know each other from a distance. An appeasement ceremony is therefore less likely to be necessary. Further, the mutual display, at all intensities, was seen between chicks and parents at the nest-relief ceremony before and during the crèche stage, and occasionally even between two chicks when alone (see p. 36). Also, Richdale calls the Yellow-eyed Penguin's nest-relief ceremony "welcome", and no suggestion of incipient threat or aggression can be found in his descriptions. Finally, after they had become familiar with me, captive chicks (p. 36) ran up to me and responded to my rather crude imitation of an adult loud mutual display or my whistling of "D'ye ken John Peel", exactly as if responding to a newly arrived parent (i.e. joining in loud mutual display with their tremulous mutual display call, followed by food begging).

Roberts (1940, p. 219), writing about the mutual display which he mistakenly supposed was confined to the pre-egg period, states that it has the function of mutual sexual stimulation. This may be so, though he admits it need not necessarily lead to copulation. I do not remember once seeing copulation follow immediately after the mutual display in the Adélie. The two acts appeared quite distinct and were in no way inter-related. While it perhaps serves the function of mutual sexual stimulation, I believe the term "greeting ceremony" with its implications of individual recognition and perhaps "joy" or "well-being" (if one dare be so anthropomorphic) at meeting again after a long period of separation during the fasting periods or during the winter (see p. 28 and Table VI), fits the behaviour of Adélies, and no doubt other penguins, better than incipient threat or appeasement ceremony.

Confirmation, reinforcement and "reassurance" of individual recognition. Simple greeting cannot, however, explain many of the situations in which the mutual display was commonly seen in the Adélie. The display as an act of "reassurance" was suggested when discussing attitudes and noises suggesting nervousness (p. 39). This may be its function when seen during fights, or it may be a displacement activity.

The example of the bird which mistook its mate when mostly covered by snow and which was pecked away after four loud mutual displays, suggests that in certain situations the display acts as a confirmation of recognition. Perhaps most convincing of all were the frequent occasions when parents arriving at their colony would go into the loud display thereby attracting chicks to them. Some might be pecked away, others join in the feeding chase (p. 46) only to be pecked away by the adult later. The film illustrates a chick

waking up and rushing to an adult in response to the sound. The same response was observed in a marked chick which was asleep when its marked parent arrived and went into loud mutual display. The sound heard in the display thus plays a vital part in recognition.

In support of it being a reinforcement of individual recognition is the fact that the same display was repeated many times in one bout and with the slightest excuse (e.g. after two at a nest had been separated for a short while during nest-building, p. 34). The intensity was highest early in the season before egg-laying and gradually decreased in intensity as the season advanced. There was also an increase in intensity during the re-occupation period among the unsuccessful breeders and non-breeders occupying territory.

ACKNOWLEDGEMENTS

BEFORE leaving Britain in 1947, I received advice and encouragement from Dr. B. B. Roberts. I am also indebted to Sir Miles Clifford, K.B.E., C.M.G., Governor of the Falkland Islands 1946–53, for his approval of and interest in the research and photographic programme on the penguins. I wish to thank members of F.I.D.S. and R.R.S. *John Biscoe* for their co-operation, especially Captain H. Kirkwood, O.B.E., R.N., Captain W. Johnston, F. Elliott, S. McNeile, B. Jefford, J. Cheal, R. Worswick and A. Venum. I wish to record my gratitude also to the late O. Burd and to those connected with F.I.D.S. who have sent information and helped since my return, especially Sir Vivian Fuchs, Sir James Wordie, C.B.E., Dr. R. M. Laws, N. B. Marshall, J. D. Andrew, Dr. J. M. Roberts, Dr. B. Stonehouse, A. Mansfield, Miss E. Todd, B. Hunt, J. Coley and A. Tritton.

Facilities for working up the field data for Part I—Methods of Study and Part II—The Adélie Penguin, were kindly provided by Dr. D. Lack, F.R.S., Director of the Edward Grey Institute, Oxford University, to whom I am much indebted for advice. I have also had the benefit of discussing various aspects of Parts I and II with Dr. N. Tinbergen, Professor K. Lorenz, Dr. L. E. Richdale, Dr. Harrison Matthews, F.R.S., R. E. Moreau, E. A. Armstrong, M. Cullen, and Dr. B. Stonehouse, to all of whom I am most grateful.

The sketches have been drawn by my wife, Brenda Sladen, who has given much valuable criticism and advice on the text. Plate IIc is of a photograph kindly provided by Dr. J. N. Pattinson of the X-ray department, Middlesex Hospital, London. Plates VIe and f and XIIc were photographed by Dr. Murray Levick (Levick, 1914) whose set of beautiful photographs are now at the Scott Polar Research Institute, Cambridge. Plates IIIb and XII f are from photographs by B. Hunt. The rest of the Plates are from photographs taken by myself.

APPENDIX

A. TABLES

	Adélie			Chin straps		Gentoos		
	A	B	C	B	C	B	C	D
Rings used:								
<i>Semi-permanent aluminium:</i>								
leg-rings	45	34	51	1	—	—	49	19
flipper-rings	—	238	—	211	1	16	37	76
<i>Total (778)</i>	45	272	51	212	1	16	86	95
<i>Temporary:</i>								
painted aluminium	—	50	—	23	—	—	—	—
overlap flipper-rings	—	—	—	—	—	—	—	—
coloured celluloid flatband	62	56	—	36	—	—	—	—
rings (mostly flipper)	—	—	—	—	—	—	—	—
<i>Total (227)</i>	62	106	—	59	—	—	—	—
Paint Marks:								
<i>Flipper numbers</i>	57	79	—	33	—	—	—	—
<i>For mass marking</i>	200	1024	—	—	—	—	—	—
<i>Total (1393)</i>	257	1103	—	33	—	—	—	—
Numbers of birds marked with semi-permanent aluminium rings:								
<i>Adults</i>	44	124	11	138	1	16	37	90
<i>Nestlings</i>	—	119	40	74	—	—	60	4
<i>Total (758)</i>	44	243	51	212	1	16	97	94

TABLE 1. Summary of the Pygoscelid Penguins marked during the period of study, 1948-51.

Notes: Column A—Hope Bay, 1948-9 (only Adélie were marked).

Column B—Signy Island, 1950-51.

Column C—Elsewhere in the Dependencies, 1949-50.

Column D—Falkland Islands, 1949-51.

	Established (experienced) breeders	Unestablished (inexperienced) breeders
Date of arrival at Rookery (p. 48).	Staggered, but generally earlier.	Staggered, but generally later.
Nest-sites (p. 49).	Old sites re-occupied, the bird coming straight back to them. May however change site if persistently disturbed.	Vacant sites in colony, or poor sites on periphery. May loiter around area or rest on snow slope nearby. If disturbed, very liable to move elsewhere. May move to a better site, if available (p. 27).
Ecstatic display of male (p. 32).	Moderately frequent but not persistent unless alone.	Very frequent, especially among unpaired males standing alone in territory. Often repeated many times in succession if bird remains alone.
Breeding success (p. 25).	More successful than unestablished. Usually lay normal clutch of two eggs.	Less successful. e.g. Eggs fall easier prey to Sheathbills and Skuas; may desert chicks more readily.
Nest-building (p. 44).	Probably do not waste time by collecting such useless objects as lumps of ice.	Abnormal nest-building activities may prove to be in this group.
Pair-bond (p. 70).	On present evidence pair-bond is maintained from year to year.	More easily upset.
Effect of loss of partner in pre-egg stage (p. 28).	Experiments (Tables VIII & IX) showed that partners were quickly replaced whether male or female, in spite of other unpaired birds (? unestablished) in vicinity.	Not definitely known, but observations suggest that female partner at any rate is difficult to replace.
Copulation (p. 40).		The incomplete act of copulation seen in some pairs may be as much the result of inexperience as lack of "intensity" (p. 25).
Fights (p. 38).	Rare, if previously established pair return to same nest, but will occur on return of the true mate, if an established bird has been "keeping company" with another. The fight would be male against male or female against female; and not male v. female.	Common, and is the chief means of sorting out territorial claims.

TABLE II. Suggested differences between the established (experienced) and unestablished breeders.

GOURLAY ROOKERY, 1950

Date seen	Sex	Weight (kgm.)	Bl. (mm.)	Notes
21 Oct.	M	3.6	SQ	Alone on edge of a Colony.
221 Oct.	M	?	SQ	With party of adults just arrived at rookery.
27 Oct	—	—	—	One seen but not caught.

HOPE BAY ROOKERY, 1948-9

17 Dec.	M	4.10	MQ	These were the first seen at Hope Bay. They were several yards from ice cliffs, and were clean and recently arrived.
	F	3.60	SQ	
18 Dec.	F	3.60	Q	On edge of a colony.
19 Dec.	M	3.65	SQ	
22 Dec.	—	3.9	—	On edge of a colony. See Plate Ve.
24 Dec.	M	?	—	
24 Dec.	M	4.60	4	Wandering with an adult.
	F	3.90	4	
25 Dec.	—	—	—	One on rocks by shore.
26 Dec.	—	—	—	Numbers increasing. Thirteen counted. Two were on edge of colonies, others either near sea or walking about slopes with the "wanderers". One attacked me; all others, as usual, fled.
27 Dec.	—	—	—	Several new arrivals seen on rocks by sea.
28 Dec.	M	4.7	7	Near a colony. This the first immature bird dissected with no evidence of intestinal parasites. Numbers increasing and now seen from time to time at edges of colonies, though none seen within colonies or at nests. Occasionally seen also with parties of "wanderers". One seen picking up a stone by a colony.
31 Dec.	M	4.3	MQ	Killed by dogs near Base. With stone in bill and standing by nest with signs of recent building on edge of Colony V. On edge of Colony V. On edge of Colony V. Numbers still increasing, and more seen around colonies. Four yearlings among 114 adult plumage birds, and seven among another group of fifty adults on a snow slope.
	—	4.10	—	
	—	3.55	—	
	—	3.60	—	
	—	—	—	
1 Jan.	—	—	—	One lying in a scoop in Colony V, but not seen next day.
4 Jan.	F	3.65	MQ	Around Base with four adults. Numbers are decreasing slightly.
6 Jan.	—	—	—	Numbers probably less.
8 Jan.	—	—	—	Fewer on edge of colonies but about nineteen counted with parties of "wanderers".
9 Jan.	—	—	—	One walking up steep slope of nearby hill.
10 Jan.	—	—	—	One with very stained pink (<i>Euphausia</i>) breast, suggesting it had been lying in a nest site
12 Jan.	—	—	—	Some wandering with (?) non-breeders.
13 Jan.	—	—	—	One seen on edge of a colony, a few with (?) non-breeders on snow slope near the sea.

TABLE III—continued opposite.

Date seen	Sex	Weight (kgm.)	Bl (mm.)	Notes
21 Jan.	F	4.90	10	Quills of new plumage in blubber. This the first indication of moult. Another lying in a nest-site in colony.
25 Jan.	M	5.5	10	Near Base Hut.
26 Jan.	M	5.20	10	Among adults.
	M	5.9	11	From a colony
30 Jan.	—	5.9	—	On a snow slope. Back feathers came out when caught.
31 Jan.	M	6.5	10	On snow slope. Quills of new plumage in blubber.
	—	—	—	In all about fifteen yearlings seen, mostly on the snow slopes but at least three in colonies. Without exception all much larger and fatter than adults and half of them showing loose feathers on back. One nearly half moulted.
2 Feb.	—	—	—	Four yearlings with nestling in one colony.
4 Feb.	—	—	—	Four yearlings still in same colony. Three others moulting in another colony among the nestlings.

PORT LOCKROY, GRAHAM LAND

14 Feb.	F	4.25	10	Immature plumage half moulted into adult. Collected from ship <i>John Biscoe</i> .
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TABLE III. Immature-plumaged (Yearling) Adélies seen in Breeding Areas at Signy and Hope Bay.

Notes: M=Male. F=Female. All these were confirmed by dissection.

Bl.=Blubber thickness. Blubber was measured to the nearest mm., but when less than 4 mm. thick measurement was too inaccurate as the quills of the plumage showed through. Thickness was then divided into the following groups: MQ=moderate amount of blubber between the quills. SQ=when the quills showed clearly with only a little blubber between. Q=when quills only and no trace of blubber between. Blubber thickness was measured from a routine position (it varied considerably in different situations) from the right side, one inch from the midline, half-way between xyphisternum and clavicle.

Stomach contents: All birds dissected were examined for stomach contents and there were only occasional stones except the bird collected January 31st which had *Euphausia*.

A. December 17th, 1948—January 4th, 1949.

	Adult Plumage			Immature Plumage		
	Number of Birds	Average weight (kgm.)	Range	Number of Birds	Average weight (kgm.)	Range
Male	39	4.6	3.7-5.9	5	4.3	3.7-4.7
Female	34	4.2	3.5-5.0	4	3.7	3.6-3.9
Unsexed	4	4.5	3.1-5.5	4	3.8	3.6-4.1
Average weight for total sample	77	4.4		13	4.0	

B. January 21st—February 4th, 1949.

Male	99	4.2	3.2-5.5	4	5.8	5.2-6.5
Female	42	4.1	3.1-5.1	1	4.9	—
Unsexed	3	4.0	3.4-4.4	1	5.9	—
Average Weight for total sample	144	4.1		6	5.7	

TABLE IV. Weights of Adélies in adult plumage compared with yearlings, Hope Bay.

	Group A Definite signs of im- maturity and non-breeding.	Group B Signs of maturity but not necessarily of breeding.	Group C Definite signs of breeding.
Incubation area	No different from that of immature bird: none, or less than 2 cm. wide.	None, or less than 2 cm. wide.	During incubation and until chick about one week old it is large, bare and often purple and never less than 2 cm. wide.
Ovary	Flattened, homogeneous appearance with no ovules or a few small ovules scattered in a homogeneous matrix (a).	Ovary heterogeneous. Ovules of varying sizes. No homogeneous matrix (b) and (c).	For several weeks after egg-laying, presence of ruptured follicles is definite evidence of breeding (d).
Oviduct	No bends; flattened and semi-translucent (a).	Tortuous, raised and usually pale flesh colour (b) and (c).	No obvious macroscopic difference from mature oviduct (d).
Testis	Flattened and usually narrow (e) or slightly S- shaped with pointed upper and lower poles (f). Some- times grey, but colour not a definite sign.	Raised, with rounded upper and lower poles. Colour usually pale flesh, but sometimes grey (g) and (h).	No obvious macroscopic difference from mature testis.
Bursa fabricalis	Present and well developed.	Residual or not demon- strable macroscopically.	No different from that of mature bird.
*Remnants of vitelline duct	Usually present.	Rarely present.	No different from that of mature bird.

TABLE V. Macroscopic evidence of breeding and non-breeding.

Notes: **Vitelline duct* is the rudiment of the yoke sac. This needs further investigation as my observations were founded on a small sample only.

The small letters in brackets refer to diagrams in Figure 12.

	A	B
Date	October 20th	October 28th
Weight	4.55 kgm.	4.35 kgm.
Blubber thickness†	6 mm.	MQ
Diameter largest ovule	2.7 cm.	3.3 cm.
Oviduct width, top	1.8 cm.	2.2 cm.
Oviduct width, uterus	2.5 cm.	3.6 cm.
Behaviour	Walked straight up to a lone male occupying a nest-site, both immediately joining in repeated loud mutual displays.	Wandering round the periphery of colonies. Visited three before being collected.
Dissection number	H451/2	H470/1

TABLE VI. Comparison of the behaviour and dissection data of two female Adélies newly arrived from the sea ice.

Notes: It is suggested that A had previous breeding experience (i.e. was an established breeder, and was returning to its former nest-site), and that B had no previous breeding experience and would thus have been either an unestablished breeder, or non-breeding wanderer.

†For description of blubber thickness, see footnote of Table III.

Ecstatic Display Seen	A	B	Total observed
1. Males alone at empty nest or site at any time during season, but most often before eggs laid. 2. Females as in 1.	*37 †1	17 none	*54 1
3. Males at empty nest with another bird (female) either standing by side or walking up in response to his display. 4. Females at empty nest with another bird (male) as in 3.	15 none	11 none	26 none
5. Males over two eggs which they were incubating alone. 6. Females as in 5.	3 none	1 ‡2	4 2
7. Males over one or two chicks when alone in nest. 8. Females as in 7.	4 4	3 2	7 6
9. Female over chick with male also at nest.	\$1	none	1
10. Two adults in the same nest, both seen in ecstatic display at any time of the season.	none	none	none

TABLE VII. Ecstatic display at nest-sites by adult Adélies of known sex.

Notes: Column A. Sex of one or both birds confirmed by dissection.

Column B. Marked birds in which sexes were confirmed by knowing incubation routine, or, in a few cases, by seeing copulation.

Each observation may represent several displays made in succession, but they were not added to the total, unless made on different days.

A rearrangement of the above data shows the following:

Males at empty nests over eggs	84
Males over chicks	7
Females during their first and second fasting periods	none
Females after their second fasting period (i.e. after the chicks should have hatched)	10

*Only five of these observations are from Hope Bay, the records made in October were destroyed but represented about thirty dissections confirming that the male only was seen in ecstatic display. The total observations would therefore be about eighty instead of fifty-four

†This was the only record of a female seen in ecstatic display at an empty nest. Dissection confirmed that the bird had bred (ruptured follicles in ovary) and, as it was December 27th, it might have just lost its young.

‡These two observations for the same bird (No. 62185) were made on successive days, January 5th and 6th, while she was still incubating two *addled* eggs.

§These (dissections H731/1-2) were both seen in the "bill to axilla" display on December 15th. The male was crouching over a newly hatched chick. The female, by the side of the nest, was also seen in ecstatic display.

	A. Pairs Before Eggs Laid	
Date and Time (G.M.T.) 1950	Nest 36	Nest 37
Oct. 30th 1400 hrs. 2200 hrs.	Female killed. Male marked, weight 4.25 kgm., returned immediately to nest. Both males seen in quiet mutual display with second partners.	Female killed. Male marked, weight 4.6 kgm., returned immediately to nest.
Oct. 31st 1630 hrs.	Still with partner at a well built nest.	May have lost his partner. Nest poor.
Nov. 1st 2130 hrs.	Both males still with partners	
Nov. 2nd 1500 hrs.	Both still with partners. Still no eggs.	
Nov. 4th 1730 hrs.	Both still with partners which were killed. They were females and had tread marks on backs.	
Nov. 6th 0030 hrs. 1630 hrs.	Both males have third partners with which they were seen in quiet mutual display. Still with third partner who was on one egg. This female not killed, so breeding routine left to continue.	Still with third partner; no eggs. This female not killed, so breeding routine left to continue.
Nov. 9th 2200 hrs.	On two eggs, his mate standing by nest.	Standing by nest, his mate on one egg.
Nov. 13th, 17th and 23rd	Both males alone on two eggs each.	
Dec. 4th 0300 hrs.	Both males away at sea. Their mates returned a few days ago and now incubating alone.	
Dec. 8th 0800 hrs.	Both males now back from sea and alone, incubating two eggs each.	
Dec. 15th 1930 hrs.	Both males alone over two chicks each. No further observations recorded.	

	B. Pair with Eggs
Date, 1948, and Time (G.M.T.)	Nest XI
Nov. 14th 2000 hrs. 2300 hrs.	Pair with two eggs. The female, which had just returned from sea to start second fast killed. Male marked, weight 3.9 kgm., returned to nest to continue first fast. Male incubating alone.
Nov. 23rd 2300 hrs.	Still alone on two eggs.
Nov. 30th 2300 hrs.	Nest empty and deserted, male not found.
Dec. 19th 0400 hrs.	Male back at rebuilt nest with a second partner. Not disturbed.
Dec. 23rd 0300 hrs.	His partner, a female, killed. Ruptured follicles in ovary and large incubation area evidence she had bred this season.
Dec. 26th 0230 hrs.	His third partner, a female, killed. Dissection showed she had probably bred this season.
Dec. 27th	Male with fourth partner. Not disturbed.
Dec. 31st 0300 hrs.	Still with partner at nest. Not disturbed but not seen again.

TABLE VIII. To demonstrate the readiness with which marked male Adélies (probably established breeders) acquired new partners if the females were removed.

Date, 1950, and Time (G.M.T.)	Nest 33	Nest 34	Nest 35
Oct. 30th 1400 hrs.	Male killed. Female marked, weight 3.9 kgm., returned immediately to nest but had run away by time Nests 34 and 35 had been marked.	Male killed. Female marked, weight 3.9 kgm., returned immediately making loud mutual display over nest, but ran away later.	Male killed. Female marked, weight 4.4 kgm. Though very aggressive, she did not run back to nest, but stood on periphery of colony.
2200 hrs.	Alone at nest; seen in "bill to axilla" display (see p. 33). Lost all stones from nest.	Had a second partner at her nest.	Alone at nest.
Oct. 31st 1630 hrs.	Still alone, at very poor nest.	Still with partner.	Still alone, at moderate nest.
Nov. 1st 2130 hrs.	On periphery of colony, very dirty. Probably been fighting as her nest occupied by an unmarked bird which made no attempt to collect stones.	Still with partner.	Still alone, at moderate nest.
Nov. 2nd 1500 hrs.	Back in her site with another bird standing by. When disturbed she ran off and was chased by this other bird all through the colony. No mutual display seen when together at nest.	Still with partner. No eggs.	Still alone. No eggs.
Nov. 4th 1730 hrs.	With a partner, which was killed—a male.	Still with partner, which was killed—a male.	Still alone but on two eggs, one quite freshly laid.
Nov. 6th 0030 hrs.	Alone, but ran away. Only a scoop now; no stones.	Nest 34 unoccupied.	Still alone on two eggs.
1630 hrs.	Still alone with one egg, but ran away leaving neighbours to steal stones from an already very poor nest. A Sheathbill took the egg.	Now with a third partner in nearby nest. This male not killed so breeding routine allowed to continue. Nest 34 occupied by a single unmarked bird.	Still alone on two eggs.
Nov. 9th 2200 hrs.	Could not find her. Nest 33 occupied by unmarked bird.	Standing by her mate who was on one egg.	Still alone on two eggs.
Nov. 11th 1530 hrs.	Not found	Gone to sea to break her fast, leaving male alone incubating the egg.	Still alone on two eggs, but ran away after being weighed (3.3 kgm.).
Nov. 13th 2200 hrs.	Not found	Away. Male on nest.	Nest 35 empty and deserted. Could not find her, nor was she seen again in the colony (see p. 54).
Nov. 17th 1900 hrs.	Not found.	Away. Male on nest.	
Nov. 23rd 1730 hrs.	Back from the sea, looking clean, standing by herself about two feet from Nest 33. Not disturbed. Half hour later seen wandering round colony lethargically.	Away. Male on nest.	
Dec. 4th 0300 hrs.	Not found.	Back from the sea and alone on one egg.	
Dec. 8th 0800 hrs.	Not found.	Alone on egg.	
Dec. 15th 0600 hrs.	A marked bird, probably this female, ran away from nest.	Standing by nest, her mate on the egg.	
1930 hrs.	Not found.	Alone on egg.	
Jan. 12th 1951	With an unmarked partner in a well built nest.	Not found nor seen again.	
Jan. 16th	She was still at large nest, probably with partner, but she was not seen again.		

TABLE IX. To demonstrate the readiness with which marked female Adélies (probably established breeders) get new partners if the male is removed.

Date 1921	Number seen	
	Complete	Incomplete or attempted
<i>A. Preliminaries to egg-laying</i>		
September 22nd-30th	4	5
October 2nd-8th	44	30
October 9th-15th	13	38
October 16th-22nd	15	28
October 23rd-30th	47	32
<i>B. Period of massed fishing expeditions</i>		
October 31st-November 6th	39	20
November 7th-13th	40	12
November 14th-29th	Numerous on most days	
November 29th	The first eggs were laid	
	Only four recorded during the period	

TABLE X. Summary of Bagshawe's (1938, Tables VII-IX) data on complete and incomplete acts of copulation seen in the Gentoo Penguin.

Copulations were seen in reduced numbers throughout the period of egg-laying, some being incomplete, but most of them complete.

Expedition and observer	Year	Arrival	1st Egg	1st Chick	Rookery and latitude South
Scotia (Brown)	1903	Oct. 7th (? before)	Oct. 29th	Dec. 6th (? Dec. 4th)	South Orkneys 61°
Scotia (Mossman)	1904	Oct. 8th	Nov. 2nd	Dec. 12th (? Dec. 7th)	South Orkneys 61°
F.I.D.S. (Sladen)	1950	Oct. 8th (? before)	Oct. 29th	Dec. 4th	South Orkneys 61°
F.I.D.S. (Tritton)	1953	Oct. 4th (before)	Oct. 27th	(? Dec. 1st)	South Orkneys 61°
F.I.D.S. (Marshall)	1945	Oct. 7th	Nov. 4th (? Oct. 31st)	Dec. 5th	Hope Bay 63°
F.I.D.S. (Andrew)	1946	Sept. 21st	Nov. 6th	Dec. 16th (? Dec. 11th)	Hope Bay 63°
F.I.D.S. (Roberts)	1947	Oct. 4th	Nov. 2nd	Dec. 8th	Hope Bay 63°
F.I.D.S. (Sladen)	1948	Sept. 30th (before)	Nov. 1st	Dec. 8th	Hope Bay 63°
F.I.D.S. (Coley)	1952	Sept. 20th	Nov. 4th	Dec. 10th	Hope Bay 63°
Swedish (Scottsberg)	1903	Oct. 12th	Nov. 1st?	(? Dec. 6th)	Paulet I. 64°
Français	1904	Oct. 15th	Nov. 3rd	(? Dec. 8th)	Wandel I.* 65°
Pourquoi Pas? (Charcot)	1909	Oct. 22nd	Nov. 9th	Mid-Dec. (? Dec. 14th)	Petermann I. 65°
French (Sapin-Jaloustre)	1950	?	? Nov. 10th (? Nov. 8th)	Dec. 13th	Port Martin 66°
Australian (Mawson)	1912	Oct. 12th	Nov. 3rd	(? Dec. 8th)	Cape Denison 68°
Australian (Mawson)	1913	Oct. 17th	Nov. 9th	Dec. 17th (? Dec. 14th)	Cape Denison 68°
Southern Cross (Bernacchi)	1899	Oct. 14th	Nov. 2nd	Dec. 9th (? Dec. 7th)	Cape Adare 71°
Terra Nova (Levick)	1911	Oct. 13th	Nov. 3rd (? Oct. 30th)	Dec. 4th	Cape Adare 71°
Nat. Ant. Exped. (Wilson)	1902	about Oct. 20th	Nov. 9th (before)	?	Cape Crozier 77°

TABLE XI. Dates on Adélies collected by various expeditions, arranged in order of latitude of expedition site.

Notes: The dates are given as recorded. All those in brackets are probable corrections, assuming that the average incubation period is thirty-six days (i.e. average for first eggs, see p. 51).

*Now named Booth Island.

1946		1947		1948		1952	
Ring No.	Nest-site	Ring No.* of birds recaptured	Nest-site	Ring No.† of birds recaptured and birds newly ringed	Nest-site	Ring No.‡ of birds recaptured	Nest-site
{ 1001 1002	1	{ 1002 with unmarked mate	1	Not found		Not looked for	
{ 1003 1004	2	{ 1003 1004	2	Not found		Not looked for	
{ 1005 1006	3	{ 1005 1006	3	1005 1006	3	Not found	
{ 1007 1008	4	Not found		60042 60043	4	Not looked for	
{ 1009 1010	5	{ 1009 with unmarked mate	5a	{ 1009 ? 60027	5a	1009 not found but 60027 seen (see Table XIII)	5
		{ 1010 with unmarked mate	5b	{ 1010 with unmarked (?) mate	5b	Not found	
{ 1011 1012	6	{ 1011 with unmarked mate	6a	{ 1011 60028	6a	{ 1011 60028	6a
		{ 1012 with unmarked mate	6b	{ 1012 with unmarked (?) mate	6b	Not found	
{ 1013 1014	7	{ 1013 1014	7	{ 1013 1014	7	Not looked for	
{ 1015 1016	8	{ 1015 1016	8	{ 1015 1016	8	Not looked for	
{ 1017 1018	9	{ 1017 1018	9	{ 1017 1018	9	Not looked for	
{ 1019 1020	10	{ 1019 1020	10	{ 1019 1020	10	{ 1019 with unmarked mate (see Table XIII)	? 10

TABLE XII. The faithfulness of Adélies to nest-sites and mates, Hope Bay, 1946-52.

Notes: *Careful search of all birds made in neighbourhood of nests during October and November (Roberts, MS).

†Birds found during daily observations, November and December (Sladen, MS).

‡Birds found during occasional visits (Hunt & Coley, MS).

For more detailed analysis of 1952 results see Table XIII.

Ring No.	Sex*	Date when first ringed	Date when recaptured 1952	If found in same nest-site	Notes
{ 1011 60028	F M	Nov. 1946 Oct. 1948	Oct. 28th	Yes	In same nest-site (6a, see Table XII) and the same pair as found in Oct. 1948.
1019	F	Nov. 1946	Nov. 4th	Probably	With unmarked partner. This female was at least eight years old. Data for 1952 too incomplete to pinpoint nest-site exactly, but certainly within a few feet of original 1946 site.
1040	---	Jan. 1948	Oct. 28th	---	One of the eighteen nestlings originally ringed by Roberts (MS) and now recaptured breeding in the same colony where originally ringed at age of four years. There were two eggs in its nest, and when last seen on Jan. 4th, 1953, it was by one chick.
60015	M	Oct. 1948	Oct. 28th	Yes	
60017	---	Oct. 1948	Oct. 28th	Probably	Data for 1948 incomplete. It might have been in original site, but certainly within a few feet of it.
60018	---	Oct. 1948	Oct. 28th	Yes	
{ 60021 60024	M F	Oct. 1948 Oct. 1948	Nov. 4th Nov. 9th	Yes Yes	In same nest-site and same pair as when originally ringed in Oct. 1948.
{ 60025 60027	-- ---	Oct. 1948	Oct. 28th	Probably Yes	This pair was probably together in Oct. 1948 but original data destroyed in base fire.
60034	M	Oct. 1948	Oct. 28th	Yes	
60036	M	Oct. 1948	Oct. 28th	Yes	
60037	F	Nov. 1948	Oct. 28th	No, but nearby	Site disturbed by building of new Argentine base nearby.

TABLE XIII. Adélies ringed in previous years at marked nest-sites, at Hope Bay, and recaptured, 1952-3 season.

Notes: *Sex was determined by incubation routine and other ways (p. 23) during the 1948-9 season.

This table has been compiled with the aid of photographs, original notes and personal communication with B. Hunt and A. Coley and their F.I.D.S. Base Report (Hunt & Coley, MS).
For previous years' results see Table XII.

For data received since going to press see Sladen, W. J. L. & W. L. N. Tickell, 1958. Antarctic bird-banding by the Falkland Islands Dependencies Survey, 1945-57. *Bird-Banding*, 29: 1-26.

Nest	First Egg			Second Egg			Third Egg		
	Date and Time	Weight (oz.)	Dimensions (mms.)	Date and Time	Weight (oz.)	Dimensions (mms.)	Date and Time	Weight (oz.)	Dimensions (mms.)
A	14th 2300	—	65 × 57	18th 2000	4	65 × 55	No 3rd egg laid		
B	13th 2300	—	69 × 56	17th 1930	4½	69 × 55	20th 1630	3rd egg laid but not collected as female had already departed to sea. Not measured.	
C	?	—	69 × 57	13th 2300	—	69 × 57	No 3rd egg laid		
D	13th 2300	—	71 × 53	No 2nd egg laid					
E	13th 2300	—	69 × 53	17th 1930	4	69 × 59	No 3rd egg laid		
F	15th 2000	4½	70 × 55	No 2nd egg laid					
G	11th 2300	—	64 × 54	15th 2000	3½	62 × 52	18th 2000	3	60 × 50

TABLE XIV. Weights and Dimensions of Eggs at Hope Bay, November 1948. This was also an experiment to see if third eggs were laid when others were removed.

Notes: Average interval (to nearest day) between first and second eggs—four days.

Average interval (to nearest day) between second and third eggs—three days.

The nests were marked and some of the birds also marked. The nests were chosen well away from the areas where more intensive work was going on and they were visited daily. The eggs were removed from the nests and also from surrounding nests as soon as observed. Weights are to the nearest ½ oz. Dimensions are length and maximum width to nearest mm. Time in G.M.T.

Nest No	First Egg			Second Egg			Third Egg		
	Date and Time	Weight (gms.)	Dimensions (mms.)	Date and Time	Weight (gms.)	Dimensions (mms.)	Date and Time	Weight (gms.)	Dimensions (mms.)
38	8th 1600	118	69 × 55	12th	No measurements		No 3rd egg laid		
43	10th 2030	98	66 × 52	13th 2200	90	57 × 49	No 3rd egg laid		
45	8th 0030	130	71 × 52	10th 2030	124	71 × 56	13th 2330	102	68 × 51
47	8th 0030	119	68 × 56	No 2nd egg laid					
48	8th 1730	No measurements		11th 1600	107	68 × 53	No 3rd egg laid		
49	8th 1730	112	68 × 54	11th 1600	111	69 × 54	No 3rd egg laid		
50	8th 1730	No measurements		11th 1600	112	69 × 53	No 3rd egg laid		
52	4th 1500	—	70 × 54	6th 1730	111	73 × 53	No 3rd egg laid		
54	9th 2130	107	66 × 54	12th	No measurements		No 3rd egg laid		

TABLE XV. Weights and Dimensions of Eggs at Signay Island, November, 1952. This was also an experiment to see if third eggs were laid when others were removed.

Notes: Average interval (to nearest day) between first and second eggs—three days.

Interval between second and third eggs in Nest 45—three days.

All nests and birds were marked. Eggs were removed as soon as observed. Nests 43, 45, 47 and 52 were in Colony IX (see Figure 11) where eggs from all nests were collected within twenty-four hours of laying. Nests 48, 49 and 50 were in Colony X where in all other nests the first eggs were left and the second eggs removed. Nests 38 and 54 were in Colony Y (see Figure 9).

The eggs were brought back to the laboratory for weighing (to the nearest gram) and measurement (length and maximum width to nearest mm.). Time in G.M.T.

A. Signy, 1950

Nest No.	First Fast			Second Fast		Notes
	Before female left	After female left	Total days	Female	Male	
53	I	*17	I	20 ¹⁸	—	*Male deserted before female returned.
65	17 ¹⁸	19	36	17 ¹⁸	13	2
67	25 ¹⁸	16	41	I	13	I
1	25 ¹⁷	16	41	22 ^{10/21}	14	5
4	22 ^{18/21}	16	38	23 ¹⁷	12	6
5	25 ¹⁷	13	38	17 ^{15/27}	16	I
6	*27 ¹⁸	13	*40	19 ^{16/27}	13	6
17	220 ^{21/27}	213	33	220 ²¹	15	6
29	18 ^{20/27}	16	34	21 ¹⁷	14	12
11	22 ^{18/21}	18	40	23 ¹⁷	I	I
40	26 ¹⁷	16	42	15 ^{28/29}	I	I
41	13 ^{26/29}	15	28	22 ¹⁷	I	I
42	28 ¹⁷	*15	*41	16 ^{28/29}	—	—
62151	21 ^{18/21}	13	34	22 ¹⁷	I	I
50	I	12	I	I	16	8
	25	15	40	21	14	6
						Signy averages from reliable data.

TABLE XVI—continued opposite.

B. Hope Bay, 1948

Nest No.	First Fast			Second Fast		Notes
	Male		Total days	Female	Male	
	Before female left	After female left		Female	Male	
12	†	<i>12</i>	†	†	<i>15</i>	9
13	†	<i>12</i>	†	†	<i>13</i>	10
19	†	<i>12</i>	†	†	<i>16</i>	7
22	†	1	†	†	<i>15</i>	7
24	†	1	†	†	<i>14</i>	9
9	†	<i>11</i>	†	†	*17	*Female deserted before male returned.
10	†	<i>17</i>	†	†	<i>14</i>	6
		<i>13</i>			<i>15</i>	8 Hope Bay averages from reliable data.

TABLE XVI. Fasting periods of marked Adélies.

Notes: Data are summarised for the fasting periods collected from some of the more important marked pairs at Signy Island and Hope Bay.

1—Incomplete data.

†—Notes for October 1948 destroyed in the fire at Hope Bay.

All numbers represent days and are estimated to the nearest day. If there was a gap of two days in the observation, the middle day was taken. Index figures indicate the date (October) when the bird concerned was first marked. If two figures are given, e.g. 22^{18/21}, it means that an unmarked bird was recorded in nest on October 18th. but not marked until 21st.

Complete data are in italics, and only these numbers have been used for the averages. Figure 15 represents these averages diagrammatically.

Age		Stages in development	Voice	Plumage	Weight in ounces (from mean growth curve, Figure 18)
1st week	GUARD STAGE	Completely under parent, or head under lower abdomen of crouching parent and hind region sticking out.	Typical chick "peeping"	1st down soon being replaced by 2nd down	3½- 13
2nd week					14- 31
3rd week		Stands up in nest and takes notice of surroundings.	First tremulous "peeping" heard at nest-relief ceremony when parents in loud mutual display.	2nd down.	32- 59
4th week		Ventures a foot or more away from parent (if colony not too crowded). [First signs of crèche formation at Signy, 1950.]	Tremulous "peeping" well developed. First <i>skwawk</i> of threat heard.		60- 87
5th week	CRECHE STAGE	First signs of crèche formation.		1st signs of moult of 2nd down.	88-104
6th week		Feeding chases (p. 46) start.	Tremulous "peeping" develops into immature loud mutual display sound.	Chin, lower abdomen and thighs free of down and showing white.	105-125
7th week		Feeding chases well developed.		More advanced chicks almost free of down.	126-130
8th week	DISPERSAL & DEPARTURE	Dispersal of crèches starts, chicks tending to lie in or near old nest-sites but bunching together when frightened. The most advanced young seen along coast.	<i>Aark</i> call notes now heard.	Most chicks free of down now.	130 but very variable.
9th week		Groups of young collecting away from colonies and along coast. Most chicks depart to sea	Constant <i>aarks</i> heard everywhere.	A few late chicks may still be seen in down.	Variable.

TABLE XVII. Stages in the development of Adélie chicks.

Parents with their own chick(s)	at their nest-site	...	38	} 69 observations
	more than 3 ft. away from nest-site	...	11	
Parents feeding own chick(s)	at their nest-site	...	19	
	more than 3 ft. away from nest-site	...	1	
Parent with strange chick at its nest-site	1	} 2 observations
Parent feeding a strange chick near its nest-site	1	

TABLE XVIII. Evidence that parents normally recognise and feed their own chicks when at the crèche stage. The data have analysed from the nest histories of marked adults and chicks after their respective chicks had reached the crèche stage.

Number of nests counted				Percentage mortality
Empty	With 1 chick	With 2 chicks	Total nests	
10	9	5	24	†60
59	26	22	107	*67
3	5	0	8	*69
8	2	2	12	*75
70	12	16	98	*78
71	12	15	98	*78
13	6	1	20	80
78	19	12	109	80
265	72	35	372	81
8	5	0	13	81
130	24	17	171	83
188	48	18	254	83
10	2	1	13	*85
372	64	20	456	89
10	0	0	10	§100
26	0	0	26	‡100
1321	306	164	1791 Totals	82 % Average

TABLE XIX. Mortality of eggs and young chicks at Hope Bay, 1948-9

Notes: These accurate counts of empty nests and nests with chicks were made at sixteen different small colonies or sections of colonies late in the re-occupation period (January 5th to 11th) just before crèche formation. Assuming that every nest started off with two eggs, these figures therefore give the mortality of eggs and young chicks up to the crèche stage.

*Indicates the colonies which were situated in a sufficiently exposed situation for the wind to keep them relatively free from snow accumulation.

†Colony IV was one of the most exposed colonies in the Hope Bay rookery and swept free by the frequent gales, whereas

‡Colony III, a few yards away but not so exposed, was buried under snow during most of the 1948-9 season (see p. 69 and Plates XII d-f).

§Was a colony in another sheltered position.

A. Temperatures (degrees Fahrenheit)			Average 17.2
Time (G.M.T.)	No. of observations	Average temperature	Range
1200	15	16.7	10.0-25.0
1800	15	18.1	13.0-26.5
2300	12	17.0	12.0-25.0

B. Winds. Observations three times daily								
Wind direction	N.E.	E.	S.E.	S.	S.W.	W.	Calm	Total
No. observations	3	1	15	1	21	1	6	48
Of the twenty-one observations of S.W. wind, on eight occasions a gale was blowing.								

C. General Conditions. Observations three times daily						
	Drifting or snowing			Not Drifting or Snowing		
	Overcast	Sunny intervals or Fine*	Total	Overcast	Fine and Sunny*	Total
No. observations	27	12	39	7	2	9

TABLE XX. Summary of weather conditions at Hope Bay at time of egg-laying and early incubation, November 9th to 24th, 1948.

Notes: *At Hope Bay with its strong winds and surrounding glaciers and snowslopes it was possible to get thick drift though the sky above might be cloudless. On two occasions only was it fine and sunny without drift. The most important weather factor causing mortality was burying of the nests under snow (p. 69).

B. NOTES ON SKINNING AND PRESERVING IN SALT

Practical experience in skinning and preserving medium sized birds before leaving the country, and reference to booklets such as British Museum Instructions to Collectors* (1938) and Blake (1949), are of help in establishing a routine procedure.

Most Antarctic birds, but particularly the penguins, have large deposits of blubber beneath and between the feather quills. Unless this is thoroughly removed by experts the skins may in later years become friable and disintegrate. Skins were therefore salted in the Antarctic and on arrival in London were treated professionally. Salted skins may keep quite well up to three years or more, but the sooner they are finally treated, the better.

The procedure recommended below has resulted from experience gained on twenty-five salted Pygoscelid Penguin skins collected by the writer in the South Orkney Islands, and later treated by Mr. J. D. Macdonald and Mr. G. S. Cowles at the British Museum (Natural History), London.

i. Kill birds with chloroform, or destroy their brains with a thick needle. The awl (Figure 7) may rupture the occipital artery and should not be used when the skin is to be preserved.

ii. A lump of firmly compressed snow can be used instead of cold water for removing fresh blood stains. If the blood freezes, brush it off immediately before taking the specimen indoors for skinning.

* A revised edition is in course of preparation.

iii. A lateral incision is preferable to a midline abdominal incision, though some collectors make theirs along the back in the midline.

iv. While skinning, blubber and blood are absorbed with a liberal supply of fine sawdust or "dead" plaster of paris powder.

v. Special care should be taken with the head region. When inside out, continue dissecting the skin right over the skull to the base of the bill; remove the brain thoroughly and dry the cavity with a little alum (use alum sparingly); check that the eyes and tongue are removed, and also the nasal glands that lie in deep grooves in the skull.

vi. Flippers and legs should be skinned as far as possible along the humerus and down as far as the tarsus, and all flesh removed.

vii. Remove the blubber as thoroughly as possible with a scraping spoon (Figure 8). This is made by sawing serrations on one side of a spoon with a hack-saw. Blubber is easier to remove when frozen and semi-solid than when warm and greasy, so the skins are best left in the cold before scraping.

viii. Rub salt well into all parts of the skin, particularly round the base of the tail. Leave in a tray of damp salt for one or two days, after which more salt should be rubbed into it.

ix. Return the skin to its normal position with feathers outside. Pack the cavity loosely with tow and salt, and stitch together roughly.

x. Wrap the feet in cotton wool, or tow, to prevent them coming into direct contact with the plumage of other specimens.

xi. Attach brass labels with reference numbers to the skins with cord. Send the standard museum labels with full details concerning the specimen separately as they disintegrate in the salt.

xii. Pack the specimens in a clean wooden barrel in damp salt so that they do not come in contact with each other or with the barrel. Blubber does not stain the plumage permanently if the salt remains damp. Most of the deterioration to salted skins is caused by contact with metal corroded by salt, so if metal is unavoidably present, the skins should be kept well away from it.

C. SUPPLEMENTARY NOTES ON PHOTOGRAPHY

1. Notes on Motion Picture Technique

The *Ciné-Kodak* special camera had certain advantages. It carried a reloadable 100 ft. magazine for film and had a reflex viewfinder. The clockwork gave a long run of film, rang a bell when in need of rewinding, and cut out quickly when exhausted.

A heavy tripod was used for this bulky camera, and especially for telephoto shots and in the prevailing windy weather.

Kodachrome film was used throughout. To avoid any slight variations in colour quality between different emulsion numbers, all the film was obtained at the same time. It was packed for transit through the tropics.

Most of the film was exposed at the speed of 24 frames per second, the normal speed for sound projection.

An exposure meter was always used, but experience was required to obtain correct light values when filming scenes with snow. All film was purposely slightly underexposed as the original was ultimately to be duplicated.

Special care was taken to keep lenses and camera gate clean.

To avoid condensation of moisture on lens and film, the camera was kept at a constantly low temperature and never suddenly introduced to a warm room or tent.

Slow running due to low temperatures can be avoided by lubricating with 'non-freezing' oil, or graphite, but precautions of this nature should be taken before leaving Britain and professional advice sought.

Each 100 foot spool was given a number which referred to detailed notes made in the field. These were later collated with the processed film.

When a *long delay before processing* is unavoidable, high humidity can do more damage to exposed film than anything else. Spools were therefore returned to their containers with a suitable desiccant, and sealed thoroughly with cellotape. Two simple desiccants used were brown paper heated in an oven until nearly charred or rice grains dried in an oven. Refrigeration was no problem in the Antarctic. For the journey back to Britain through the tropics, the films, with packets of silica gel desiccant, were placed in large metal tins, sealed with solder and stored in the ship's refrigerator.

All the film was sent to Kodaks in one package, thus avoiding possible variations in colour quality as a result of differences in processing.

After processing, valueless material was removed and the 100 foot lengths spliced together in sequence on 800 ft. reels. The spool reference numbers, and also individual shot numbers, were scratched in the black margin between the perforations.

This original (sometimes called the "master") was protected from scratches and possible damage in handling by the poliwx* treatment and then duplicated. Projection, analysis of movements and behaviour in correlation with field-notes, and editorial work was carried out on this duplicate, and eventually the Kodachrome original cut to match it. Further duplicates could then be made of the edited original.

As the original could not be projected, for fear of damage to the emulsion, an *animated viewer* proved indispensable for analysis and editing.

2. Limitations of the ciné-camera in the Antarctic

- i. Some training and experience in ciné-photography and maintenance of the camera are required.
- ii. The photographer must be familiar with the normal behaviour of the birds and refrain from filming abnormal behaviour resulting from camera noise and close proximity. In this respect individual birds vary considerably, but a telephoto lens will overcome most of these difficulties in the Pygoscelid Penguins.
- iii. Time taken to rewind the clockwork and reload film may break the continuity of long shots on behaviour.
- iv. The clockwork may run slowly in very cold weather, and only the simplest mechanical faults in the camera can be rectified in such isolated places.
- v. Film, especially colour, may deteriorate as a result of delay in processing.
- vi. The ciné-camera cannot take the place of direct observation, it is essentially complementary to it.

3. Still Photography

Equipment. A number of cameras ranging from 35 mm. to half-plate size was used but the best all-purpose camera proved to be a 35 mm. camera with a coupled range-finder. It was easy to carry and was taken everywhere in all weathers, in bad weather it being carried in the rucksack in a drift-proof and water-proof bag. In addition to this, two other cameras were often used for special subjects: a second 35 mm. camera for colour film, and a reflex $2\frac{1}{4} \times 2\frac{1}{4}$ inch camera for monochrome film.

For the professional photographer who visits the Antarctic, the large plate-camera is undoubtedly the most suitable. One recalls the beautiful work by Ponting of Scott's last expedition.

To avoid condensation, cameras were kept at a constantly low temperature and never suddenly introduced to a warm room or tent. Shutters were lubricated with a "non-freezing" oil or graphite before leaving Britain.

Technique for Photographing Penguin Populations. All routine photographs were taken from fixed points situated at a distance at which the birds would behave naturally. The photographer's position was marked by paint, and close by a painted arrow indicated the direction his camera should face. Daily photographs were started at Hope Bay in October 1948, and were to be continued throughout the season. The film and camera were, however, lost when the base was burned down, and it was not until the sledgers returned with their camera and a little film towards the end of the month that these could be resumed on a less ambitious scale. These methods were improved at Signy (see Plates III and IV). For permanence, small rock cairns were built to mark the photographic points and their positions were marked on the large scale map of the rookery (p. 22) so that they may be found easily by future workers. The direction in which the camera should face was still indicated by an arrow and the magnetic compass bearing was recorded in case the arrow was obliterated.

* Poliwx, 49 Praed Street, London, W.2.

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- †FILM 2. *Life History of the Adélie Penguin*. 16 mm., silent, colour, 30 minutes. Photographed and edited by W. J. L. Sladen from Film 1, above, and submitted as part of a D.Phil. thesis on the Pygoscelid Penguins at Oxford University, 1954.
- FILM 3. *Adélie Penguins of the Antarctic*. 16 mm., sound, colour, 20 minutes. Produced by the New York Zoological Society (1957). Distributed by McGraw-Hill Text-Films, New York. Photography and sound by W. J. L. Sladen (from Film 1, above) on behalf of the Falkland Islands Dependencies Survey. Narrated by Dr. R. C. Murphy.
- †FILM 4. *Le Manchot Adélie*. 16 mm., silent, black-and-white, 250 metres. Producers, Dr. J. Sapin-Jaloustre and J. Cendron for Expéditions Polaires Françaises, Paris. Filmed in Adélie Land, 1949-52.
- †FILM 5. *Le Manchot Empereur*. 16 mm., silent, black-and-white, 220 metres. Producer J. Prévost for Expéditions Polaires Françaises, Paris. Filmed in Adélie Land, 1952-3.

*Deposited at the British Film Institute, London.

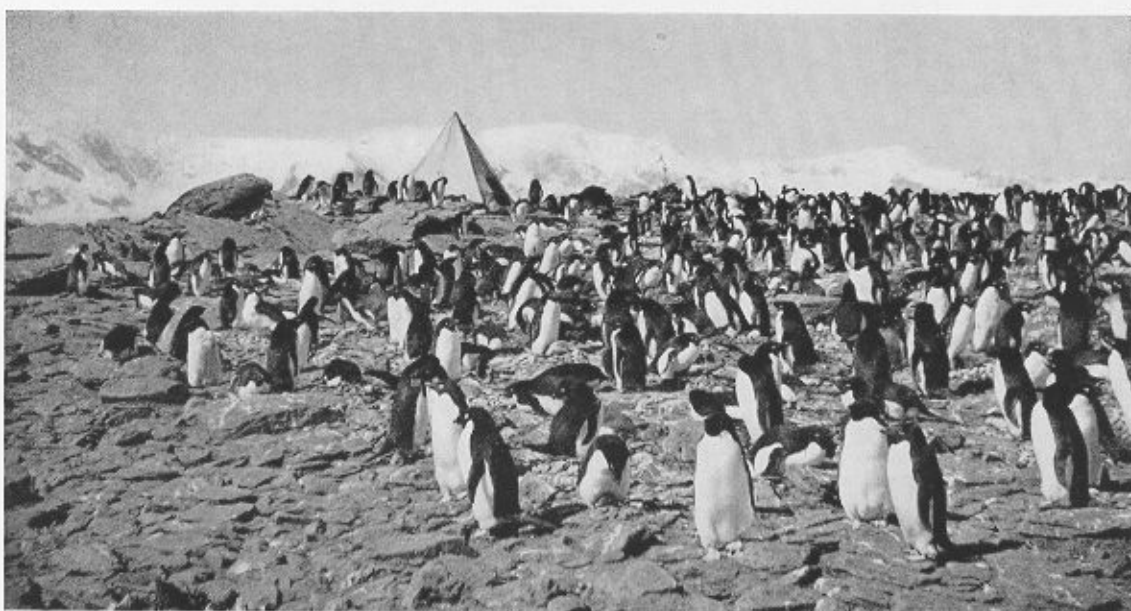
†Shown at the XIth International Ornithological Congress, Basel (see Sladen, 1955a).

PLATE I

- a. Observation tent, Hope Bay, 1948-9.
- b. Observation tent, Gourlay rookery, Signy Island, 1950-1.
- c. Sledging from Base over ice cap to the rookery, Signy Island.



a



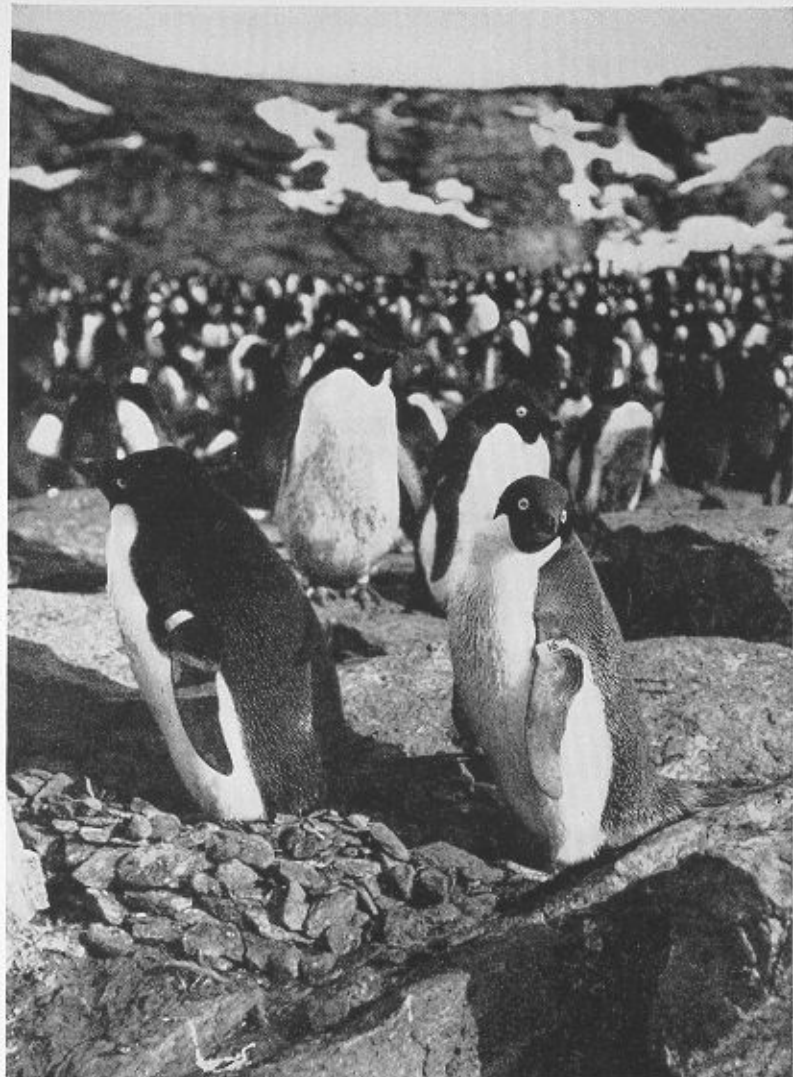
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PLATE II

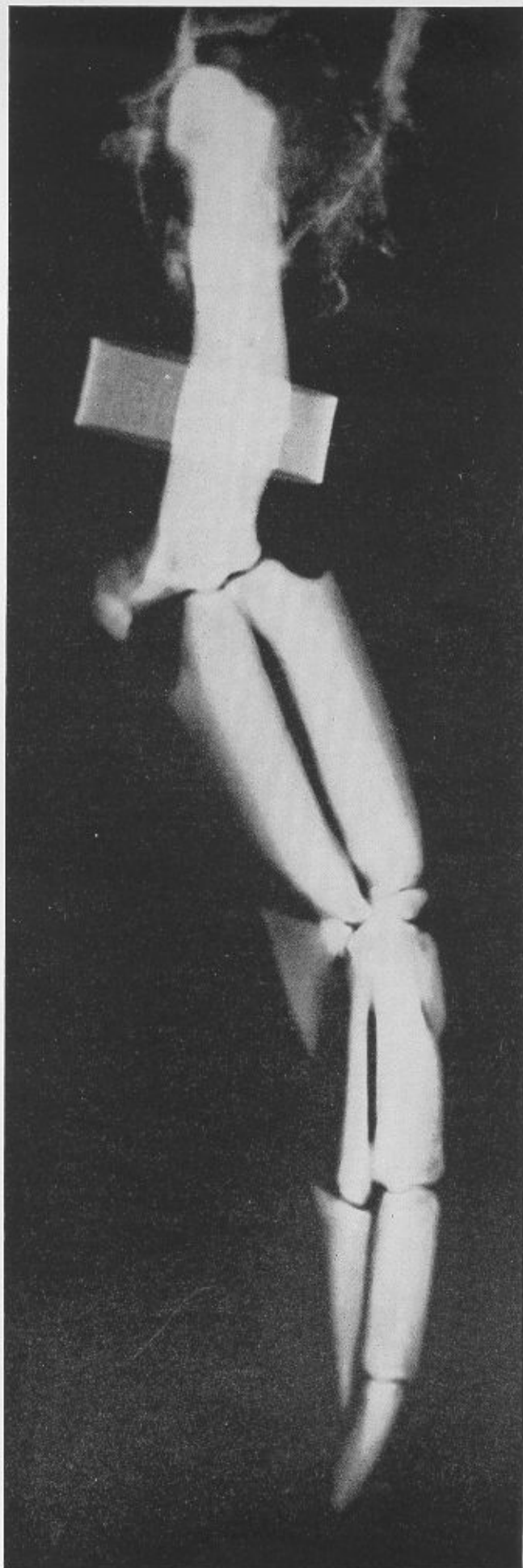
- a. A pair of Adélies at their nest before egg-laying. The male has 17 painted on his left flipper and a semi-permanent aluminium flipper-ring. The female has a temporary, painted aluminium overlap flipper-ring with 16 painted on it (see pp. 13-18).
- b. Chinstrap Penguin with semi-permanent aluminium flipper-ring, crouching over two chicks.
- c. X-ray of Gentoo Penguin flipper with semi-permanent flipper-ring (see p. 15).



a



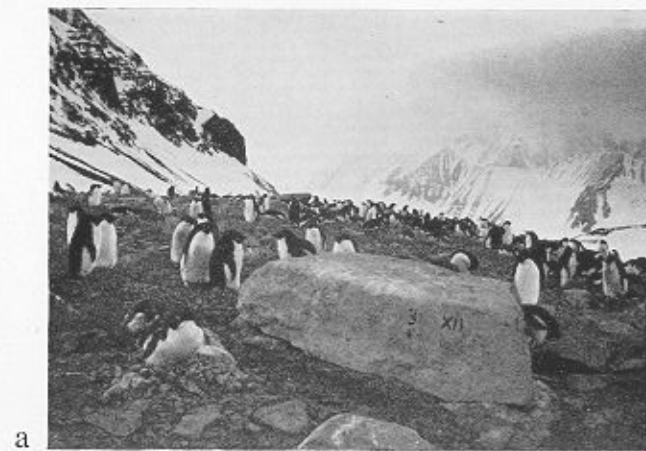
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PLATE III

- a. A method of marking nest-sites and colonies. Nest 3 in Colony XII at Hope Bay, 1948. The pair have lost their eggs and are away at sea (p. 57).
- b. The mark on a vertical rock-face of Colony VI, photographed four years after it was painted (p. 20).
- c-i. Colony VIII, Signy Island, seen throughout the breeding season from a fixed photographic point. This is a mixed colony of Adélies and Chinstraps.
 - c. October 17th, about ten days after the arrival of the first Adélies at the rookery. The more central nest-sites are occupied first while the colony is still snowbound.
 - d. October 22nd, some snow still over nest-sites.
 - e. November 2nd, four days after the first eggs have been laid. Population at its maximum.
 - f. November 23rd, the Adélies are incubating, the Chinstraps are back but have not yet laid eggs. The Chinstraps, mostly standing in pairs, occupy the more rocky portion of the colony, behind the Adélies.
 - g. December 13th, about a week after the first Adélie eggs have hatched. Most of the Chinstraps are now incubating eggs. All snow has gone from the colony and surrounding terrain.
 - h. February 18th, the Adélie colony is deserted, all the chicks having left for the sea. The Chinstrap chicks are at the crèche stage.
 - i. March 20th, the Chinstrap chicks have left for the sea, but most of the adults have returned to moult in their own nest-sites. (The adult Adélies did not moult at the rookery at Signy.)



a



b



c



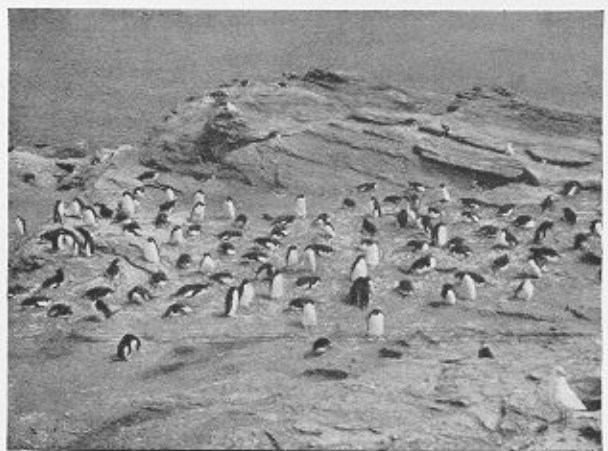
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i

PLATE IV

a-j. Colony V, Signy Island, seen throughout the breeding season from a fixed photographic point (P4—see Map IV). Colony V is about forty feet away from three larger colonies, though the one on the right is almost continuous with it. Colony XI is in the middle distance. In 1950-1, Colony V had a maximum population of fifty-eight Adélies (see Figure 9).

- a. October 17th, about ten days after the first Adélies had arrived at the rookery. Nine birds counted.
- b. October 22nd, nest-sites mostly clear of snow; twenty-five birds counted.
- c. October 30th, five days before the first egg-laying in this colony; fifty-two birds counted.
- d. November 2nd, two days before the first egg-laying in this colony. The nest-sites are free from snow. Maximum population of fifty-eight birds counted.
- e. November 8th, fifty-two birds counted. The females are beginning to depart to sea to break their fasts.
- f. December 13th, nearly a week after the first chicks hatched. The re-occupation period has started.
- g. December 27th, forty-four birds counted, the maximum number seen in this colony during the re-occupation period (Figure 9).
- h. January 16th, the chicks are in a crèche; only one adult counted.
- i. January 25th. The colony is abandoned, all the chicks having joined others in the crèche of one of the adjoining colonies.
- j. February 6th. Colony V still abandoned. The chicks have shifted to another position. They are now nearly free of down and almost ready to depart to sea.



a



b



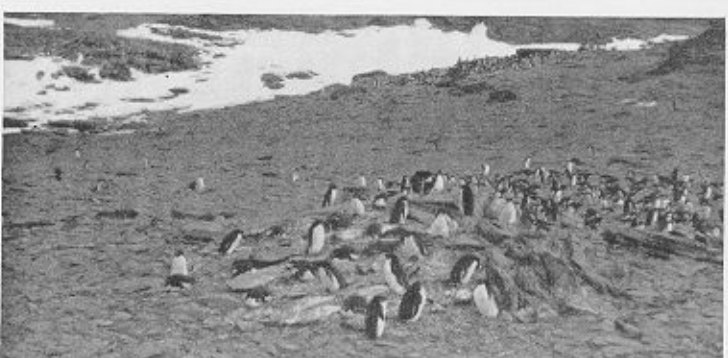
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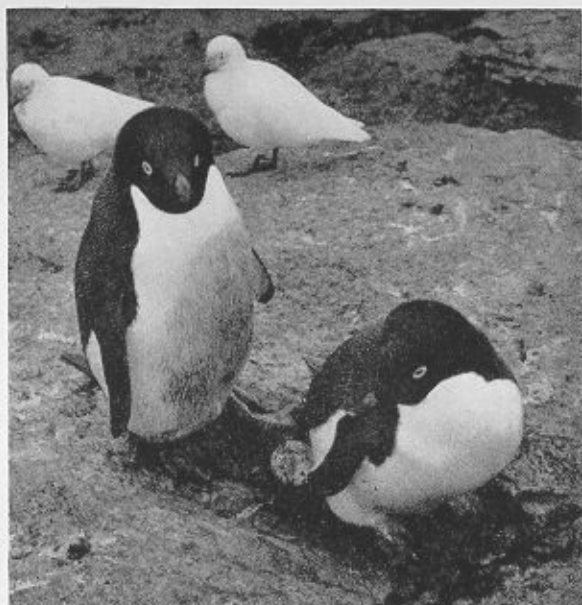
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PLATE V

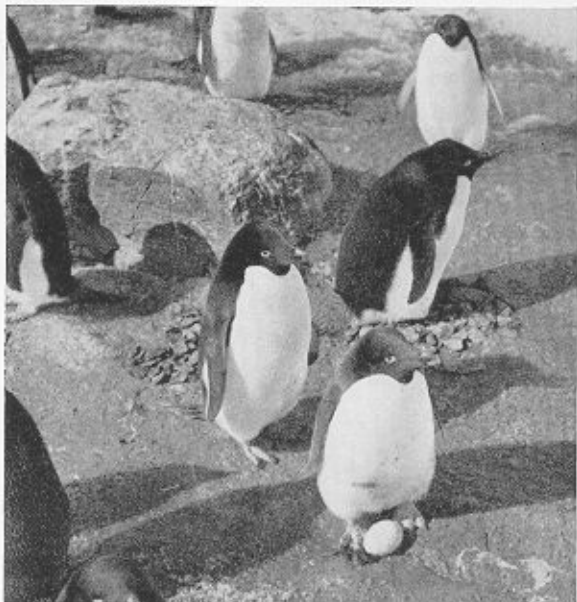
- a-d. Two pairs of unestablished ("inexperienced") breeders, each with one egg. Note that the nest-sites are on the edges of the colonies and contain only a few stones, and that there are Sheathbills in the background waiting to steal the eggs.
- a-b. The bird on the nest has scraped away the egg with the stones when settling on the nest.
- d. A Sheathbill about to peck through the egg, which has rolled away from the nest (p. 25).
- e. December 22nd, 1948, Hope Bay, during the re-occupation period. A party of non-breeding "wanderers" on the edge of a colony. It includes one Adélie in immature plumage (yearling) on the extreme right. Note that these yearlings have white eyelids like the adults.



a



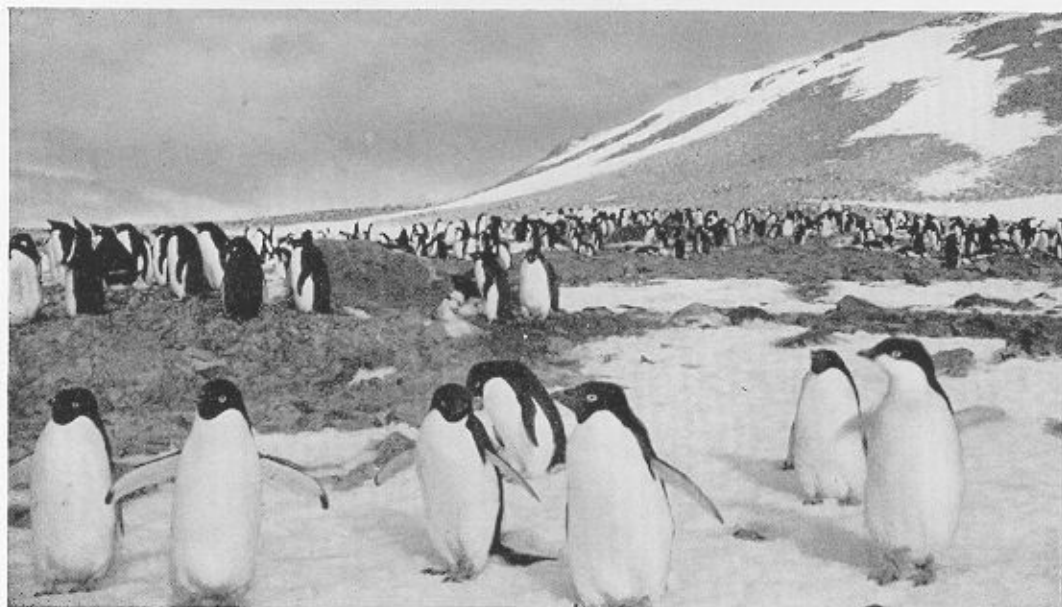
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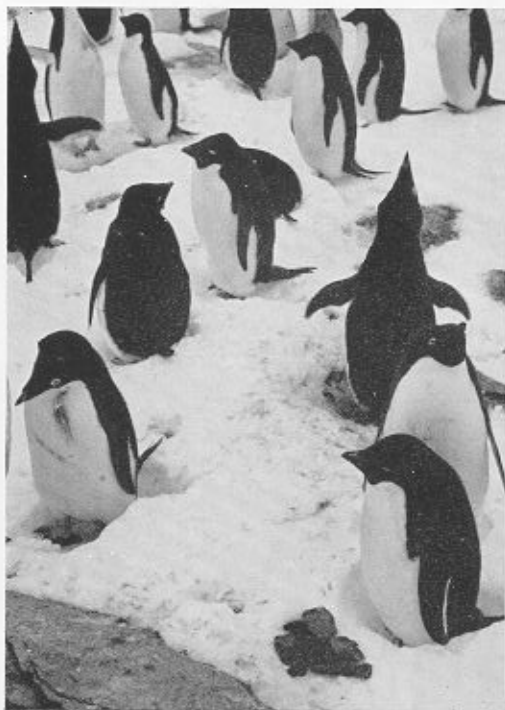
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e

PLATE VI

- a. Ecstatic display at the beginning of the season in a colony covered by snow. One bird (top left with bill out of picture) has a partner by his side. The other two in display are males alone at their nest-sites. There is a pile of newly collected stones (bottom right) in front of a bird in its nest-scoop.
- b. Ecstatic display during the re-occupation period. The two birds at empty nests are unsuccessful breeders, or non-breeders. A third on the left is over one chick. On the extreme right another bird is starting the "bill to axilla" display.
- c. The quiet mutual display. A pair early in the occupation period at a nest-site covered by at least one foot of snow. (The ice-axe provides a size-scale.) This picture was taken in the subsidiary colony shown in Plate XI a and b.
- d. Parent showing one of the postures of threat (p. 37) and crouching over two young chicks.
- e. A fight.
- f. A yawn.



a



b



c



d



e



f

PLATE VII

- a. Walking.
- b. About to enter the sea.
- c. Walking and tobogganing.
- d. Porpoising.
- e-f. Landing from the sea.
 - e. These Adélies are probably jumping 7 feet (p. 46).
 - f. They usually jump higher than the icefoot. The freshly arrived birds pause for intensive preening.



a



b



c



d



e



f

PLATE VIII

- a-l. The nest-relief ceremony of a marked pair at Nest 40. The female has just returned from the sea and is clean. No. 40 on her left flipper is upside-down and on the right she has an aluminium flipper-ring with the clip in the anterior position (see p. 15). The male has a temporary coloured celluloid flatband ring on his right flipper. He has now completed a forty-two-day fast (Table XVI and p. 52).
- a. The greeting; bills are wide open in loud mutual display.
 - b. Bowing (p. 33).
 - c. The quiet mutual display. One dirty egg shows, resting on the feet.
 - d. Bowing again.
 - e. Male moves off the eggs.
 - f. Female takes over immediately and crouches over the eggs, while they both repeat the loud mutual display.
 - g. Female pushes the eggs under her.
 - h. Completes the act.
 - i. Repeat of the quiet mutual display.
 - j. The male has brought a stone for the nest and, after dropping it, stretches into the quiet mutual display with his mate.
 - k. The female has now changed position and lies down, incubating. The male stands by between bouts of collecting stones to build up the nest.
 - l. The male is off to sea to break his fast.

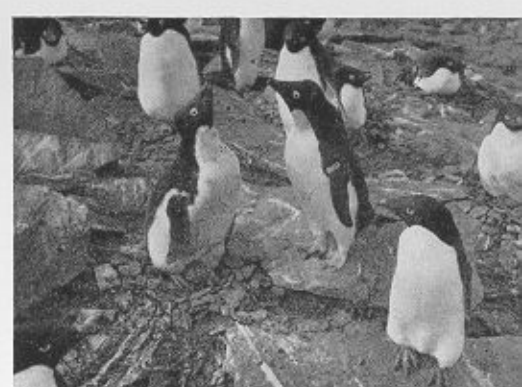
Note: The bird on the right and in front of Nest 40 in c-g is typical of the non-breeding "wanderer", or unestablished bird, seeking territory (p. 26). The raising of its forehead crest and smoothing of the occipital crest is a posture suggesting nervousness (p. 39). It ran off as soon as the male went into a posture of threat.



a



b



c



d



e



f



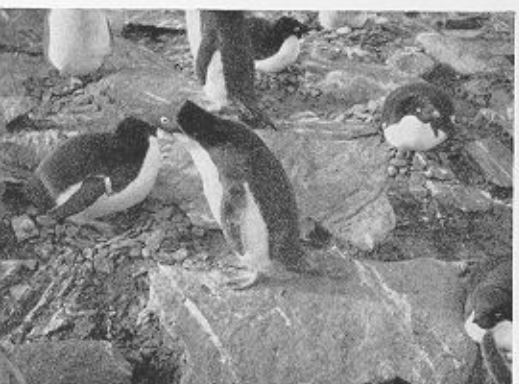
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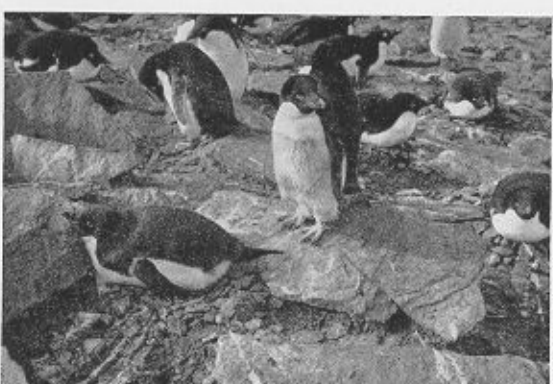
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i



j



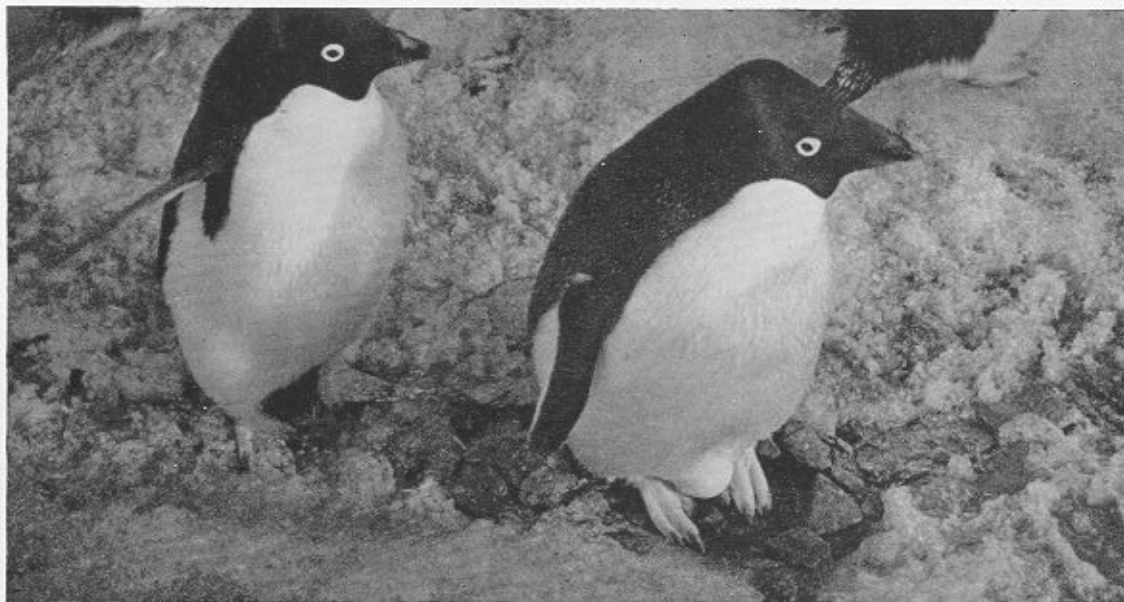
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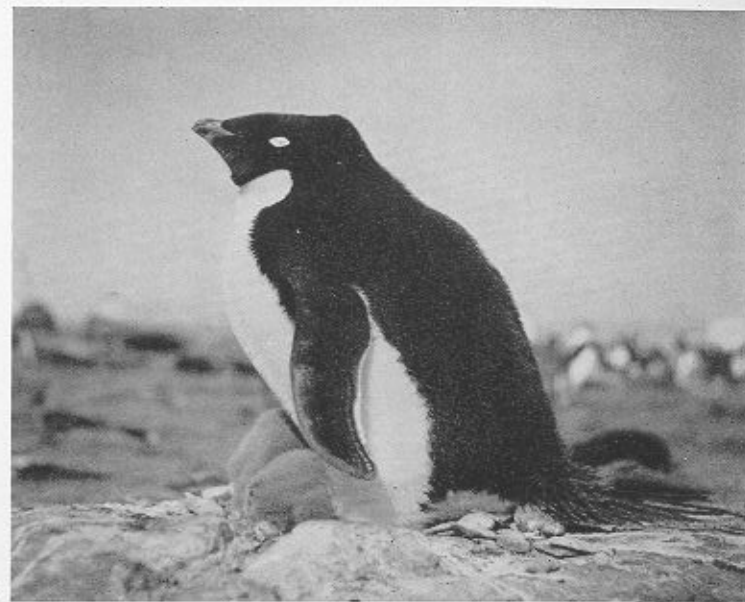
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PLATE IX

- a. The crouching posture over a newly laid egg (p. 46).
- b. The same posture over two small chicks. Note the density of the semi-erected feathers which contribute to protection when the bird is dashed against rocks in rough seas (p. 46).
- c-e. A parent returns from sea to feed its chick.
 - c. The greeting (mutual display; compare with Plate VIc).
 - d. Food-begging.
 - e. Feeding; food is regurgitated from the parent's stomach (p. 46).



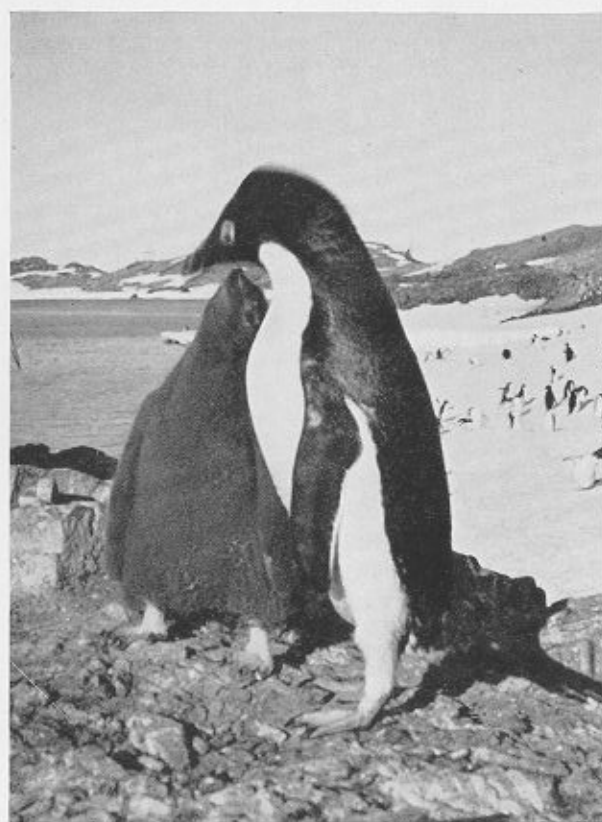
a



b



c



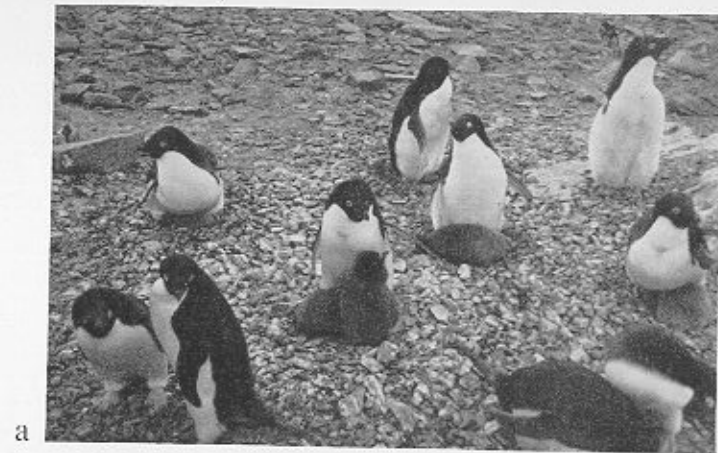
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PLATE X

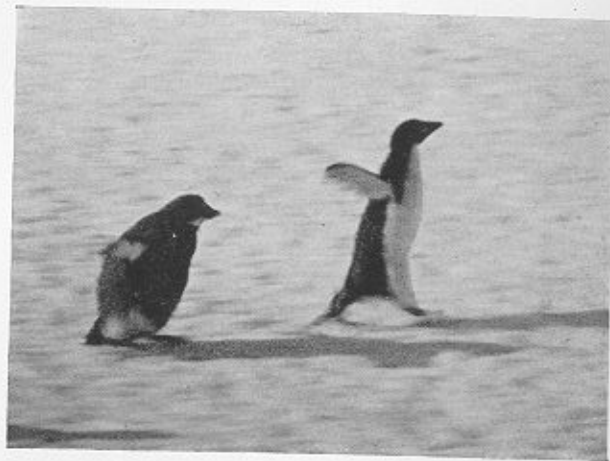
- a. Chick begins to stand up in the nest during its third week.
- b. Chick ventures a foot or more away from the nest during its fourth week.
- c. The feeding chase is well developed during the chick's seventh week.
- d. The crèche stage in Colony III at Signy; January 25th, in the morning.
The group on the right has about 150 chicks in it. There were only about five adult Adélies in the area when the photograph was taken, and these were probably parents feeding their chicks. A Skua (indicated by the arrow) is lying on the edge of the crèche. The adults on the far edge of the colony are Chinstrap Penguins which nest on the steeper slopes on the seaward side.
- e-g. The re-occupation period. There are no "guardians" to the crèches. Chicks will crowd near adult penguins of any kind. These adults are usually unsuccessful breeders re-occupying territory (e) after recuperation at sea, or non-breeding "wanderers" staking a claim on new territory. They usually build large nests. The adult in (f) having built a nest, guards this and not the chicks which stand around just out of pecking range.
- g. A small crèche of Adélie chicks gathered around adults of a different species, the Gentoo Penguin. How could these Gentoos possibly be "guarding" the Adélie chicks? (see p. 61).



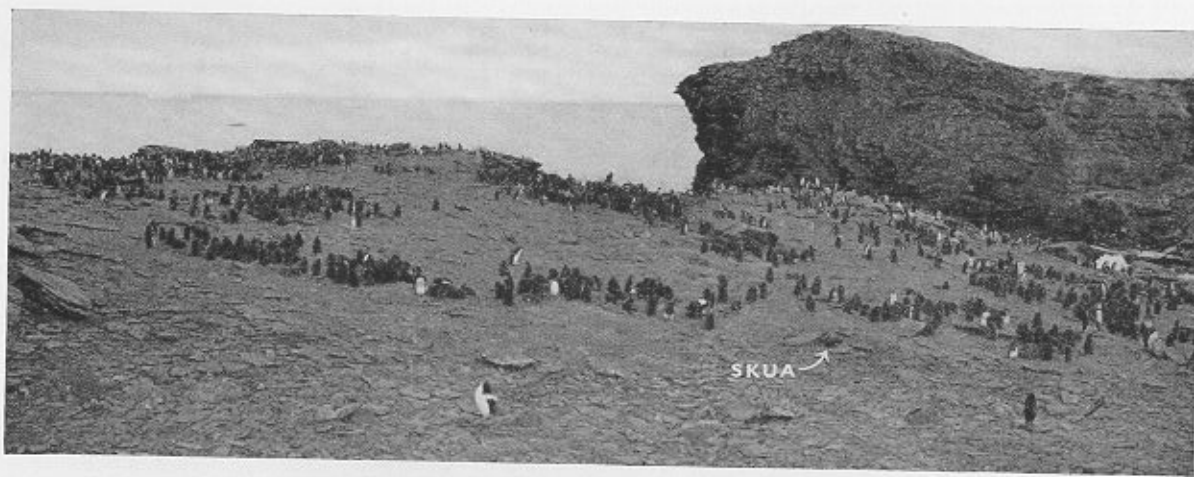
a



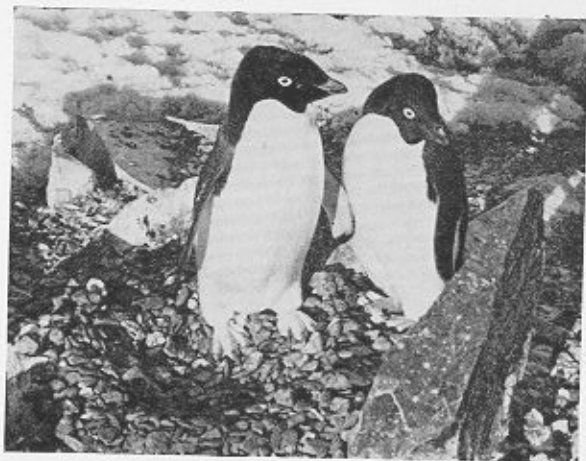
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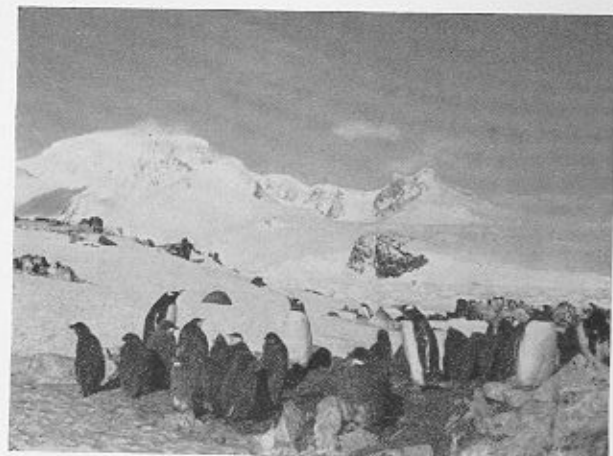
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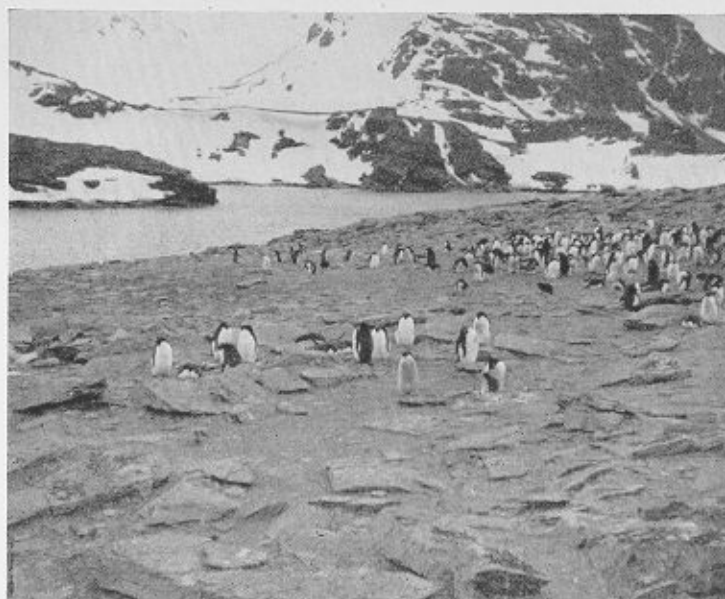
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a



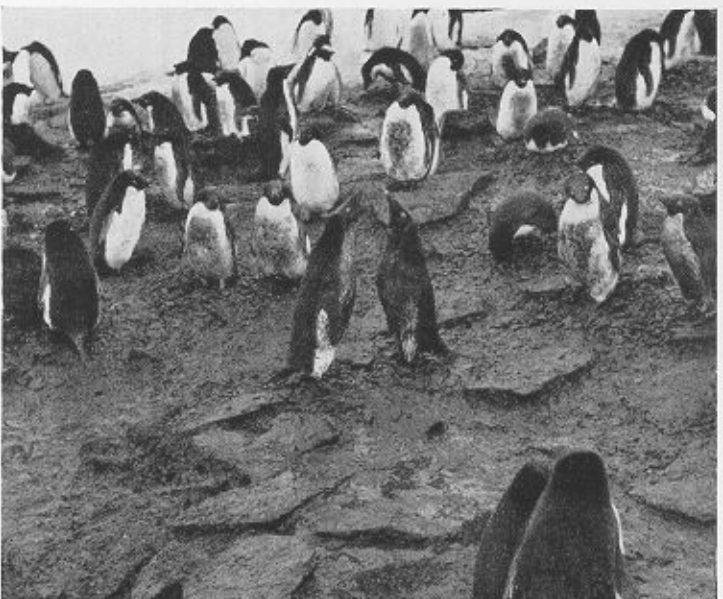
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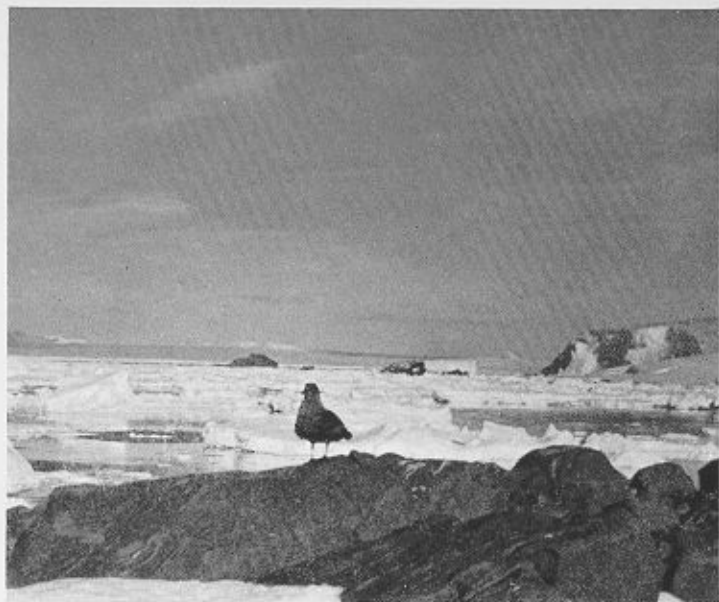
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PLATE XI

- a-b. A colony at Signy near the store tent showing (a) a subsidiary colony on snow on November 4th, and (b) the appearance on December 27th during the re-occupation period when all the snow has gone. The only successful nest in this subsidiary colony was the one with a chick in it in the right foreground. The store tent is flattened in (b) because two Elephant Seals lay on it.
- c-f. A fight between two females on October 24th during the occupation period.
- c. A male occasionally, but half-heartedly, enters into the fray.
- d. One female gives up. It is very dirty.
- e. The remaining pair join in mutual display, while
- f. The ousted female lies exhausted on the snow-slope near the colony (see pp. 67-68).

PLATE XII

- a. The Skua, *Catharacta skua*.
- b. A well-nourished chick (left), and a starving, emaciated chick which would be an easy victim for the Skua.
- c. A Leopard Seal lurking below the icefoot.
- d-f. Colony III at Hope Bay (see pp. 69-70) from a fixed photographic point.
 - d. On December 8th, 1948; all the eggs have been lost and the nests buried under the snow.
 - e. On January 30th, 1949; the colony is deserted except for one adult. The nest-sites are covered by snow several feet deep. There was 100% mortality of eggs during the 1948-9 season in Colony III. Colony IV on top of the hill, being kept clear by the gales, had a much lower mortality (see Table XIX).
 - f. The same colonies from the same position during the 1952-3 season.



a



b



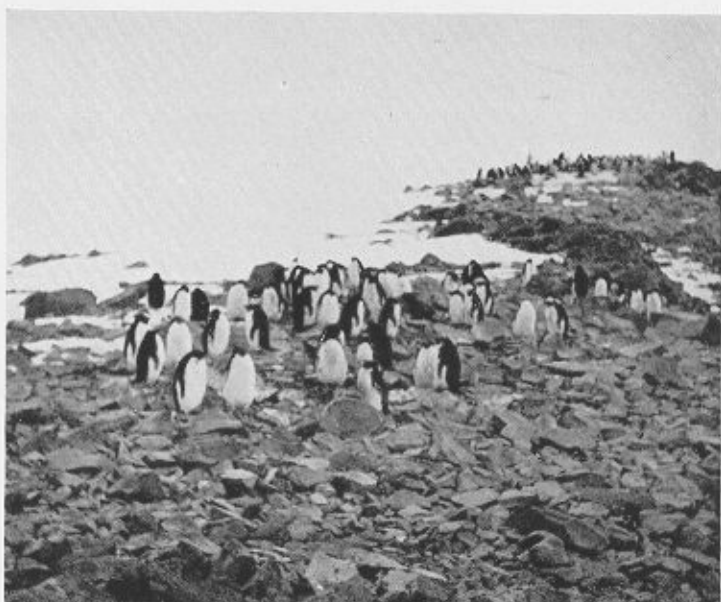
c



d



e



f