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THE ELEPHANT SEAL

(*Mirounga leonina* Linn.)

II. GENERAL, SOCIAL AND REPRODUCTIVE BEHAVIOUR

By

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I. INTRODUCTION

A. General Remarks

THE elephant seal first became known to science in 1748 but the earliest reliable account of the habits of the species was a brief paper by Murphy (1914). Ring (1923) and Matthews (1929) gave superficial accounts of the behaviour of elephant seals at the Iles de Kerguelen and South Georgia. These three papers contained the only important information on the habits of the species at the time the present study commenced in 1948, but since then Sorensen (1950) has published an interesting account of the herd at Campbell Island embodying original observations, and very recently Angot (1954) has produced a paper on the elephant seals at Kerguelen. Unfortunately, this author's methods do not appear to be entirely suitable.* The most important contribution to the study of the behaviour of elephant seals is Bartholomew's (1952) very detailed account of the social and reproductive behaviour of the closely related northern elephant seal (*Mirounga angustirostris* Gill). In many respects the behaviour of *leonina* appears to be identical with that of *angustirostris* but the two species live under very different conditions. "*M. angustirostris*' principal rookeries are in the subtropics. Water temperatures in midwinter are above 55°F. and where fresh water is available on the islands, palm trees grow" (Bartholomew, private communication). In contrast, the southern species occasionally breeds on sea ice at the southern limits of its range and is able to keep open breathing holes in the ice for several weeks during the autumn and spring.

B. Field Localities

1. *South Orkney Islands*

The present study was made during three Antarctic seasons while the author was serving with the Falkland Islands Dependencies Survey. From February 1948 to February 1950 field work was carried out at the South Orkney Islands from a base on the east coast of Signy Island in latitude 60°43′ S., and longitude 45°36′ W. (see Figure 1).

The majority of the seals hauling out at this group of islands (about 10,000) come ashore to moult their hair coat in the summer months and are thought to come from the breeding stock at South Georgia (Laws, 1953d, p. 753), while the *breeding* population in the South Orkneys numbers less than 250 individuals of which about 100 are breeding cows. A detailed preliminary analysis of the behaviour was facilitated by the small size of the population, especially during the breeding season. Indeed, certain aspects of the behaviour would have been extremely difficult to study at South Georgia.

Signy Island is roughly triangular in outline, with the south coast forming a base about three miles long and North Point lying about four miles to the north. A permanent ice cap covers most of the southern half of the island and the only extensive low-lying land is in the north-east where, between Berntsen Point and Stygian Cove (Figure 1 and Plate Ia), there is a coastal strip which extends inland a quarter of a mile at the most before the 100 foot contour is exceeded. The coastline is very indented, and has many small coves. There is a thin covering of glacial drift with, here and there, outcrops of limestone or metamorphic rocks. Vegetation is confined to small patches of mosses, lichens and occasional clumps of grass, *Descampsia antarctica* (Hooker) and *Colobanthus crassifolius* (Hooker), on the north-facing slopes.

A valley runs from Elephant Flats in the south to Stygian Cove and holds four freshwater lakes. The western boundary of the area is the main north-south escarpment of the island which rises steeply in rock cliffs or steep snow slopes to Snow Hill (801 feet) and Jane Peak (696 feet). Robin (1948) has shown that the majority of elephants seals on Signy Island are to be found on this stretch of coast and the nearest beaches outside the area are approximately a mile distant; they are near North Point, and in Paal Harbour. Because of its accessibility from the base on Berntsen Point and because it was a relatively isolated geographical area, Borge Bay was chosen for detailed field work.

The remainder of the island, which has a precipitous rocky coastline, was inspected at approximately monthly intervals. It is separated from the larger Coronation Island to the north by a deep strait and, owing to difficulties of travel, only a small part of the coastline of Coronation Island was visited in summer

* Many of his more important conclusions are derived from a statistical analysis of the lengths of samples of elephant seals seen at different dates during the year. He claims to be able, by virtue of experience gained in a few weeks, to estimate the lengths of seals (from nose to base of tail) with an accuracy of ± 10 cms. in the case of females and ± 25 cms. for males; throughout his paper he calls these *estimates* measurements. In a previous paper I have given it as my opinion that in measuring a *dead* elephant seal with a tape measure an accuracy greater than ± 3–6 ins. (8–15 cms.) cannot be expected, and Bertram (1940) states that ± 2 ins. (5cms.) was the expected error in measuring Weddell seals.

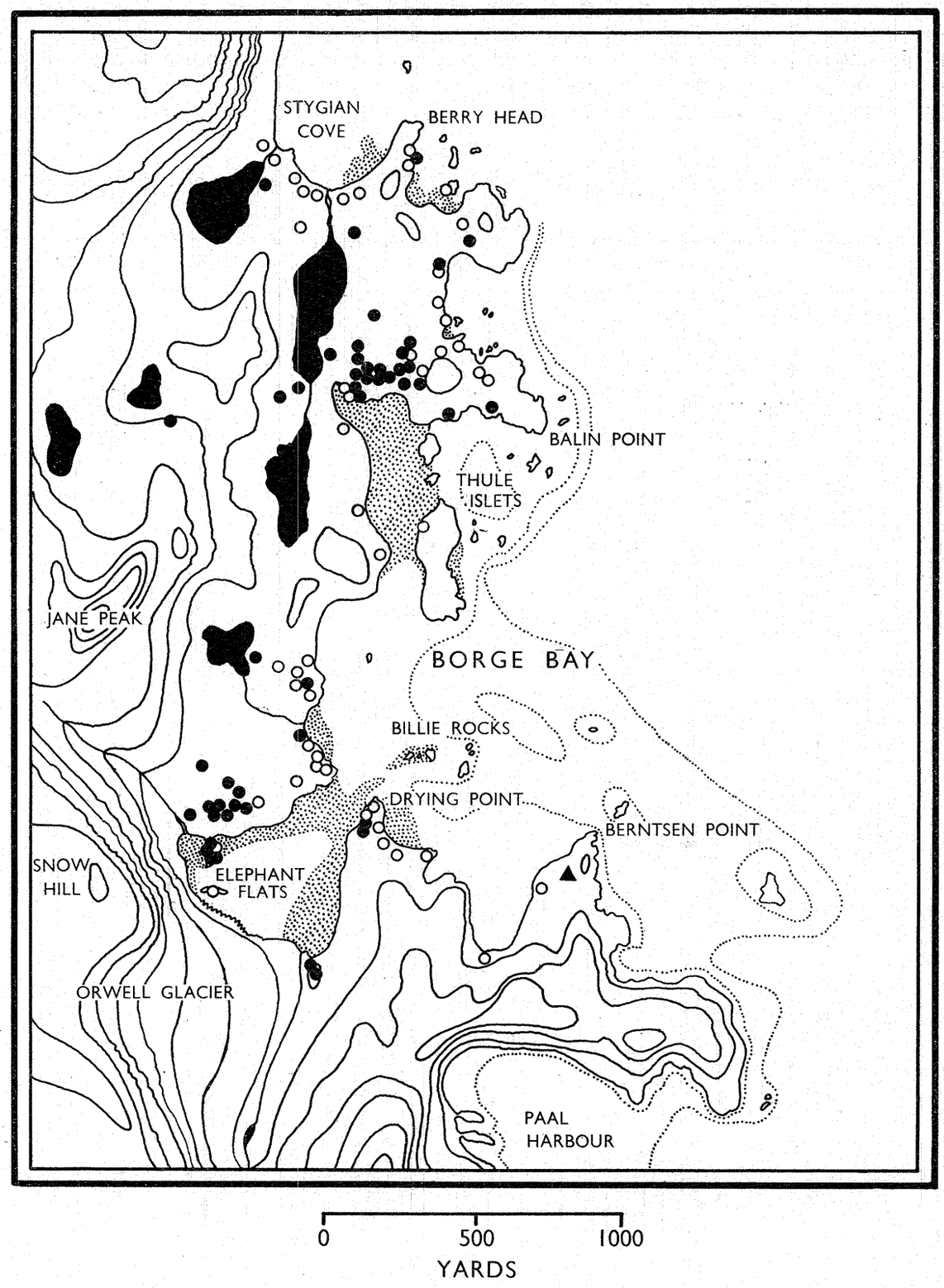


FIGURE 1. Borge Bay, Signy Island, South Orkney Islands, showing the distribution of the sexes during the summer haul-out of the elephant seals. Each circle represents a "pod" of approximately fifty individuals. (White, male; black, female.) The position of the F.I.D.S. base is marked by a small triangle.

(in the vicinity of Cape Hansen, due north of Borge Bay). Winter journeys, however, showed that there were few suitable seal beaches elsewhere on the south coast.

Owing to the late break-up of the fast ice around the island in 1948 and 1949, the greater amount of the work on the reproductive behaviour in these seasons was carried out on a large area of fast ice off the east coast of Signy Island. The average extent of the fast ice during each of these seasons is shown in Figure 16.

2. *South Georgia*

From March to December 1951, the field base was located on King Edward Point, Cumberland East

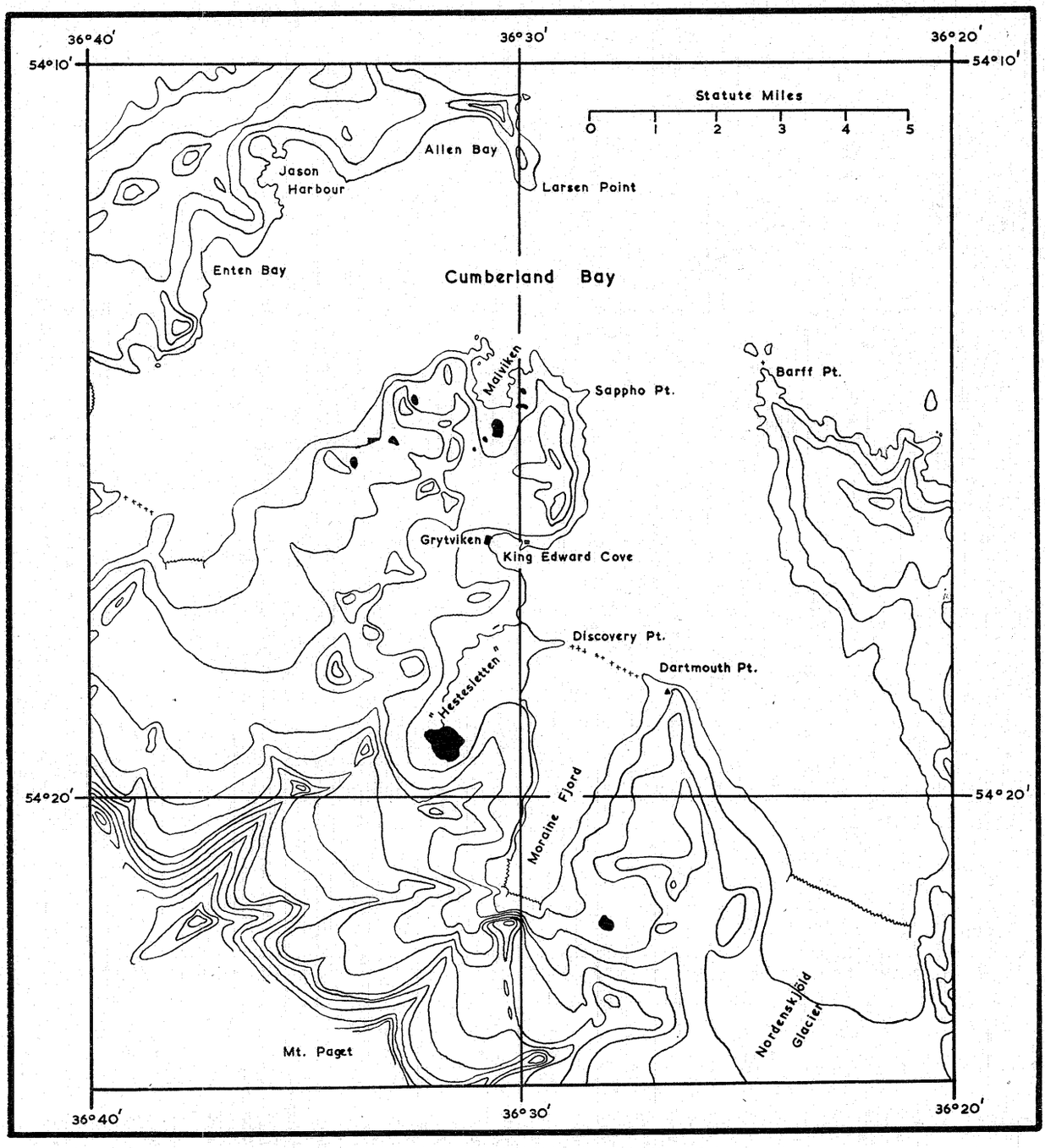


FIGURE 2. Cumberland Bay, South Georgia.

Bay, South Georgia, in latitude 54°17′ S., and longitude 36°30′ W. Observations were mainly confined to the large breeding rookeries in Cumberland Bay, from August to December. The non-breeding behaviour was less completely studied there than at Signy Island, but there is reason to believe that it is essentially the same.

Cumberland Bay is the largest bay in South Georgia and is formed by the confluence of three fjords marking the former extent of valley glaciers. The mountain range to the west culminates in Mount Paget (9545 feet) and Mount Sugartop (7823 feet) and the principal glaciers flowing from it into Cumberland Bay are the Nordenskjöld Glacier, Neumayer Glacier, Lyell Glacier, Geikie Glacier, Harker Glacier and Hamberg Glacier. With the exception of the last, their fronts reach the sea in ice cliffs of considerable height (Figure 2).

Owing to its proximity the coast south-east of Grytviken was frequently visited. The greatest concentrations of elephant seals were on the seaward fringe of the extensive moraine plain known as "Hestesletten"* (Plate IVb) and on the flat ground near Discovery Point (Figure 20), but the long beach from Penguin River to Discovery Point is largely composed of coarse material which discourages the haul-out of seals. Skottsberg (1912, p. 26) has described the vegetation: "Only along the edge is there a tussock association. Otherwise the vegetation may be described as a grass tundra with dominant mosses, *Polytricha* and others, forming low, compact cushions. . . ." His photographs give an accurate impression of the area.

The extensive growth of tussac grass (*Poa flabellata*), and the existence of Penguin River and numerous small ponds, make it a favoured hauling out ground for elephant seals and it was the site of a breeding rookery of about 1100 females in the spring. Unfortunately, the area was disturbed by sealers who visited it once during 1951. For the purpose of studying what was thought to be a completely undisturbed breeding rookery,† a camp was occupied by the author for a short period in the spring (September 18th to October 12th) on Dartmouth Point (Figures 2 and 19). The topography and vegetation of this area are very similar to that of Discovery Point. Counts and behaviour studies were made on the peninsula bounded by the Nordenskjöld Glacier and Moraine Fjord, and daily (or more frequent) counts and observations were carried out in the vicinity of Dartmouth Point itself, in the area shown in Figure 19. It supported a breeding herd of about 1200 females in 1951 and is classified as a reserve which the sealers have not been permitted to work since 1918.

Less frequent visits were paid to the small beaches on the east shore of Maiviken, in Cumberland West Bay, where there is a breeding population only about one-fifth the size of the herds in the two localities already mentioned.

In the course of five journeys around the coast of South Georgia, the regular studies were supplemented by other observations made as the opportunity presented itself. On four of these voyages, aboard the seal catcher *Albatros*, the author was able to study the commercial sealing methods (Laws, 1953d).

3. *Falkland Islands*

Through the kindness of Mr. P. H. Tilbury of the South Atlantic Sealing Company, a few additional observations were made in the Falkland Islands during a voyage on the sealing vessel *Protector*. These were mainly confined to Arch Island in the Falkland Sound.

It should be mentioned that most of the work was carried out without assistance, and on that account is not as complete as could be wished.

C. Methods

This paper is the second of a series on the biology of the southern elephant seal. In an earlier paper (Laws, 1953b) a general account of the life history has been given and the external appearance of all age groups described in some detail. The average, maximum and minimum growth rates have been established for both sexes, and the probable extent of mortality has been discussed.

Conclusions arising from field observations have been checked, where possible, by reference to material collected for laboratory study. A paper on the physiology of reproduction is in preparation and will be published in this series. It is substantially the same as part of a dissertation submitted for the degree of Doctor of Philosophy in the University of Cambridge (Laws, 1953e).

* This name is used locally but is not officially accepted.

† Later shown to be an incorrect assumption.

1. *Counts*

At Signy Island weekly counts of the numbers of elephant seals hauled out in the Borge Bay area were made throughout the year. Additional counts were carried out at less frequent intervals over the remainder of the coastline of Signy Island and on Coronation Island.

After some experience had been gained in the autumn of 1948, size and appearance were used as criteria to divide the population counts into seven classes, four male and three female. Later, the age groups represented by this classification were worked out by reference to dentine rings in the teeth of representative individuals (Laws, 1952b and 1953a).

Class I males were large bulls over seven years old and strong enough to control a harem in the breeding season. They are identified by great size, full development of the proboscis and extensive scarring. Class II males are large males, somewhat smaller than those in Class I and are aged from six to seven years. They are not so massive in stature and have fewer scars and usually a less well developed proboscis; they are the "subordinate" bulls in the breeding season. In a few cases distinction between these classes is difficult outside the breeding season. The Class III males are of medium size, aged from three to five years, usually sexually mature but not large enough to take part in the activities of the breeding rookeries. The Class IV males are small and from one to three years old.

The Class I females are distinguished from the medium sized Class II females by their greater size, scarring and extent of tooth wear. Their age is in excess of eight years. The Class II females are from three to eight years old and the small Class III females are yearlings and two-year-old animals.

The cows can usually be distinguished from the younger males by the shape of the head, which is not so broad and square, and by the type of scarring in the neck region. With experience it is quite practicable to make a constant distinction between the classes in the field counts. On several occasions two indepenpendent counts were made on the same day in order to check the accuracy of the classification, and the differences between them were found to be negligible. It is thought, however, that there may be significant differences between the classification of the counts by different observers although the total numbers are comparable. Moreover, in January and February when the seals were congregated in large "pods" in certain areas, it was necessary to determine the proportions of the various classes in several samples, and then to apply these proportions to the figures for the total numbers present. As a result, the classification of such counts may be slightly inaccurate; the corrected curves suggest that on no occasion was the error more than a few per cent.

In addition to the classification of the individual seals based on physical characters, counts were made according to geographical divisions. For this purpose the area was divided into beaches and other natural geographical areas and the numbers of seals were listed accordingly.*

At South Georgia similar, but less extensive counts were undertaken during the autumn at "Hestesletten" and Maiviken. During the breeding season the counts were made with greater frequency, and the number of harems was recorded. During the period of detailed observation at Dartmouth Point counts were made at least once daily.

Specially prepared sheets in tabular form were used for recording the counts in the field, as they were made.

2. *Marking Experiments*

Many opportunities for observing the behaviour of the seals occurred while the counts were being taken, but in order that more detailed and extensive studies of individual movements and behaviour might be made, marking experiments were undertaken at Signy Island and to a lesser extent at Cumberland Bay, South Georgia.

The results of the recent long term marking experiment on the elephant seal have been described in previous papers (Laws, 1952a and 1953b). Lack of assistance in the very arduous work of permanent

* For census purposes the coastline of Signy Island was divided into Areas A to P and each of these areas subdivided into smaller areas or beaches such as F1 to F7. The scattered harems were known usually by a colour with which the majority of the cows were painted (Red, Yellow, Green, etc.). Their distribution bore no relation to the census areas because the majority of them were located on the sea ice.

At South Georgia the coastline in Cumberland Bay was divided into geographical areas (e.g., Dartmouth Point, D1 to D12). The harems forming in these areas were designated alphabetically according to the time of formation. Thus, the first harem in Area 1 was known as Harem 1a, followed by 1b, 1c, 1d, etc.

marking and the discovery of a reliable method of age determination led to the abandoning of the permanent marking programme.

For short term behaviour studies, confined to three breeding seasons, experiments with both paints and oxidation dyestuffs were carried out at Signy Island in 1948. The latter medium proved unsuitable for use on a large scale, but paint marking is a satisfactory method of identifying individual elephant seals for short periods. A variety of cellulose aircraft paints made by Imperial Chemical Industries Ltd., to Air Ministry Specification D.T.D. 751/5, were found most suitable.* After experimenting with various types of pneumatic sprays, it became apparent that the paint must be rubbed into the hair and, even so, the marks usually had to be renewed at intervals of from seven to ten days. The paint was carried in 1 lb. Kilner jars and applied by means of interchangeable brushes (for the various colours) which fitted onto the end of a bamboo rod. At first a rod ten feet long and in two sections was employed, but with experience one five foot section was sufficient. Cows were marked, usually on the flank, with a number, such as a yellow "9". Some aggressive females and all the bulls were painted with either a spot of colour on the proboscis ("Red-nose", etc.) or a positional sign (such as "Yellow-left-spot" or "Red-tail") or a combination (e.g., "Red-left-spot and nose"). They were entered in the field notebook under abbreviations of these names (e.g., Y/9, R/n, Y/1/s, R/t, and R/1/s and n) and the system proved quite satisfactory. As a rule the animals of each harem were painted with the same colour or colour combination. It was frequently necessary to harry the bulls until they tired, before they could safely be painted.

Individual marking on a relatively large scale was possible at Signy Island because of the scattered distribution of the breeding population on the level sea ice. Daily tours of the breeding area were made during most of the season and the movements of twelve males and twenty-six females were recorded in 1948 and of twenty males and thirty-nine females in 1949 (ninety-seven in all). A small number of individuals, mainly bulls, were identified by means of physical characteristics, such as distinctive scars or unusual colouring. The lengths of all marked individuals were measured photographically (Laws, 1953b).

A less discriminating system was employed when working at "Hestesletten" and Dartmouth Point owing to the crowded state of those beaches. Some bulls were marked individually but the cows were usually marked according to the date on which parturition took place. For example, all cows under observation which gave birth to a pup on September 22nd, were marked "Red-X" on the left flank.

3. *Field Notes*

Large scale maps of the areas studied were prepared, and on them were noted the positions of harems, of marked and unmarked individuals (in the breeding season), and of "pods" and individuals (outside the breeding season). Where possible the conspicuous tracks of individuals over the snow at Signy Island (Plate IVa) were followed and plotted so as to give a complete record of their movements.

Bartholomew (1952, p. 370) says of his methods that: "The technique used . . . was the simple and obvious one of careful observation of the undisturbed animals and the detailed recording of their behaviour at the time of observation." Such a method was not possible in the present study. The observations on behaviour were subsidiary to the study of growth, age and reproduction, which necessitated killing animals for specimens and weighing pup seals. Some disturbance was therefore unavoidable, but it was kept to a minimum and in view of the fearless and lethargic nature of the elephant seal, is thought not to have impaired the value of the observations. The detailed observations of behaviour were therefore made as the opportunity presented itself in the course of population counts, weighing young, or collecting specimens, but several hours were spent each day at Dartmouth Point in the breeding season, watching groups of undisturbed animals. Fortunately, the behaviour patterns of the elephant seal are relatively simple, especially outside the breeding season. As far as possible the field notes were confined to objective observations, and selection was exercised in order to avoid amassing the very large quantities of notes which would have resulted from indiscriminate observations. Some experiments were made to determine the influence of certain factors on behaviour.

All notes were transferred at the end of each day into clean notebooks, and these, together with photographs and other original data, have been deposited with the Falkland Islands Dependencies Scientific Bureau in London.

* The colours employed were dull red (212–5010), yellow (212–5009), white (212–5021), grey-green (212–1132) and dull blue (212–1122).

II. DISTRIBUTION

A. Geographical Distribution of Mirounga Leonina

BOTH species of elephant seals were formerly of much wider occurrence than they are now, but owing to the lucrative oil industry they were hunted to extinction in many localities. However, with the cessation or restriction of elephant seal hunting during the past forty years, the southern species has again increased greatly in numbers and has begun to recolonise many of its former breeding localities.

In South America they were found breeding as far north as Juan Fernandez, but Murphy (1936) stated that they were "practically exterminated" there. Molina (1872) states that the elephant seal was common on the coast of southern Chile, near Arauco (37°10′ S., 73°20′ W.). They are still seen as far north as the island of Chiloé on the west coast of South America but Carrara (1952) lists only one breeding rookery on the coasts of Argentine territory. This is located on Peninsula Valdes near Punta Norte (42°07′ S., 63°50′ W.) and averages a total of eighty animals, the maximum count being 115 individuals. Elephant seals are once again more common on Tristan da Cunha and Gough Island (Elliott, 1953), on the islands of Marion, Crozet, St. Paul and Amsterdam. The species breeds in Tierra del Fuego, the Falkland Islands, South Georgia, Gough Island, Marion Island, Iles Crozet, Iles de Kerguelen, Heard Island, Macquarie Island, Campbell Island and other islands south of New Zealand.

Fraser (1935) has discussed an early account of the elephant seal at St. Helena by P. Mundy (1656), and Dampier who visited the island in 1691 convinced himself that the animals were "sea-lyons" (i.e., elephant seals) and not manatees as had been suggested by other voyagers. Mortensen (1934) and Hamilton (1940) support these conclusions. The date of the latest record appears to be 1810 (Kitching, 1936). This is the most northerly authenticated record of *M. leonina* (latitude 16° S.). A specimen said to be from the Tinian Islands, Marianas group, which Desmarest used as the type of his *M. byronia*, is thought to have been given the wrong locality by its collector (Lydekker, 1909). The Tinian Islands are situated in latitude 15° N., and no elephant seals have been reported there either before or since. The nearest known colony of elephant seals was that which Peron (1816) found on King Island in Bass Strait, in latitude 40° S. If Desmarest's specimen was correctly assigned to the Tinian Islands, which is doubtful, then it is much more likely to have been a wanderer from the Californian coast, and re-examination of the skull might show it to be *M. augustirostris*.

Elephant seals are often seen around the coasts of New Zealand, and great numbers of elephant seal bones have been found in the superficial deposits of the North and Middle Islands (Murray, 1866). Since Peron's remarkable account of the seals that he found on King Island in Bass Strait and nowhere else, only occasional stragglers have been reported from the Australian coasts but the generic name *Mirounga* is derived from an Australian aboriginal name, which suggests that formerly it was not uncommon on the shores of this continent.

The most northerly of the recent records are from Algoa Bay, South Africa. A male was collected there in February 1918, and two females, one in January 1932 and the other in January 1937, have been reported (Roberts, 1951). Matthews (1929) mentions that an elephant seal was seen in South Africa by the staff of the *Discovery* in 1926.*

Southwards the species ranges as far as the pack-ice and even to the shores of the Antarctic continent. The most southerly known breeding stations are in the South Shetland Islands (King George Island, latitude 62° S.) and South Orkney Islands (Signy Island, latitude 60° S.). The species may also breed in the South Sandwich Islands.

B. Migrations

Unfortunately, Lydekker (1909) did not state the nature of the evidence which Rothschild communicated to him, purporting to show that migration formerly took place between the San Juan (Juan Fernandez) and Guadeloupe Island elephant seal herds. The Humboldt current might facilitate such a movement, but these two populations are undoubtedly specifically distinct, and such migration cannot have taken place in

*Kettlewell and Rand (1955) give more recent reports. Males were seen in March, 1949 and February, 1950 on Cape Peninsula (34° S.). On October 6th, 1953 a cow with suckling pup, 3–4 days old, was observed on the Bredasdorp coast near Cape Agulhas. They point out that this is the first birth recorded from South Africa, and that the nearest rookeries are on the Prince Edward Islands (900 miles to the south-south-east) and the Tristan da Cunha group (1500 miles to the west).

historical times. Doutt (1942) suggests that the harbour seal *Phoca vitulina mellonae* (subsp. nov.) has been isolated in Seal Lake, Ungava Peninsula, for approximately 4000 years, and assumes that this is the length of time required to make a *subspecies* under conditions of a changed environment.

The recolonisation of island groups in the north and south of the southern elephant seal's range, shows that there is a north to south migration which may perhaps more properly be called a dispersal. Thus, at Tristan da Cunha MacGillivray (1854) wrote that the "sea elephant" was almost extinct, and Moseley (1893) said that although still present in Inaccessible and Nightingale Islands it was becoming scarcer every year. Elephant seals were occasionally seen by Barrow (1910) during his three years on Tristan da Cunha, but Elliott (1953) implies that the species does not breed there at present although it is becoming steadily more numerous and will probably breed there again. This visiting population is presumably from Gough Island not far to the south (see footnote on p. 8).

The increase in the elephant seal populations at the South Orkney Islands, South Shetland Islands, South Sandwich Islands and Falkland Islands, was first considered to be an extension of the range owing to pressure of population on the crowded beaches at South Georgia. Recent work (Laws, 1953d) has suggested that there has been some over-hunting at South Georgia and the movement of seals southwards is probably an extension of the movement in recent years from the larger bays of South Georgia to smaller, less accessible coves. The fact that the estimated total of 10,000 elephant seals hauling out in the South Orkney Islands includes only about 100 cows which breed there, suggests that the larger summer populations in this group and in the South Shetland Islands and Falkland Islands represent a genuine migration southwards and westwards from South Georgia after the breeding season.

In 1914 fair numbers of elephant seals were recorded at Signy Island, South Orkney Islands, for the first time since Dallmann visited the group in 1873 (Marr, 1935). Scientists of R.R.S. *Discovery II* reported large herds in both the South Orkneys and South Shetlands in the middle "thirties", but it was not shown to breed in the former group until 1947, and in the South Shetlands until 1948. Breeding was first confirmed (in recent years) in the Falkland Islands in 1934. In the South Orkneys and South Shetlands this has probably been due to the presence of migrating cows early in the season when there was open water inshore. The majority of the animals hauling out on Signy Island between 1947 and 1952 were mature females.

The more southerly records are mainly of young males (only three are females), and their distribution seems for the most part to be limited by the edge of the pack-ice. These records are given in Table I. The males recorded are of all ages.

Some information on the direction of movements from Signy Island is now available.

Locality	Lat.	Long.	Sex	Authority
McMurdo Sound	77°40′ S.	166°30′ E.	male	Wilson (1907)
Cape Denison	67°00′ S.	142°40′ E.	male	Mawson (1915)
—	65°30′ S.	52°00′ E.	male	Christensen (1942)
—	66°30′ S.	49°31′ E.	male	,,
Scott Island	67°24′ S.	179°55′ E.	—	Marshall (1930)
—	65°08′ S.	163°00′ E.	female	Wilkes (1845)
Terre Adélie	66°45′ S.	141°30′ E.	males(2)	Sapin-Jaloustre (1953)
Neny Fjord	68°16′ S.	66°50′ W.	male	F.I.D.S.
Port Lockroy	64°49′ S.	63°30′ W.	males(8)	F.I.D.S.
"Waterboat Point"	64°48′ S.	62°43′ W.	males(20) female(1)	Bagshawe (1939)
—	60°41′ S.	48°32′ W.	female	Kermack (1946)

TABLE I. Southern records of the elephant seal.

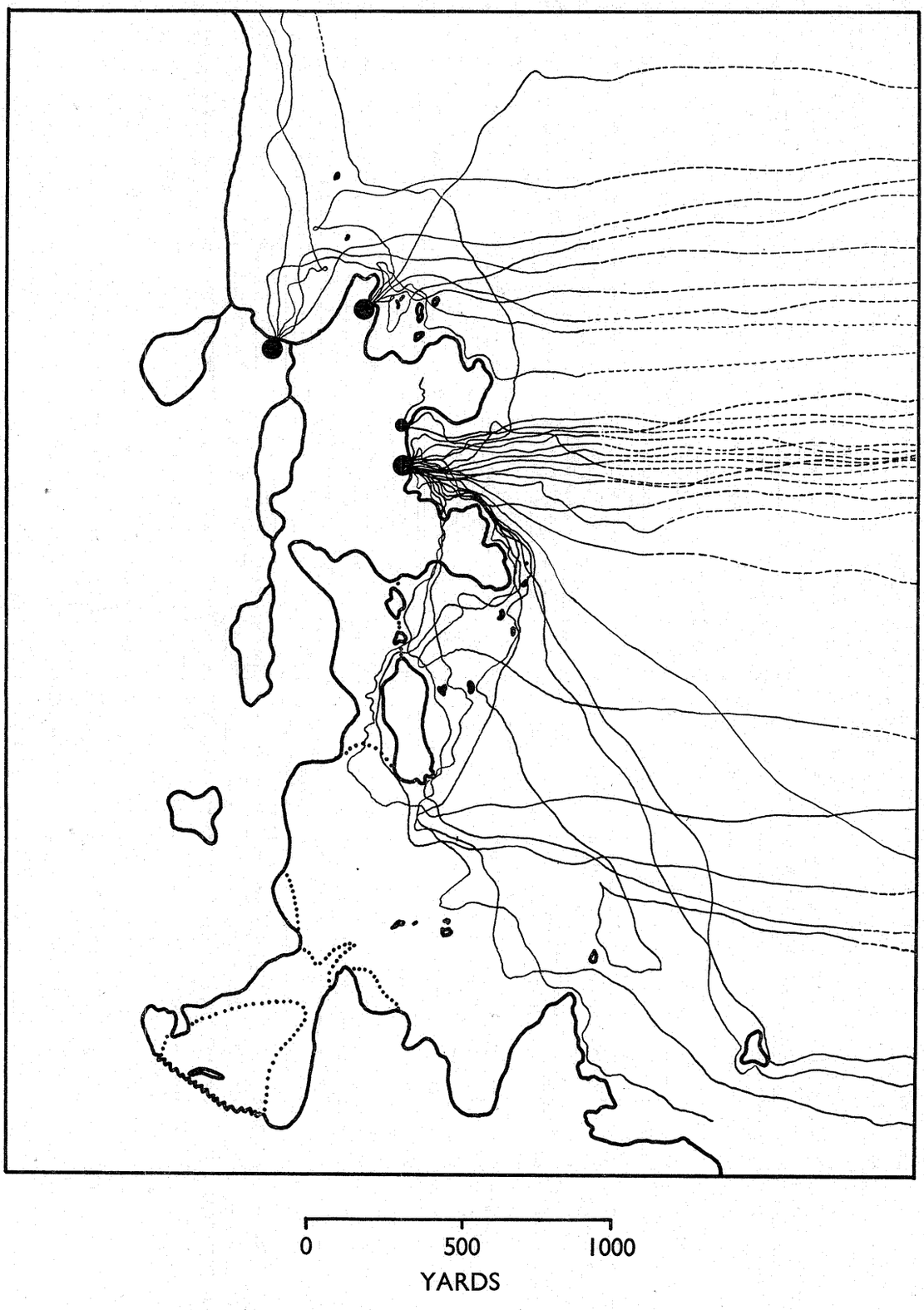


FIGURE 3. Borge Bay, Signy Island, showing the tracks made by thirty-six male elephant seals leaving four "pods" between June 2nd and June 11th, 1949. The dotted portions of the tracks are uncertain.

In the autumn of 1948 the sea was frozen over when the last seals left and they travelled away over the ice (see p. 14). During the first half of June tracks of these departing seals were plotted on a map of the area. With but three exceptions they all trended eastwards (Figure 3). In the springs of 1948 and 1949 fast ice surrounded the island and all seals approaching the area at this time came from the east or south-east, although there were patches of open water to the west also. In 1948 the author came to the conclusion that the first cows moving inshore were following a course to one particular beach (Drying Point) and were "navigating" by sight, and after a week's observations he had no occasion to modify his original impressions. In 1949 nearly all the breeding animals hauled out near a large iceberg, about 200 feet high, and their movements suggested that they "navigated" by conspicuous landmarks.

We may conclude that there is probably a dispersal to pelagic feeding grounds in winter, covering a wide area of the southern ocean, although the majority of the seals probably feed in the vicinity of the pack-ice. Some individuals reach high southern latitudes, one having been seen at nearly 78° South in the Ross Sea; others probably range northwards to 40° South and in some regions even further north (see footnote on p. 8).

There also appears to be some evidence of a true migration in the Falkland Islands Dependencies for there is a more directed movement to the south and west of South Georgia. This movement takes place after the breeding season at South Georgia and, as a result, perhaps fifteen per cent. of the South Georgia herd haul out during the summer months at the Falkland Islands, the South Orkney Islands and the South Shetland Islands. However, no large groups of elephant seals have been seen in the water at any time, nor have they been reported by whalers or sealers who would certainly have seen such herds if they were present in the area. The migration, if it may be so called, is certainly not as important as those of other species such as *Callorhinus ursinus*, and *Phoca groenlandica*, nor are the distances involved so great.

III. NON-REPRODUCTIVE BEHAVIOUR

A. General Behaviour and Attributes

THE southern elephant seal is an aquatic mammal and as such spends probably three-quarters of its life in the open seas surrounding the Antarctic continent, mostly north of the region of pack-ice, and knowledge of its behaviour is necessarily confined to observations made on land and in the coastal waters of oceanic islands. Although the author has made several ocean voyages in the Falkland Islands Dependencies, and in sealing and whaling vessels at South Georgia and the Falkland Islands, he has rarely observed elephant seals outside coastal waters and whalers and sealers report a similar experience. When at sea the species probably spends at least 80 per cent. of its time under water, and when it does surface (see p. 12) only the head appears; moreover, it does not advertise its presence by conspicuous spouts as do the cetacea. Therefore, in describing the behaviour of the species we can deal factually only with the short period of the annual cycle which is spent on or near land, and are reduced to conjecture about its pelagic life.

Although the behaviour of the elephant seal may be conveniently divided into non-reproductive and reproductive activities, these are related and certain patterns are common to all behaviour. Since a comprehensive knowledge of all aspects of behaviour is essential to an understanding of the mode of life of the animal, no apology is made for covering ground which has already been surveyed by earlier writers.

1. *Terrestrial Locomotion*

Bartholomew (1952, p. 372) has rightly stated that, "of these nonsocial activities locomotion is the most important, because the elephant seal's limited mastery of terrestrial locomotion and its complete mastery of aquatic locomotion exert a controlling influence over much of its social and sexual behaviour".

The locomotory patterns of both species and sexes of *Mirounga* appear to be practically identical, and have already been described in some detail (Bartholomew, 1952); only a brief general account will be given here.

Locomotion movements are usually initiated by vertical lumber flexion which draws the pelvic region forward; the fore part of the body is then raised and carried forward by a downward thrust of the fore flippers, aided by pelvic thrust and extension of the body, so that the animal hitches forwards about ten

or twelve inches. As soon as the sequence is completed the fore limbs are brought forward and the lumber region is arched, thus initiating another movement. When the animal is moving quickly a series of dorso-ventral undulations take place at a rate of about two per second. The hind flippers are held loosely with the plantar surfaces uppermost. Several writers have likened the locomotory pattern to that of a looper caterpillar, to which it bears only a superficial resemblance. In prolonged movement, such as is common in the breeding season, the animal bounces along like a large partly-deflated rubber tyre, the extreme flexibility of the vertebral column making it quiver pneumatically. The rhythmic nature of sustained locomotion is surprisingly graceful for such an apparently unwieldy animal.

Under certain circumstances there are modifications of the basic pattern. Pregnant cows near term carry the hind flippers off the ground, and the pelvic component of the locomotory rhythm is lacking or reduced. Nevertheless, they manage to cover considerable distances (later, p. 59). Both sexes are able to climb very steep slopes if there is sufficient friction. Travelling downhill the fore limbs are held in to the sides and not used, the anterior point of traction being the chest. In some large and vigorous bulls in the breeding season a similar modification was observed when they were moving over level sea ice.

Tracks left on the snow cover of the level sea ice (p. 14 and Plate IVa) facilitated measurements of the rate of progress. In the autumn when covering long distances to open water, the bulls moved about ten yards in a burst of locomotor activity, then they stopped and rested a few moments before continuing. When travelling similar distances in the spring, they move much more rapidly and with fewer and shorter halts. Observations of the track of bull "Scarred-eye" in 1949 (p. 70 and Figure 23) established that the shortest distance between halts was 14 yards, the longest 181 yards, and the average 56 yards. When travelling short distances the bulls move more rapidly, the maximum speed observed on level ground being six miles per hour, though it is much less on rough ground. The maximum speed of cows on level ground is about three to four miles per hour.

2. *Swimming and Aquatic Behaviour*

Even very young pups can swim. The youngest seen swimming was two days old, but the circumstances were unusual (related to the break-up of fast ice) and they do not usually enter the water until they are over thirty-four days old. They are then confined to the very shallow water along the shore and do not leave the beaches for another week (Plate VIId). They leave the mother when they are weaned at an average age of twenty-three days (Laws, 1953b, p. 28), and, contrary to popular belief, the mother does not teach her pup to swim. It takes the pup about a week to learn, but at first its movements are uncoordinated and there is a great deal of splashing when it finds itself out of its depth. The hind flippers are held half out of the water, and instead of being firmly extended as in the case of the adults, are limp. The fore flippers make "dog-paddle" strokes and the head is usually held well clear of the water but in some cases dives of up to five minutes duration were observed when young pups were swimming. In abnormal situations occasioned by the break-up of the fast ice on which the harems are placed, young pups fall into deep water and manage to keep afloat for about half an hour before weakening and drowning.

There is little to add to Bartholomew's (1952) description of the swimming of the northern elephant seal. The hind flippers are extended and the animal swims by lateral undulations of the body, synchronised with alternate medially directed thrusts of the hind flippers. The fore flippers are normally pressed against the side of the body but may be used for turning or balancing at low speeds. The reader should see also Scheffer and Slipp (1944) for a relevant description of swimming in the harbour seal (*Phoca vitulina richardii*). The maximum speed of free swimming adult elephant seals was about twelve to fifteen miles per hour; Bartholomew (1952) gives a speed of ten to twelve miles per hour.

Typically, when surfacing to breathe, they float vertically in the water, motionless, and usually with the head pointing straight up into the air. This position is the opposite of that adopted by the *Lobodoninae* and may be related to the more ventral opening of the nostrils. After respiring gently for a short time, the animal exhales strongly and sinks smoothly beneath the surface before swimming away. This is in marked contrast to *Hydrurga* which submerges like a porpoise showing the curve of the back. In sheltered inshore waters the elephant seal often floats at the surface with the body strongly arched so that the head and hind flippers appear above the surface and the rest of the body is submerged (Figure 4).

The elephant seal apparently does not swim ventral-side-up as other species may, but in sheltered coves they were often seen sleeping motionless in this position (or the reverse), either on the surface or submerged.

FIGURE 4. Young male elephant seal in characteristic resting position in the water.

Animals were often seen sleeping on the bottom in three or four feet of water, rising at intervals to the surface in order to breathe, without opening their eyes and apparently automatically (Figure 5). They seem to rise by expanding the thorax and so reducing their specific gravity. Just before submerging they breathe out strongly prior to closing the nostrils and presumably call upon oxygen stores in the blood when submerged. The most common rhythm consists of periods of submergence and apnoea of from five to ten minutes duration alternating with periods of emergence and ventilation lasting from one to three minutes. The maximum length of submergence recorded was fifteen minutes, but longer periods are probable in other circumstances. The caval sphincter in this species is very well developed, suggesting that dives of long duration are possible.

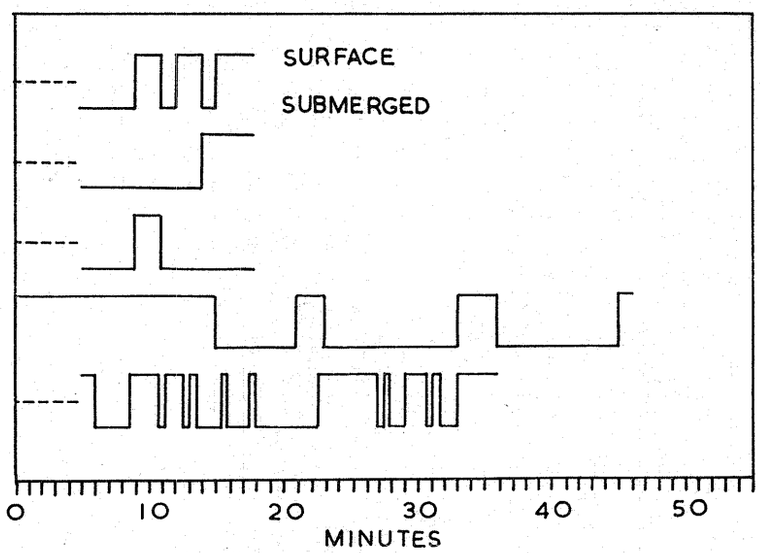


FIGURE 5. Diagrammatic representation of the respiratory rhythm of sleeping elephant seals.

When hauling out onto fast ice the elephant seal swims up to the ice edge and rests the fore part of its body on the ice. Then, by traction movements of the fore part of the body, assisted by swimming movements of the hind flippers, it slowly pulls itself out of the water (Plate Vd). Owing to its great weight out of the water the action requires much effort and animals usually lie motionless for a few minutes after hauling out.

3. *Relation to Sea Ice*

The influence of the fast ice on the breeding organisation of the elephant seal at Signy Island, and the effect of pack-ice and land-fast ice on the numbers of elephant seals hauling out are discussed elsewhere in the paper (pp. 35 and 36). This section is chiefly concerned with the maintenance of breathing holes in the spring and autumn.

Prior to the present study, the breeding of elephant seals on sea ice had not been observed. Under the normal conditions of its life the genus does not come into contact with sea ice to any great extent, and Bertram (1940) in his valuable table comparing the bionomics of the pinnipedia of the world, indicates that the distribution of the species has no relation to sea ice. It is only in the extreme southern limits of its distribution that the elephant seal comes into contact with either pack or fast ice, and it is likely that the behaviour resulting from contact with land-fast sea ice is of recent origin.

In 1949 the waters off the east coast of Signy Island remained open until April 8th, when the pack-ice moved inshore and the sea froze over. There were two brief clearances during the month but after April 26th the fast ice remained unbroken and gradually increased in thickness until it broke up the following spring. Small numbers of male elephant seals remained on and around the island until June 24th, some of them living in close relationship with the sea ice for over two months. In 1948, when the sea froze over much later than usual, elephant seals were present only until June 6th. It is therefore probable that the presence of fast ice delayed the departure of the elephant seal rearguard at Signy Island in 1949.

While the ice was less than three inches thick, breathing holes were made by using the crown of the head as a battering ram from underneath the ice, as does the walrus (*Odobenus rosmarus*), (Johansen, 1910). The circular hole formed is about two feet in diameter and is surrounded by a rim of ice fragments (Plate IIIb); it is kept open by use as the ice thickens. Breathing holes were always made in this way and, in contrast to the ice-sawing method of the Weddell seal (*Leptonychotes weddelli*), the teeth were never used. The distance between adjacent breathing holes was usually about twenty to fifty yards, but one (at least) was located over two hundred yards from the nearest tide crack or breathing hole. Three of these breathing holes can be seen in Plate IVa. In addition to these circular holes, elephant seals also utilised natural openings in the ice cover, notably along the tide cracks where the sea ice abuts on the land or on grounded icebergs. On two occasions a seal at a breathing hole was seen to give a start as if disturbed, and then submerge; another head then appeared at once. In view of these occurrences and the small number of breathing holes kept open, it appears that breathing holes are shared indiscriminately by all elephant seals in the area. They may also make use of the few Weddell seal (*Leptonychotes weddelli*) blow holes seen at the same time.

The elephant seals attempting to travel over the surface of newly frozen bays, invariably fell through because the ice was not strong enough to bear their weight. They made persistent attempts to travel on it, leaving a trail of broken ice extending for several yards, before submerging and swimming beneath (Plate IVa). Within a few days of the ice first forming the surface was strong enough to bear the weight of all but the heaviest bulls, and the last individuals to leave the island travelled over the surrounding fast ice for a distance of ten miles before reaching a large lead of open water. On June 30th, 1949, a grounded iceberg four miles east of Signy Island was visited in order to verify that a large seal lying-out there was a bull elephant seal. It was, no doubt, using the tide crack for fishing purposes. Several others were seen on subsequent occasions in the area of consolidated pack-ice to the east of the island, and it seems likely that some spend the winter months in the ice. Throughout the remainder of the winter, fast ice and consolidated pack-ice extended to the limits of visibility (approximately twenty-five miles) but during a sledge journey to the eastern end of Coronation Island in July, Lewthwaite Strait was found to be lightly frozen and northward from Petter Bay open water extended to the horizon.

In the spring of the 1949–50 season, when the fast ice was over two feet thick, bulls hauled out at a lead of open water near a large iceberg some three miles south-east of Borge Bay. When pressure from the south closed the lead for a short time, two large hauling out holes were made by breeding males and used

by both sexes. These were made at the junction between the fast ice and the drift ice by the same actions as produced the autumn breathing holes, but they were large enough to allow the animals to haul out. A similar sequence of events prevailed in 1948 and was followed from a distance using binoculars.

Most of the cows breeding at Signy Island in 1948 and 1949 hauled out at the ice edge to the east of Borge Bay. Some gave birth to their pups out there, but of those which moved inshore to do so, the majority travelled over the surface of the ice, though at least two cows marked at the ice edge, are known to have swum considerable distances under the ice before hauling out to give birth.

> Female "Red-neck" swam under the ice for a minimum distance of 500 yards before hauling out at the tide crack of a grounded iceberg, and then travelled two miles over the surface of the ice before pupping. Female "Blue-left-spot", after being marked at the ice edge, hauled out at the tide crack between Outer Islet and the main island (a distance of over two miles from open water) before pupping. Several other cows travelled considerable distances over the fast ice before parturition; female "Green-neck", which was the first cow in 1949 to give birth to a pup inshore, wandered over seven miles. These and other tracks are shown in Figure 23.

The bulls (see pp. 69–70) covered even greater distances during the breeding season. One interesting record relates to bull "White-nose" which was seen and marked on the ice edge to the south-east on October 7th, 1949. On October 9th it approached Borge Bay from the north and subsequent investigation showed that it had hauled out at the pool of open water near Cape Hansen, Coronation Island (Figure 16). A search throughout the area confirmed that it had not travelled over the ice in order to reach this pool, so it must have swum underneath. If it followed a straight course (which is improbable) then it covered a minimum distance of five miles under the ice.

Bertram (1940, p. 9) has drawn attention to the problems faced by Weddell seals, when navigating under the ice and having to find breathing holes. He has suggested that, in certain circumstances, there are pockets of air under the ice and that seals are able to make use of them. In this connection the new information about the behaviour of elephant seals in relation to sea ice is especially interesting, and it seems likely that only if small pockets of air were present, could a seal unused to such an environment successfully negotiate long distances beneath the ice. In any case, it is open to doubt whether a special type of navigation is involved, for the number of elephant seals which have to solve these problems is very small.

4. *Feeding*

After weaning takes place at an age of twenty-three days, the pups live for about a month on the reserves of blubber laid down during suckling. During the latter part of this period they begin to take to the water and often lie in the shallows, facing in towards the beach with head submerged and back out of the water. With open eyes, they nuzzle under pebbles for the amphipods which cluster there. After this transition period they gradually acquire the adult diet as their swimming ability improves.

The adult southern elephant seal feeds exclusively upon cephalopods and fish. Crustacea and other invertebrates which are occasionally found in the stomachs of adult elephant seals probably originate from the gut of the fish present, or are taken accidentally. The animals were, of necessity, killed on land so that of the 139 stomachs which have been examined only six contained any fresh food substances, and none were full; twenty-three contained cephalopod remains, six contained fish remains and three had both fish remains and squid beaks (Table II). However, when occurrences of the different types of fresh material in the stomachs are compared, we find only one stomach with squid (from Signy Island) to five with fish. Matthews (1929, p. 241) found cephalopod beaks in thirty-five per cent. of the stomachs he examined and no trace of any other food substances.

At Signy Island a cephalopod was caught by hand from the dinghy and identified as an Oegopsid (probably an Onychotenthid). Comparison with the partly digested specimen taken from the stomach of H340 (a male) and with the beaks found in other stomachs, indicates that this species and possibly one other are usually taken by the elephant seal. Of the fish remains examined, the various species of *Notothenia*, especially *N. coriiceps*, predominate.

On the evidence given above, it is reasonable to assume that elephant seals, in the localities studied, probably feed mainly upon fish in inshore waters and upon cephalopods elsewhere. Since cephalopod beaks are digested very slowly, if at all, and fish bones are digested rapidly, the proportions of fresh material alone are significant. Most of the animals having fresh food in their stomachs were killed when still wet from the sea. Havinga (1933) has established that digestion in the harbour seal (*Phoca vitulina*) is very rapid. This may

Nature of food	Occurences	
	Male	Female
Cephalopod beaks	10	13
Fresh cephalopods	1	0
Fish vertebrae	0	1
Fresh fish	3	2
Amphipods	4	0
Lamellibranchs	2	0
Brachiopods	0	1
Algal fragments	8	1
Empty of food	58	55

TABLE II. Summary of stomach contents of 72 male and 67 female elephant seals, at Signy Island and South Georgia.

also be true of the elephant seal since their stomachs are often found to contain little food material. However, it must be remembered that they often fast for long periods when on land.

The depths at which the elephant seal customarily feeds are not known. The food is usually swallowed under water, for only one individual was seen eating at the surface. The relevant passage from the field notes says that, "an elephant seal poked its head out of the pancake ice just offshore. With its head thrown back it was trying to swallow a large *Notothenia* of over a foot in length. It masticated the fish between the canine and post-canine teeth before swallowing it head first and submerging again." The water here was about two fathoms deep. Osburn (1911) says that the California elephant seals (*M. angustirostris*) in the New York Aquarium were fed on fish, but differed from other seals in masticating it with the blunt conical teeth. Huey (1930) has, however, stated that he has watched captive elephant seals being fed and, "while the fish were dead when tossed to the animals, they were speedily bolted head first, without the least motion of mastication". The same writer has listed the stomach contents of a large male elephant seal harpooned and shot by fishermen in deep water forty miles off the California shore. He records ratfish (*Hydrolagus colliei*), sharks (*Squalis sucklii*, and *Catulus uter*), skates (*Raja* spp.) and squids (*Loligo opalescens*), some of which are customarily found in from 50 to 120 fathoms. The ratfish is never taken in less than fifty fathoms, and usually in deeper water. It is generally stated, in discussions of the dentition of elephant seals, that the teeth are adapted for seizing soft prey but not for masticating it.

Since digestion is usually well advanced by the time the stomach is examined on land, it is difficult to determine the amount of food eaten by an elephant seal. Some indication is given by Boulenger (1937) who states that, "an eighteen foot example in the Berlin Zoo consumes eighty to two hundred pounds of fish per day, according to season, being considerably less voracious in summer than in winter". Probably in the wild state the amount is much greater. Murphy (1914) mentions that as many as a hundred squid beaks are found in a single stomach, but these may be the residue of several meals. More relevant is his observation that in the stomach of a cow elephant seal killed as soon as it had come ashore he found fifteen fish each about 25 cm. long.

5. *Fasting*

The elephant seal feeds only at sea and as it spends long periods on land during the summer months it has to be able to endure protracted fasts. Adult bulls are known to spend over eight weeks on land during the breeding season (p. 69) and a slightly shorter period when moulting. The adult cows spend only twenty-eight to thirty days ashore during the breeding season, but it has been shown that while suckling the pup they probably lose at least 700 pounds weight (Laws, 1953b); during the moult they remain ashore for about thirty-two days.

Seals of both sexes are reluctant to enter the water when moulting, even if driven, and the cows, owing to their distance from the sea, rarely do so. (The probable influence of the moult process on heat loss is discussed on p. 20.) It is therefore certain that the cows fast throughout the period of the moult and they are known to become much more emaciated than the males. This is confirmed by the pattern of their dentine rings which are presumed to be a result of fasting. The males, on the other hand, enter the water more readily and therefore never become as emaciated as the females although they take longer to complete the moult process. In this connection it is perhaps significant that four males had fresh fish or squids in their stomachs while only two females had fresh fish remains. A male (H340) which was killed on December 20th on beach B2 was, "solitary—recently hauled out—moulting" (field notes) and the stomach contained a large, very fresh cephalopod. Another male (H360), killed on January 5th on beach G2, was "In good condition—moult almost complete" and there were amphipods in the stomach. This suggests that the males take to the water to feed during the moult, but perhaps only during the later stages of this process. The dentine rings of the canine teeth (if they reflect periods of fasting) again support this conclusion, because the rings laid down at the time of moulting are usually less marked than those in the dentine of female teeth (p. 44 and Laws, 1953a).

Of the 139 stomachs examined (see p. 16) few contained food, but 84 per cent. contained sand and stones, the amount varying from a few ounces to several pounds. Individual stones were rarely larger than an inch in greatest dimension, in contrast to stones found in the stomachs of sea-lions (*Otaria byronia*) which may be up to three inches in diameter. This material must be deliberately swallowed, for it is unlikely that it is taken in with the food, which is free-swimming. At Signy Island very few beaches were composed of material similar to that found in the stomachs, as they were mostly pebble or boulder beaches. It seems likely, therefore, that the stones and sand are taken from the sea bottom. One female at Signy Island, and one male at South Georgia were seen eating shingle on land.

Matthews (1929) suggests that the function of the stones is to triturate the food. Schroeder and Wegeforth (1935) state that seals and sea-lions voluntarily swallow stones but that they are not a pre-requisite to complete gastric digestion. Hamilton (1933), in a discussion of this habit in other species, suggests two more theories: one that it is used for ballast, and the other that it serves to grind up and destroy the parasites in the stomach.

Let us deal with these suggestions in order. The first may be doubted because, of the stomachs examined, only 16.8 per cent. of those containing stones or sand also contained food remains, whereas 34.2 per cent. of those without sand or stones held food. The fresh remains were invariably found in stomachs with few or no stones. As regards the second suggestion, it has been observed that the stones are often regurgitated on land, together with some of the stomach parasites, in the autumn months, but the majority of the nematode worms which infest the stomach remain attached to the mucosa. Some are concentrated in deep clefts resulting from pathological growths, presumably induced by mechanical irritation (Schroeder and Wegeforth, 1935). Moreover, when a stomach is cut open, the nematodes are seen to be unaffected even by large quantities of fine sand.

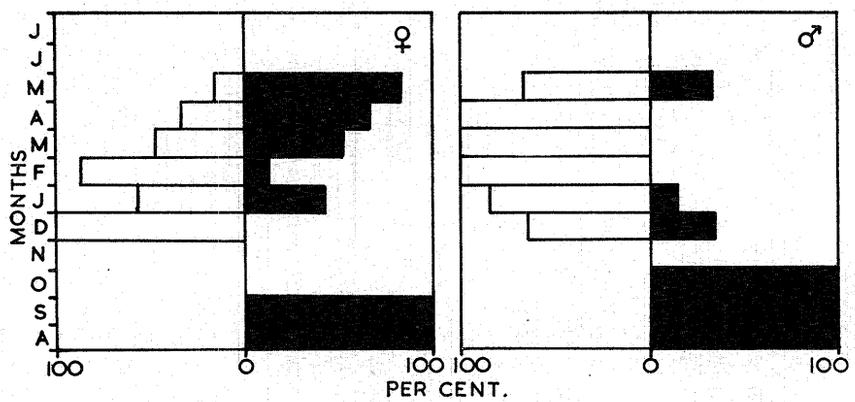


FIGURE 6. Incidence of sand and stones in elephant seals' stomachs. Black—empty of sand or stones; white—containing sand or stones.

Figure 6 was drawn up in order to show the incidence of sand and stones in the stomachs throughout the year. It represents the percentage of stomachs examined which contained stones or sand, set out month by month, separately for the sexes. Because of the observed differences in the habits of the pup and yearling elephant seals, data relating to them have been omitted. It is apparent that sand and stones are present in the stomachs mainly during the summer months and that the proportion of empty stomachs is greater in the spring and autumn. The inference drawn is that solid matter is ingested just before the animals come ashore and eliminated when they return to sea. It has been observed that this material is often regurgitated on land during the autumn months. Surely, if the sand and stones had a "ballasting" function, the stomachs examined in spring and autumn would contain at least as much material, if not more, than stomachs taken in the summer during long periods of lying out on land.

The most probable explanation of the observed occurrence of solid matter in the stomachs during the periods of fasting is that it serves to relieve "hunger pangs", by providing the stomach muscles with bulk, upon which they may contract. A suggestion to this effect made by Shaw (1801, p. 271) appears to have been unnoticed by later workers. Referring to the "Leonine seal" (apparently *Otaria byronia*) he remarks that, " . . . during the breeding season they are said to fast for three or four months, during which time they swallow a number of large stones, in order to keep their stomachs in a distended state". We may have here a parallel with human "earth-eaters".

Sand and stones are also found in the stomachs of young pups which have not yet left the beaches and are fasting prior to attaining nutritional independence. In these circumstances it cannot have been swallowed accidentally, and the habit is therefore evidently well-established.

The value of the adaptation to lengthy periods of fasting is readily apparent during the breeding season. It means that the harem bull can maintain his position for many weeks without serious challenge, and that the cows can suckle their pups without interruption for three or four weeks. The reason for the long period of fasting connected with the moult process is less apparent. It may be related to the "catastrophic" nature of the moult process in the elephant seal, as compared with most other mammals (see below).

6. *The Moult*

After shedding the natal fur at an age of about one month (Laws, 1953b, p. 30), the hair is next moulted at an age of from twelve to fourteen months, and thereafter once a year. The place, time and duration of the moult is discussed later in this paper (pp. 34 and 35) and only the process will be described here. It is unique, not only among the pinnipeds but among the mammals, so much so that Troll (1928, p. 327) has called it "reptile-like". Speculation as to the evolution of such a characteristic would be out of place here.

In sections of the skin and hair made before the moult process becomes apparent externally, a layer of new hairs, lying at a more acute angle than the old hairs, is seen beneath the epidermis. As the moult begins the sub-cuticular layers of the old skin are autolysed, the new hair straightens and pushes upwards both the hairs and epidermis of the old coat. The last season's hair is then shed in patches or large sheets (Plate IIIa) which are composed of the former epidermis holding together the displaced hairs with their roots projecting on the underside for about 2 mm. (see Laws, 1953b, Plate Vb). The new hair is relatively short and soft but grows in length and becomes more springy after the old epidermis is shed. In males over four and a half years old, the new hair frequently does not make its appearance until a week or ten days after the shedding process so that there are large bare patches of new epidermis for a time. The animals assist in the shedding of the hair by scratching themselves, rubbing on rocks and by frequenting muddy wallows at this time. There is no regular order of shedding, although the head, back and flippers usually seem to be the last to clear.

The normal colour is dark grey, weathering through various browns to a straw-yellow colour. Occasionally, individuals of both sexes are seen which have an unusually light-coloured coat, looking almost white when dry. They are most conspicuous in the spring and usually below average size. Although the elephant seal normally moults annually, it is likely that these individuals have not undergone a moult in the previous season with the result that the degree of fading is at least twice as great as in normal individuals. Moreover, the hairs are usually more curly and more sparse. Such individuals are probably comparable with "isabelline" plumaged penguins (Wilson, 1907b). Large barnacles were occasionally observed on elephant seals of this variety, suggesting that they had spent a considerable time at sea.

The blood supply necessary for a moult process of the type undergone by the elephant seal, leading to

Male No.	Condition	Blubber thickness	T°	Female No.	Condition	Blubber thickness	T°
H308	M+,G	3.0	36.0	H289	M,G	1.5	36.1
H309	M+,G	1.25	35.8	H290	M,P	1.5	35.2
H311	M+,G	3.0	36.4	H320	L,P	2.0	37.1
H312	M+,G	2.75	37.2	H341	M—,G	3.5	37.5
H322	Br+,G	2.0	35.8	H346	M—,G	3.5	34.8
H325	M,P	2.0	32.2	H352	M+,G	2.75	35.3
H326	M,G	3.5	35.0	H362	M,G		36.9
H327	M—,G	3.5	35.0	H363	M—,G	2.0	37.2
H332	M,G	1.5	35.2	H368	M,G	2.0	36.6
H330	M,P	1.0	37.3	H372	M—G,	2.5	37.2
H331	M+,G	1.5	36.5	H373	M+,G	3.25	36.7
H334	M,P	1.25	36.6	H374	M,G	4.0	37.1
H335	M,P	1.25	35.8	H379	M+,G	1.0	36.4
H340	M,P	1.75	36.4	M5	M+,G	2.25	36.9
H337	M+,G	1.25	34.6	M6	M+,G	1.75	37.0
H343	M+,G	1.25	37.2				
H344	M+,G	2.0	37.0				
H350	M,G	2.5	36.6				
H353	M,G	2.0	37.2				
H354	M,P	3.0	36.7				
H355	M,G		35.8				
H356	M+,G	1.25	36.4				
H357	M—,G	1.0	38.2				
H358	M,P	1.0	38.4				
H359	M,G	1.0	36.2				
H360	M,G	1.25	37.0				
H361	M—,G	1.25	37.1				
H369	M,G	.75	37.8				
H370	M+,G	3.0	35.8				
H377	M+,G	3.6	36.8				
H378	M+,G	2.2	36.1				
JB2	M+,G	1.0					

TABLE III. Body Temperatures: Elephant Seal. Taken immediately after death with a 5 cm. immersion thermometer, inserted into the thorax. Temperature read in °C. Blubber thickness on chest in inches. Condition: M=moulting, M—=pre-moult, M+= post-moult, L=lactating, P=poor, G=good.

an enlargement of the sub-epidermal capillaries, may well explain the need for terrestrial moulting. Such increased peripheral circulation would increase the rate of heat loss to the surrounding medium and make it impossible for the animal to maintain for long a high body temperature in water near freezing point. The rate of heat loss in air during the moult may then be of the same order as the normal heat loss in water when the peripheral circulation is reduced, so that the effect of low air temperatures and wind is enhanced. Since the efficiency of the layer of blubber as an insulator is reduced by the enlargement of peripheral vessels, thinning of this layer during fasting probably makes little difference to heat loss.

Thoracic temperatures were often taken in freshly killed animals but no significant difference between that of moulting and non-moulting animals was detected.

> For twenty-five moulting individuals of both sexes, the body temperature averaged 36.3°C (range 32.2°C to 38.4°C) and for twenty-one non-moulting individuals the average body temperature was 36.5°C (range 34.6°C to 38.2°C).

The greater range of body temperature in moulting animals may perhaps be significant. Unfortunately, Angot (1954) gives no details of the number of records which provided his average temperatures of 39.8°C. and 37.8°C. for moulting and non-moulting individuals.

7. *The Sand-throwing Habit*

An interesting pattern of behaviour which has received comments from most writers, is what may be termed the sand-throwing habit. Not only sand, but stones, snow or water may be flipped onto the back with the fore flippers, or the motions may be made, displacing only air. It is convenient to apply the term "sand-throwing" to all these activities.

The fore flippers are used alternately or in unison, being brought forward towards the neck and then swept in an arc slowly backwards, scooping up a quantity of sand on the palmar surface. When the flipper is at right angles to the body it is suddenly flipped backwards and upwards so that the sand is thrown obliquely upwards several feet into the air, most of it falling on the ground or on other seals. On certain days when flipping is frequent, the animals are often almost covered in sand and shingle. They scoop away the material on either side to such an extent that they sink into a trough which may be ten inches deep.

The incidence of sand-throwing varies from day to day in the rookeries and appears to be correlated with the humidity of the air. It is greatest when the humidity is low, such as on hot sunny days or on overcast days when a föhn wind is blowing from the mountains. (Under such conditions the relative humidity may be as low as 1.5 per cent. at South Georgia.) At the South Orkneys the annual range of average monthly relative humidity is 86–92 per cent, and the sand-throwing habit is uncommon; in South Georgia the range is 70–79 per cent (Antarctic Pilot, 1948) and sand-throwing is of common occurrence. Thus Matthew's (1929) suggestion, that "it is to keep the skin moist that the habit has been developed", is most probably correct. The skin is always wet in the water, for the hair encloses no layer of air and when it dries a feeling of irritation may be produced. The eyes react to the drying effect of the air by producing a copious lacrimal secretion.

However, other manifestations of the sand-throwing habit cannot be explained as a reaction to lowered humidity. Bulls often flip snow onto wounds on their backs immediately after a fight, and flipping motions are often carried out by seals on beaches where there are no loose stones or sand to be scooped up. Cows which have just given birth to a pup make rapid flipping motions, and the incidence of flipping is much higher in post-partum cows than in parturient cows or bulls. Females unwilling to copulate have often been seen to make flipping motions when pinned down by the bull.

Thus sand-throwing may either be a practical response to physical irritation (generally caused by low humidity of the air) or a displacement activity resulting from emotional conflict. It conforms to the general rule that displacement activities are more intensive than the same actions performed in a practical manner. That the motion is instinctive, is shown by the fact that pups a few days old and even near-term foetuses show it. It may perhaps be compared with a similar behaviour pattern in the grey seal (*Halichoerus grypus*), of which Davies (1949, p. 675) writes, "Immediately before and after parturition, cows will often dig in the shingle with their forepaws and in doing so will often scoop out quite a large depression". Similarly, the ice-sawing behaviour of the Weddell seal (*Leptonychotes weddelli*) may be either a practical action, or an aimless displacement activity under stress (personal observation).

8. *Vocalisation, Hearing and Vision*

A wide variety of snorts, sneezes, whistles, grunts, yawns and internal noises which are produced by the elephant seal appear to have no especial significance. Nearly all the socially significant sounds are concerned with territorial protests or threats, that is, except for certain sounds made by the post-partum cow and the young pup, and the elephant seal is less vocal in the non-breeding season than in the breeding season when social relations are more complex.

The pup emits a sharp, querulous yap or bark ("barf, warf, warf . . . barf") which becomes deeper with age. This sound is the response to most new situations and is not directed at any individual. The mother occasionally responds to it.

Cows at all times produce various throaty grunts and harsh barking sounds ("waaarf, waaarf . . .") and often give vent to harsh protracted growls of a few or many seconds duration. In the breeding season, and especially just after the birth of a pup, the cows make a high pitched querulous sound which is either an ululating falsetto or a long drawn out, wolf-like moan. It may be termed the "yodelling" vocalisation. In producing it the tip of the tongue is pressed against the back of the floor of the mouth and the body of the tongue is arched upwards so that it almost fills the back of the mouth. Often the cow apparently struggles for a few seconds to produce the "yodel", but no sound comes except for the forcible exhalation of air. This sound was never heard before the birth of the pup. It is sometimes heard during the process of birth, but more usually is produced in response to the first bark of the new-born pup (see p. 62). It may be used for calling the pup when separated, as Matthews (1929) states, but is singularly ineffective. Its use is more general, not necessarily directed, and it is produced in response to a situation rather than an individual.

In the bull the equivalent of the harsh growl of the female is an expiratory roar of very low pitch, which sounds like a small two-stroke engine. It is made by drawing the tongue backwards towards the throat and then expiring forcibly, as in gargling, which results in a harsh rattling sound of great power. The proboscis is erected and, in the older bulls, hangs down so that the nostrils open immediately in front of the mouth. The expiration, as evidenced by condensation of the breath, is by the mouth (not by the nostrils) and particles of mucus from the back of the mouth are forcibly thrown out. Small stones thrown to the back of the throat during the production of this type of vocalisation are returned to the observer by the forceful expiration. The diverticula of the proboscis may act as resonating chambers to amplify the sound-waves but the "snoring" vocalisation described by Bartholomew (1952) is not produced by the southern species. The proboscis of the smaller subordinate males is not sufficiently developed to give much resonance, which may account for their higher-pitched, shallower roar. The bubbling roar of a large bull carries for several miles and is either long drawn out or in a series of short bursts. It may be used as a threat to a specific individual, as a generalised response to a situation, or merely spontaneously.

On one occasion, a subordinate bull was driven backwards by the author into the harem of the "Scarred" bull. When it was suddenly confronted with the latter it emitted a protracted high-pitched, tremulous, whinny and fled. The "Scarred" bull ignored the intruder, so it may perhaps be interpreted as a submissive vocalisation. It was never heard on any other occasion, probably because, owing to the complicated heirarchical system (p. 78), subordinate bulls low in the dominance heirarchy never find themselves in such a position.

The external opening of the auditory meatus in the elephant seal is only about 2 mm. in diameter, and masked by hairs; there is no pinna. In common with all other phocids the internal ear is characterised by very large auditory ossicles (Doran, 1878) suggesting that they are considerably modified for aquatic use. The otariids, which are less aquatically specialised, have small ossicles. Consequently, the elephant seal only pays attention to relatively loud noises and, in view of the anatomy of the ear it may be assumed that the sense of hearing is not very acute on land. Certainly, in the course of the field work, it was found that man-made noises had little effect, but this may be interpreted either as meaning that the animals did not hear them, or more likely, heard but did not react.

The structure of the eyes suggests either nocturnal, or deep water feeding habits, but blind individuals are able to feed adequately (Sorensen 1950, p. 26). On land the aquatically adapted eye is kept moist by a copious secretion from the lacrimal glands (see p. 20), which has led writers to credit seals with human

emotions. As the refractive index of air is so different from that of water, it is not surprising that on land their sight is poor; they appear to be unable to discriminate between stationary objects, even at moderate distances, but when alert are quick to detect a moving object.

9. *Mock-fighting*

When they leave the mother, young pups of both sexes congregate at the top of the South Georgia beaches to the landward of the harems. Here they lie in large "pods", often for several weeks, before entering the sea. They pass their time sleeping, and in play. The play takes the form of short battles between pairs of pups, in which they attempt to rear up on the hind part of the body and, facing their opponent, lunge forwards and downwards at his face or chest. Although they make frantic and renewed attempts to execute these actions, on account of their obesity they rarely succeed at first. Later, as they lose weight and become more active, their technique improves. Although they may strike with open mouths no damage is ever suffered in these conflicts, which may be called "mock-fights".

Later in the summer both the pups of the year, of both sexes, and the younger bulls up to three years old, engage in mock-fighting. The sparring bouts take place either on the beaches or in shallow water, and, occasionally, in deep water. Again no serious damage is ever inflicted, but numerous small scars on the necks and shoulders are the results of cuts received during this form of play. Emphasising the essentially playful nature of these fights, the combatants which often take hold of their opponent's neck, face or flipper, always do so in a gentle way. The mock-fights between members of one pair often continue sporadically throughout the day, and occasionally at night. There can be little doubt that they serve to accustom the bulls to the tactics of fighting, so that when the time comes they are able to engage in the more serious battles which are such a conspicuous feature of the breeding rookeries.

The females do not indulge in mock-fighting after the establishment of nutritional independence, because they lead an almost exclusively pelagic existence for the first three years of life.

10. *Interspecific Relations*

Other Pinnipeds

In the three localities visited by the author in the course of the present study, the elephant seal comes into contact with the following species:

Southern fur seal (*Arctocephalus australis*, Zimmermann).
Southern sea-lion (*Otaria byronia* De Blainville)
Weddell seal (*Leptonychotes weddelli* Gill)
Crabeater seal (*Lobodon carcinophaga* Gray)
Leopard seal (*Hydrurga leptonyx* De Blainville)

Of these only the southern sea-lion is present in any great numbers in the same areas and the moulting rookeries are occasionally mixed. In the course of a very short voyage around the Falkland Islands, in February 1952, no extended observations were possible. It was noted that sea-lions and elephant seals are usually indifferent to each other's presence, but that there may be minor conflicts between them. Bartholomew (1952) as a result of more detailed observation came to a similar conclusion about the interspecific relations of *Mirounga angustirostris* and *Zalophus californianus*.

At South Georgia in 1951 a very young fur seal (*A. australis*) was seen on a beach in Wilson Harbour among a herd of elephant seals. When approached, it moved off making a hissing sound and the large elephant seals nearby drew away from it. The nature of the terrain chosen by the fur seals for their breeding rookeries renders it unlikely that they come into conflict with elephant seals on many occasions.

The Weddell seal has large breeding aggregations around the coasts of Signy Island totalling about 500 females, but their pupping season begins over a month earlier than that of the elephants, so that by the time the elephant seals haul out, the young Weddells have begun to take to the water. On the large expanse of fast ice the chances of contact are again slight, for the Weddell seal chooses areas of broken ice for the purpose of pupping and retires from any elephant seal harems which may form in her vicinity. This preference ensures that the two species rarely meet. However, when the fast ice breaks up, some Weddell pups come ashore and may become involved with groups of elephant seals on the beaches as, for example, at Drying Point on November 1st, 1948, when the weighing procedure had caused considerable confusion amongst the elephant seals and three Weddell pups were lying out on the beach. Although they were at the centre of the commotion, the huge bull elephant seals charging headlong after a rival invariably deviated

from their course when confronted by a relatively tiny, hissing Weddell pup. The large bulls ignored the bigger and more vociferous pups of their own species which are occasionally seriously injured by being squashed and rolled under the bull in the course of one of his mad rushes.

Another example was observed at Larsen Harbour, South Georgia, where there is a small colony of Weddell seals. On September 7th, 1951, on landing with a party of sealers from the *Albatros* to kill elephant seals, nineteen Weddells with two pups were seen. Most of them were lying on the snow-covered area behind the beach, though some were on the beach itself. A few elephant seals were lying nearby, the nearest only a few yards from a gravid female Weddell seal, and each species ignored the other.

The crabeater seal, being an animal of the drifting pack-ice rarely comes into contact with the elephant seal, but on two occasions when young crabeaters were seen in the vicinity of groups of elephant seal the indifference was mutual.

The leopard seal, especially at South Georgia, often hauls out on the same beaches as the elephant seal but the two are usually separated by an interval of several yards. In the water the leopard seal has often been seen to attack young elephant seals and the sealers assert that it occasionally attacks adult elephant seals (Laws, 1953b, p. 57).

There is no record of contact between the elephant seal and the rare Ross seal (*Ommatophoca rossi*).

Birds

A number of species are partly dependent on the elephant seal for food. Of these, the sheathbill (*Chionis alba*) and the giant petrel (*Macronectes giganteus*) are the most important.

The sheathbill is found at all times in the vicinity of the elephant seal rookeries, although during the nesting period of the penguins it is concentrated in the vicinity of their rookeries. It is exceedingly persistent in harrying the bulky and cumbrous elephant seals and stalks around them, pecking at their scars and sometimes even alighting on their backs. This attention drives the elephant seals frantic with irritation and precipitates many squabbles between adjacent animals. In the breeding rookeries the birds peck at the placenta, the umbilical cord and even the pup itself (see p. 63).

The cowardly giant petrels have none of the engaging jauntiness of the sheathbills and although in aggregate they probably cause less trouble in the harems and are practically absent from the moulting pods, they go further than the sheathbills in their attacks. They are concerned mainly with the placenta but will eat dead seal pups and even weak pups that have been deserted by their mothers. One occasionally comes upon the carcase of an elephant seal pup which is quite hollow—just skin and bones—and with only one small hole in the skin, either in the axilla or at the umbilicus. Obscene groups of giant petrels crowd round such a carcase, each with the head and neck soaked in blood from their victim. They are the vultures of the Antarctic.

The Dominican gull (*Larus dominicanus*) and the skua (*Catharacta skua*) also parasitise the elephant seal though to a much lesser extent (pp. 62–63).

In their relations with other birds the elephant seals are as a rule very peaceful. The penguins, in travelling between their nesting rookeries and the sea, often have to walk in and out among the elephant seals, and sometimes even over them. Only on one occasion out of many hundreds did an elephant seal react aggressively to a penguin. This was a moulting male at Gourlay Peninsula, which took hold of the flipper of a Ringed penguin (*Pygoscelis antarctica*) with its teeth, shook the bird violently from side to side several times and flung it several yards away. The penguin picked itself up and hurried into the sea, apparently none the worse for the experience.

Man

As Bartholomew (1952, p. 384) has emphasised, "From the standpoint of the elephant seal, by far the most important interspecific relation is that between it and man, because on this relationship the very survival of the species depends". He gives instances of the extreme indifference of the northern elephant seal to man, and many of his statements about *angustirostris* apply with equal truth to the southern species, although at all times the southern elephant seal is not so incredibly indifferent to man as is the northern species. No one who has worked on the southern elephant seal could endorse for that species his comment that in the course of his field work "it has been repeatedly possible to approach isolated sleeping individuals, examine them carefully at close range, take their pulse, remove ectoparasites from them, insert thermometers into their rectums, and even sit or lie on them—all without awakening them,

or at least without evoking an overt response" (p. 386). Rarely will the southern species permit such familiarity.

The males of *leonina* in the breeding season show much more belligerence towards man than does *angustirostris*. They will rarely allow him to approach to within three or four feet. In fact, they usually show an aggressive response when one is within twenty feet. His statement that the females with pups are more aggressive is nevertheless true for *leonina* also. They roar and threaten vigorously when a man is in sight within thirty to fifty yards of them, but do not advance more than a few yards towards him.

Judging by the history of commercial sealing, elephant seals show little evidence of disturbance by man. It is possible to kill five or six male elephant seals which are lying in close proximity without their evidencing any alarm as their companions are killed one by one. This is, however, exceptional. Females are always more nervous than males and usually withdraw.

In the non-breeding season males and females retreat slowly and individually according to temperament. Usually, only about one-third have withdrawn by the time a man reaches the group, another third retreat when he is within a few yards of them and the remainder usually stubbornly hold their ground until touched. Occasionally an animal will attack a man in the non-breeding season but when this occurs the animal concerned is usually a male.

In spite of their seeming indifference to man, there are signs that the elephant seals at South Georgia are now retreating to haunts less accessible to man (see p. 9). In the breeding season of 1951 it was observed that the large open sandy beaches (such as Fortuna Bay and the Bay of Isles) were thinly populated, whereas the more rocky and inaccessible coves (such as those in King Haakon Bay) were relatively heavily populated. This tendency was remarked upon as long ago as 1936 in the Magistrate's Annual Report. It was stated that there was no sign of a diminution of numbers but that it was obvious that the animals were vacating the large open beaches for the smaller and often inaccessible ones. The Magistrate commented upon this again in 1939 and 1943. It is shown elsewhere (p. 9) that over 95 per cent of the elephant seals hauling out at the South Orkney Islands are visitors, probably from South Georgia. The increase in the numbers of this summer population appears to have been first noticed in the early nineteen-thirties, when the group was visited by the R.R.S. *Discovery II.*

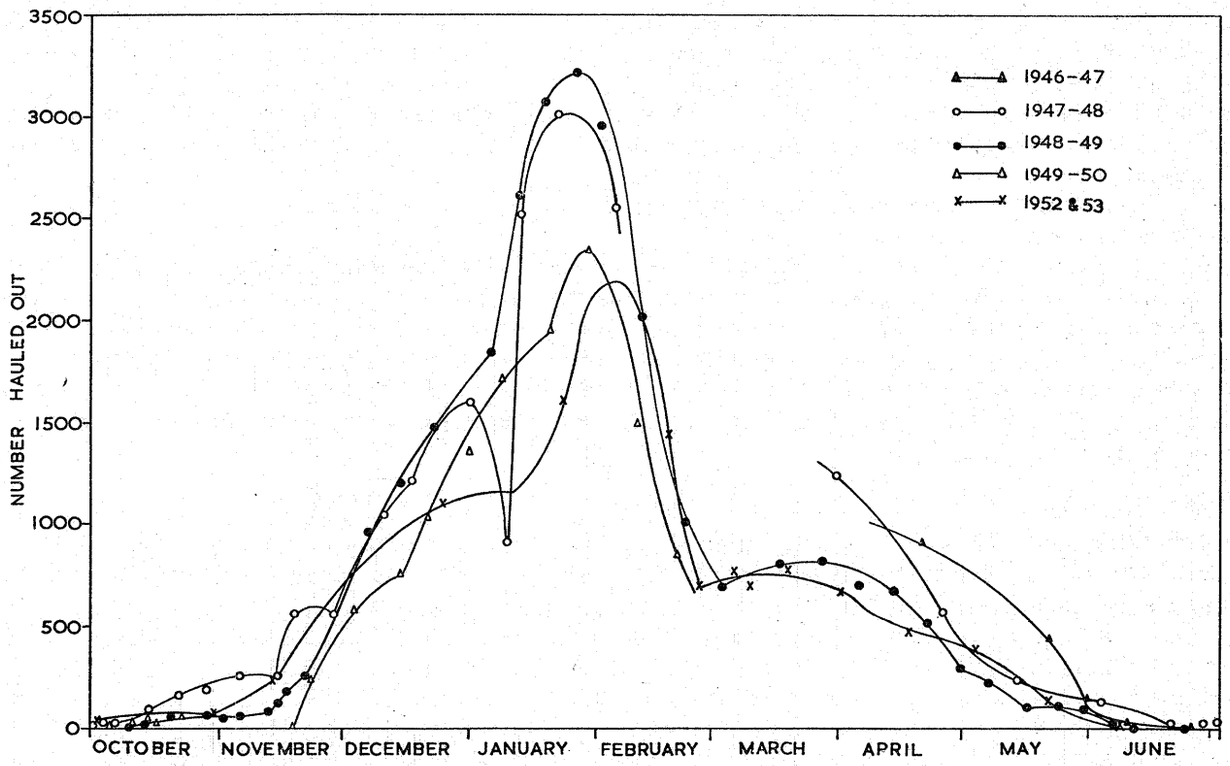


FIGURE 7. Variations in the total numbers of elephant seals ashore in Borge Bay throughout the years 1947 to 1950.

At Signy Island the very obvious decline in numbers ashore in the vicinity of the F.I.D.S. base (from Drying Point to Berntsen Point) was attributed to the killing of specimens in this area. Man was absent from the island from 1928 to 1947, and the decline in the number ashore during more recent seasons (Figure 7) suggests that human interference may have been responsible.

B. Population Dynamics

At Signy Island and South Georgia classified counts of the elephant seal population on shore were made at approximately weekly intervals (see p. 6).The data are set out in Tables IV to XIII and in Figures 7 and 8. The counts made in Borge Bay, Signy Island, cover the periods March 31st, 1948, to February 20th, 1950, and from February 25th, 1952, to March 3rd, 1953. (The data for the second period were provided by A. W. Mansfield.) In addition, counts of the total numbers hauled out in Borge Bay were made by Robin (1948) covering the period April 21st, 1947, to February 4th, 1948. In other words, data relating to four seasons are available.

At South Georgia, the counts made on "Hestesletten" relate to the period March 30th, to November 17th, 1951. At Dartmouth Point, daily counts are available from September 19th to October 11th, 1951, and counts at Maiviken cover the period September 24th to October 30th, 1951. Thus, at South Georgia, only the breeding season is adequately documented.

It is unfortunate that, although the fluctuations in numbers throughout the year should be known in detail for Signy Island, at South Georgia almost four summer months are unrepresented by the counts. Moreover, the breeding population at Signy Island is extremely small in proportion to the summer population there, so that direct comparison of the population curves for the two localities is not possible. Nevertheless, it is thought that the temporal relations of the haul-out of the different classes of seals at Signy Island, if not their numerical proportions, are comparable with those obtaining at South Georgia.

Figure 7 shows the total numbers of elephant seals of both sexes ashore at different times in Borge Bay from 1947 to 1953. They are ashore in varying numbers from the end of September until the end of June, and the same applies to South Georgia ("Hestesletten" Figure 8). The annual peak in numbers ashore at Borge Bay occurs at the end of January, but there is a considerable variation in the size of this maximum and in the configuration of the population curves for the different years. The maximum number of elephant seals hauled out at Signy Island during the breeding season is only about 5 per cent of the maximum summer population of Borge Bay and less than 3.5 per cent of the summer population of the entire island. Figures for the highest count in different years are: 3018 on January 21st, 1948; 3252 on January 26th, 1949; 2358 on January 29th, 1950; and 1629 on January 24th, 1953. The curves drawn in Figure 7 show that these figures are probably lower than the actual maxima. It may be that human interference since 1947 has been responsible for the decline in numbers over the period.

Date	Males			Females			Total
	I	II & III	IV	I	II	III	
March 31	441	195	177	0	74	168	1055
April 26	313	138	15	0	0	0	466
May 14	161	68	8	0	3	0	240
June 3	94	24	0	0	0	0	118
June 20	3	12	0	0	0	0	15
July 3	8	18	0	0	0	0	26
July 7	0	0	0	0	0	0	0

Table IV. Classified elephant seal counts in the Borge Bay area, Autumn 1948.

Date	Males			Females			Pups	Total Excluding pups
	I	II & III	IV	I	II	III		
Sept. 26	1	0	0	0	0	0	0	1
Oct. 6	1	0	0	0	6	0	0	7
Oct. 8	2	0	0	4	7	0	2	13
Oct. 12	4	0	0	12	10	0	14	26
Oct. 14	8	0	0	13	11	0	22	32
Oct. 20	13	0	0	14	27	0	30	54
Oct. 28	8	3	0	14	39	0	44	64
Nov. 4	15	8	4	12	11	0	13	50
Nov. 5	16	12	5	16	11	0	13	60
Nov. 12	13	21	38	13	2	0	11	87
Nov. 14	17	32	64	12	0	1	12	126
Nov. 16	18	69	89	12	0	0	21	188
Nov. 21	10	68	152	11	4	6	16	267
Dec. 6	2	265	687	1	1	0	6	962
Dec. 14	8	934	250	0	0	9	13	1214
Dec. 22	41	1393	21	1	18	7	5	1486
Jan. 5	4	1476	1	0	370	2	—	1852
Jan. 12	11	996	8	3	1596	15	—	2629
Jan. 19	5	811	1	0	2266	6	—	3089
Jan. 26	34	417	6	604	2180	11	—	3252
Feb. 2	24	335	1	512	2073	18	—	2963
Feb. 11	30	157	7	844	1081	6	1	2026
Feb. 22	60	127	23	572	312	28	18	1128
March 3	146	259	65	136	80	6	—	692
March 17	197	346	196	4	32	34	—	809
March 27	247	341	161	0	24	52	—	825
April 5	248	407	13	1	22	20	—	711
April 14	240	394	42	0	7	3	—	686
April 22	120	357	20	0	4	11	—	512
April 30	74	217	11	0	0	6	—	308
May 7	39	180	8	0	1	0	—	228
May 16	13	86	0	0	0	0	—	99
May 24	1	109	0	0	0	0	—	110
May 30	1	95	0	0	0	0	—	96
June 6	0	33	0	0	0	0	—	33

Table V. Classified elephant seal counts in the Borge Bay area, 1948–1949.

Date	Males				Females			Pups	Total Excluding pups
	I	II	III	IV	I	II	III		
Sept. 24	2	0	0	0	0	0	0	0	2
Sept. 25	5	0	0	0	2	0	0	0	7
Sept. 29	6	0	0	0	2	0	0	0	8
Oct. 1	7	1	0	0	3	0	0	1	11
Oct. 5	8	2	0	0	2	0	0	2	12
Oct. 10	12	0	0	0	6	7	0	4	25
Oct. 12	10	0	1	0	6	12	0	8	39
Oct. 15	10	0	0	0	6	25	0	16	41
Oct. 25	15	1	0	0	43		0	19	59
Oct. 28	17	1	0	0	46		0	21+	64
Nov. 18	4	10		0	1		0	—	15
Nov. 22	6	212		19	1	3	0	—	242
Dec. 3	1	552		25	2	2	0	1	581
Dec. 14	0	689		11	34	30	0	2	763
Dec. 21	0	865		64	22	89	0	3	1040
Dec. 31	0	756		44	51	514	5	1	1370
Jan. 8	0	634		11	188	887	0	2	1720
Jan. 20	0	156		3	450	1339	10	—	1958
Jan. 29	0	174		4	929	1250	1	—	2358
Feb. 10	0	138		4	620	735	6	—	1503
Feb. 20	2	23	30	111	313	355	29	—	865

TABLE VI. Classified counts of elephant seal in the Borge Bay area, 1949–1950.

Date	Males				Females			Pups	Total excluding pups
	I	II	III	IV	I	II	III		
Feb. 25	4	37	22	64	86	399	79	—	692
March 6	42	42	71	331	60	116	104	—	775
March 20	111	27	43	451	8	49	69	—	778
April 1	129	27	109	302	11	28	53	—	679
April 18	105	97	132	127	1	6	3	—	474
May 3	80	121	124	48	2	8	8	—	391
May 14	—	—	—	—	—	—	—	—	281
May 21	37	35	44	5	0	1	0	—	122
June 6	6	6	1	0	0	0	0	—	13
June 16	12	6	1	0	0	0	0	—	19
June 25	1	0	0	0	0	0	0	—	1

TABLE VII. Classified counts of elephant seal in the Borge Bay area, Autumn 1952. (Made by A. W. Mansfield.)

Date	Males				Females			Pups	Total excluding pups
	I	II	III	IV	I	II	III		
Sept. 25	4	2	0	0	1	0	0	0	7
Sept. 27	4	1	0	0	3	0	0	0	8
Sept. 29	5	1	4	0	4	0	1	2	15
Oct. 6	5	1	1	0	8	0	1	4	16
Oct. 28	6	4	0	0	22	24	1	44	57
Nov. 14	12	25	111	41	5	6	6	41	206
Dec. 24	74	389	433	147	45	5	6	44	703
Jan. 24	51	62	42	10	690	674	100	—	1629
Feb. 18	20	28	16	66	316	965	25	—	1436
March 3	57	22	95	333	19	54	116	—	696

TABLE VIII. Classified counts of elephant seal in the Borge Bay area, 1952–1953. (Made by A. W. Mansfield.)

Date	Males				Females			Pups	Total excluding pups
	I	II	III	IV	I	II	III		
March 30	0	0	10	2	0	0	0	8	12
April 6	6	6	12	10	0	3	5	4	42
April 13	3	1	12	15	0	0	6	3	37
April 24	3	2	20	12	2	2	4	22	45
May 1	0	1	18	16	2	2	3	16	42
May 8	0	1	30	2	0	2	1	7	36
May 15	0	1	73	12	0	3	3	14	92
May 26	0	0	19	10	3	0	0	19	32
June 20	0	1	9	2	0	0	0	14	12
June 26	0	4	2	1	0	1	1	14	9

TABLE IX. Classified counts of elephant seal in the "Hestesletten" area, Cumberland Bay, South Georgia, Autumn 1951.

Date	Bulls		Cows			Pups	No. of harems	Cows per harem	Cows per bull
	Classes I and II	Class III	Scattered	In harems	Total				
Sept. 20	4	0	3	0	3	0	0	—	0.75
Sept. 26	17	2	3	49	52	0	3	15	3.0
Oct. 2	30	2	6	113	119	14	5	23	3.9
Oct. 8	33	3	32	287	319	100	10	29	9.6
Oct. 15	40	0	9	612	621	310	20	31	15.5
Oct. 22	39	2	14	924	938	—	20	46	24.0
Oct. 31	41	6	2	843	845	—	20	42	20.6
Nov. 9	41	3	5	535	540	949	17	31	13.1
Nov. 13	40	4	—	—	300	1113	16	19	7.5
Nov. 17	41	23	—	—	192	1023	16	12	4.8

TABLE X. Analysis of the "Hestesletten" elephant seal rookery, September to November 1951. (Includes all coastline shown in Figure 20.)

Date	Bulls		Cows			Pups	No. of harems	Cows per harem	Cows per bull
	Classes I and II	Class III	Scattered	In harems	Total				
Sept. 19	55	2	22	11	33	0	2	5.5	0.6
Sept. 20	50	0	23	16	39	1	2	8.0	0.7
Sept. 21	57	1	22	36	58	4	4	9.0	1.0
Sept. 22	46	0	19	52	71	7	5	10.4	1.6
Sept. 23	56	0	16	83	99	7	6	13.8	1.8
Sept. 24	69	0	21	97	118	12	8	12.1	1.7
Sept. 25	57	0	26	134	160	14	11	12.2	2.8
Sept. 26	62	0	30	180	210	19	13	13.8	3.4
Sept. 27	64	0	33	219	252	31	10	21.9	3.8
Sept. 28	58	2	25	267	292	41	15	17.8	5.0
Sept. 29	70	3	29	356	385	50	16	22.2	5.5
Sept. 30	59	0	14	433	447	73	19	22.8	7.5
Oct. 1	74	0	30	461	491	106	20	23.0	6.6
Oct. 2	77	2	57	516	573	132	20	25.8	7.4
Oct. 3	70	2	50	563	613	158	23	24.4	8.7
Oct. 4	63	4	43	678	721	201	27	25.1	11.4
Oct. 5	60	4	40	720	760	249	30	24.0	12.7
Oct. 6	61	7	29	738	767	254	34	21.7	12.5
Oct. 7	63	8	63	868	931	360	45	19.3	14.7
Oct. 8	82	8	37	844	981	391	48	19.6	11.9
Oct. 10	84	3	36	1011	1047	552	54	18.7	12.4
Oct. 11	84	10	40	1026	1066	621	52	19.7	12.7

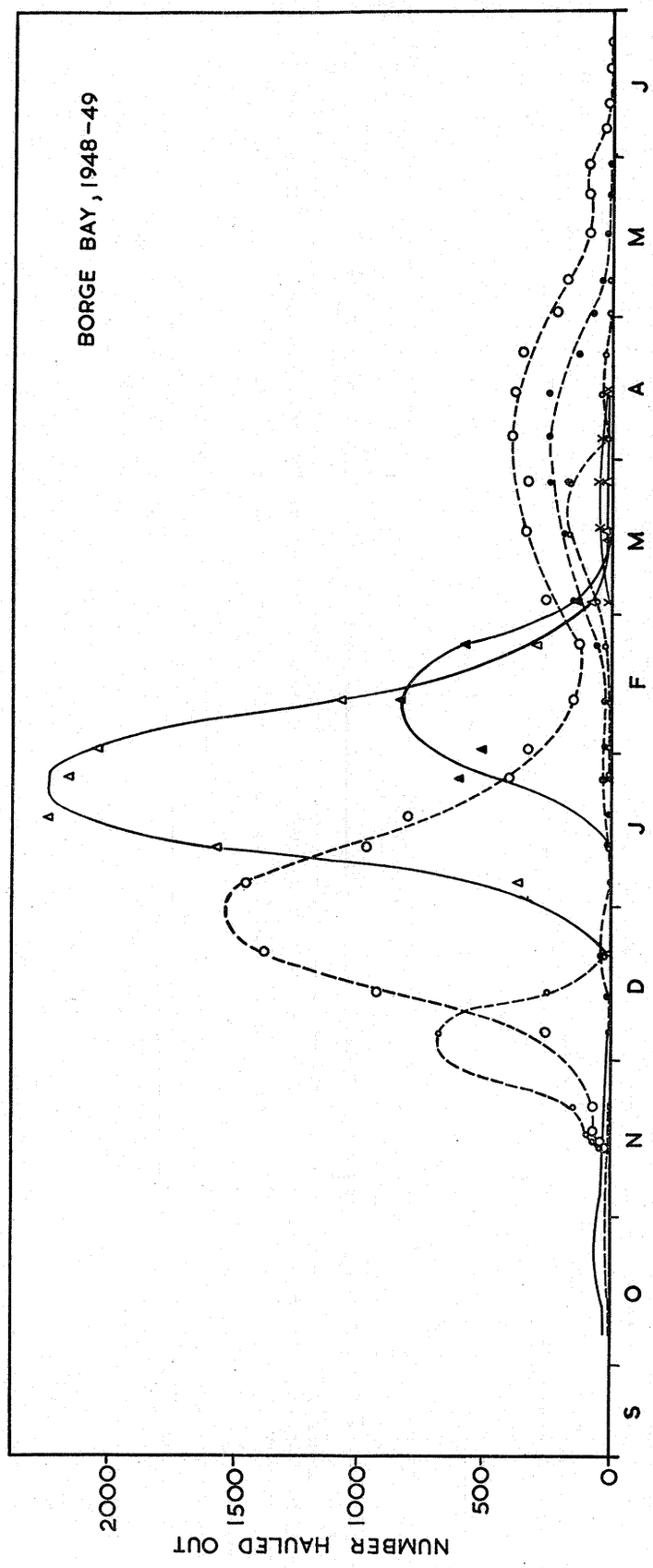
TABLE XI. Analysis of the Dartmouth Point elephant seal rookery, September to November 1951. (Includes all coastline shown in Figure 19.)

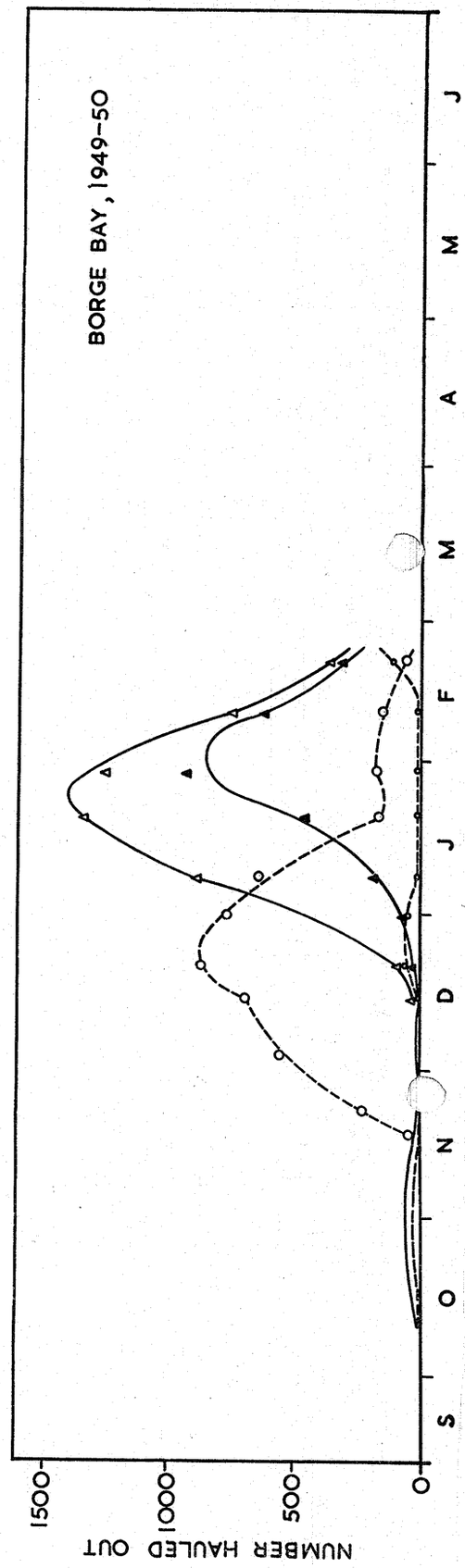
Date	Bulls		Cows			Pups	No. of harems	Cows per harem	Cows per bull
	Classes I and II	Class III	Scattered	In harems	Total				
Sept. 24	1	0	0	0	0	0	0	0	0
Oct. 6	4	0	1	16	17	2	3	5.3	4.2
Oct. 11	3	1	0	57	57	9	4	14.2	19.0
Oct. 24	7	0	12	184	196	122	6	30.7	28.0
Oct. 30	4	2	22	185	207	182	4	46.2	51.7

TABLE XII. Analysis of elephant seal population of the east shore of Maiviken, September to October 1951.

October				November			
Date	Bulls	Cows	Pups	Date	Bulls	Cows	Pups
2	2	4	0	1	14	30?	28
3	1	5	0	3	8	21	27?
4	2	5	0	4	11	19?	28?
5	4	5	1	5	7	17	28?
6	2	7	1	6	10	19	25?
7	2	12	1	7	17	15	28?
8	1	13	1	8	14	12	29
9	4	14	3	10	34	10	28
10	4	17	6	14	45	9	20
11	6	18	10	16	67	7	29
12	4	19	12	17	—	5	29
13	4	18?	12	18	100	4	29
14	4	20	14	21	92	2	28?
15	5	22	17	23	117	1	27
16	6	21?	17?	24	—	1	28
17	8	15?	17?	26	136	1	26
18	12	22	20	28	155	0	?
19	13	23	21				
20	12	23	19?				
21	10	25	21				
22	8	25	19?				
23	10	25	21				
24	9	24	21				
25	9	29	24				
26	15	28	25				
27	11	30?	22?				
28	12	28	26				
29	8	30?	22?				
31	13	29	28				

TABLE XIII. Analysis of elephant seal population in the vicinity of Drying Point, Signy Island, October to November 1947. (From counts by members of the F.I.D.S. (Robin, 1948).)


BORGE BAY, 1948–49
NUMBER HAULED OUT
0
500
1000
1500
2000
S
O
N
D
J
F
M
A
M
J


BORGE BAY, 1949–50
NUMBER HAULED OUT
0
500
1000
1500
S
O
N
D
J
F
M
A
M
J

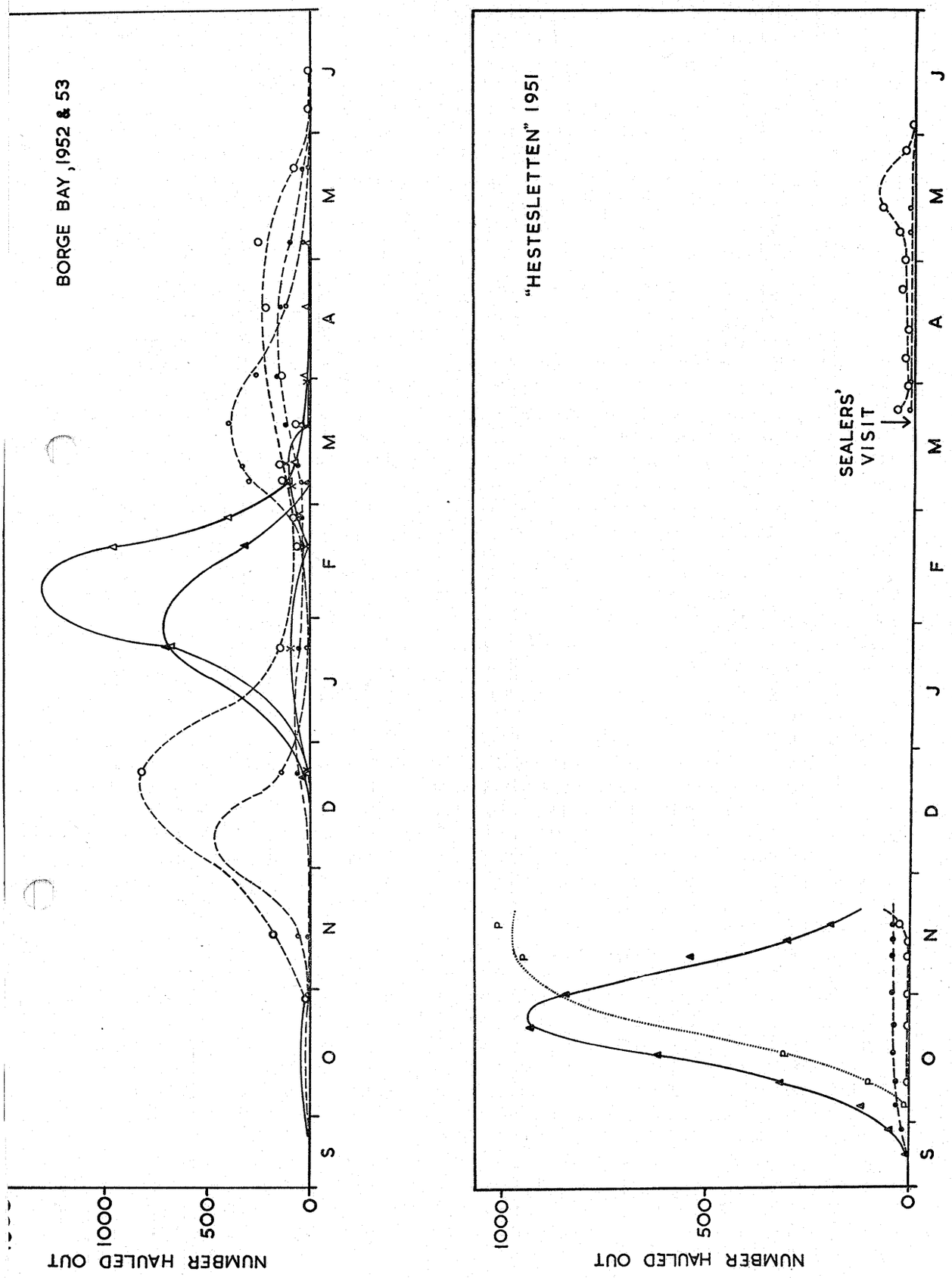


FIGURE 8. Variations in the numbers of the different classes of elephant seals ashore at Borge Bay in the seasons 1948–49, 1949–50, 1952 and 1953 and at "Hestesletten" in 1951. Male: Class I = ●; Classes II & III = O; Class IV = o. Female: Class I = ▲; Class II = Δ; Class III = X. At "Hestesletten" breeding females = ▲; breeding males = ●; pups = P.

In plotting the curves showing the presence on land of the different classes (Figure 8), it was found convenient to group Classes II and III males together. Thus, the male groups represented by the separate curves are: I, over seven years; II and III, three to seven years; IV, one to three years. The corresponding female groups are: I, over eight years; II, three to eight years; III, mainly yearlings. In order to simplify the diagrams for the Signy Island population, the parts of the curves representing the breeding season are modified to show the total numbers of each sex and pups are not shown. This means that the curve for males hauled out during the breeding season comprises Classes I and II. The numbers observed on shore at this time are so small that they are unimportant. Also, human error in some counts, owing to the large numbers involved and the difficulty of distinguishing old Class II females from young Class I cows, resulted in the partial overlapping of these groups. Small adjustments have been made so as to give consistent curves, but the extent of the changes necessary is less than 2 per cent, which suggests that the counts themselves are reasonably accurate.

The importance of these graphs is that they give an analysis of the curves representing the total numbers hauled out (see Figure 7). It is shown that the hauling out period of the two sexes and of the various age groups are represented by a series of maxima. Thus, at Signy Island in the 1948–49 season there was a peak of small males on December 6th, followed by Classes II and III males which reached their maximum numbers on January 1st. A very large peak number of Class II females coincides with the total maximum number for all classes about January 25th, and the greatest number of Class I females was present on February 11th. There was a second influx of small and medium sized males (Classes II to IV) in March and April and the majority of the large males (Class I) were hauled out in these two months, but there is no sharply defined peak of numbers in the last three curves.

In the analysis for the 1949–50 season a similar order obtains but, probably as a result of the late break-up of the fast ice in that season, there was no great influx of small males.

In the 1952–53 season (this is a composite diagram from two sets of data, Tables VII and VIII) the counts are less frequent and are the work of a different observer. Even so, a similar order of haul-out seems to prevail. The peak number of large females (Class I) precedes that for Class II females and there is a relatively large number of small (Class IV) males ashore in March. The difficulties of distinguishing between the two older classes of females are considerable and it seems likely that the variation in the form of the population curves in the 1952–53 season is the result of different observational methods. Although there are fewer counts covering the critical period in that season, the maximum total of about 2200 apparently occurred about a week later than in the previous seasons.

Yearling and two-year-old females are represented in all seasons by very small numbers, but since the younger age groups should be numerically greater than the older, their absence from land is attributed to a difference in habits. Either the majority of young animals do not come ashore at all, or they come ashore for very short periods. In both these instances they would be under-represented in the censuses. A third possibility is that the proportion of the younger age classes visiting the South Orkneys from South Georgia is small compared with the proportions of the older groups which do so. However, the latter possibility can probably be eliminated because there are no reports of large numbers of small seals at South Georgia, except for the pups of the year which are easily distinguishable, and very few were seen either by the writer or by Mansfield in the 1950–51 season.

At South Georgia, counts of the non-breeding population are available only from the end of March to the end of June. The figures for "Hestesletten", which are given both in tabular form and graphically (Table IX and Figure 8), were influenced by a visit of a sealing crew from Compaña Argentina de Pesca, on March 23rd, 1951, so that they are not truly comparable with the Borge Bay results. In spite of this complication, the date of the final departure from land at the end of June is in agreement with the departure of the rearguard from Signy Island, and the rapid increases in the numbers of Classes II and III males hauled out on "Hestesletten", after the main breeding season in the latter half of November 1951, is also comparable with the numerical increase of the same age groups at Borge Bay (Figure 8). The absence of large (Class I) males during this period is accounted for by the sealing operations.

If the summer population of the South Orkneys does come from the beaches of South Georgia, then it is likely that the time relations of the haul-out of the various classes are much the same in both groups of islands although the presence of fast ice or pack-ice will lead to minor differences. In view of the correspondence of the haul-out in the two localities for which comparable data are available, the time relations will in future be considered identical, although the numerical proportions of the classes, especially of the

younger animals, may well be very different. These conclusions agree less well with those of Matthews (1929, p. 242) than with Sorensen's (1950, p. 21), neither of whom produce adequate qualitative or quantitative data for comparison. Angot (1954) gives qualitative and quantitative data but, as previously pointed out, his application of statistical methods to samples of estimated lengths can hardly be justified. His general conclusion that the classes of females of increasing average lengths haul out at successively later dates agrees broadly with those put forward above, but his estimates of the length of time spent ashore are at variance with the writer's figures (Figure 8). The same comments apply to his information about the males.

As the data are more complete for the breeding populations they can be directly compared (p. 47).

C. Factors Influencing The Summer Haul-Out

1. *The Moult*

The most obvious factor responsible for the summer haul-out of elephant seals is the apparent necessity for moulting on land. The catastrophic nature of the process in the elephant seal has been described (p. 18), and although it is open to doubt whether the moult is the primary factor leading to hauling out, it is unlikely that the animals would spend lengthy periods on land, during which they are unable to feed, without such a cause.

By making use of Figure 8, and assuming that the behaviour of individuals of the same age group is alike, the average length of time spent ashore by each group can be calculated. Thus, at Signy Island Class I males spend fifty-six days ashore, Class II and III males forty days, and Class IV are ashore for twenty-four days. Females of Classes I and II are ashore for thirty-two days and Class III females for about twenty-four days. Second year females of Class III appear to spend very little time ashore at Signy Island, but may haul out at South Georgia during the period for which data are lacking. It is probable that the duration of the shedding process is only a few days shorter than the time spent ashore. The only definite evidence relates to the cows, which move further inland and do not leave until the moult is complete (p. 43), and to a few marked individuals.

Therefore, the length of time taken over the moult process seems to increase with age, or more properly with size, since Classes I and II females, which differ greatly in age though not in size, are ashore for the same length of time. Can it be connected with an increase in surface area? Or is it related to differing habits during the moult process?

The second peak of males of Classes II, III and IV is not solely connected with moulting, for only a small proportion of these animals are seen to be moulting at this time and they do not usually remain on shore for long periods in the autumn as they do earlier in the season. The pattern of the tooth rings, which are thought to be a reflection of fasting periods lends support to these conclusions (Laws, 1953, Figure 3). The last formed dentine rings in each season's growth of male teeth are a series of thin concentric layers, suggesting an interrupted fast (see p. 17).

2. *Sea Ice*

In Figure 9, the curve representing total numbers of elephant seals hauled out in Borge Bay at different dates during the 1948–49 season can be compared with the sea ice conditions throughout the season. It shows that during the months when the majority of elephant seals are hauled out, the pack-ice is almost entirely absent from the South Orkney Islands.

It has already been shown (p. 25) that the date on which the maximum numbers of elephant seals are hauled out at Signy Island varies only slightly from year to year, but that the shape of the curves of total numbers varies greatly. In the seasons 1948–49 and 1949–50 the curves of total numbers are smooth, but in the 1947–48 curve there are two discontinuities (Figure 7). Comparing the latter with the curves representing the haul-out of the various classes (Figure 8), the first discontinuity probably represents an interval between the peak numbers of small and medium sized males. On this assumption the peak number of small males occurs twelve days earlier than in 1948–49, and is related to the early break-up of the fast ice in 1947. The next discontinuity corresponds to the decline after the peak numbers of Classes II and III males (Figure 8) and the date of this maximum is the same as in 1948–49. The maximum number ashore at any one time corresponds with the peak of Class II females. Both of these discontinuities in the 1947–48 curve are correlated with the presence of thick pack-ice around the island and in Borge Bay at these times. They can best be

explained by assuming that the pack-ice discourages incoming seals from hauling out at the usual time, while not deterring those individuals which have finished moulting (and have therefore fasted for several weeks) from departing to the feeding grounds. Consequently, as seals are leaving the beaches and not being replaced by incoming animals, as is usual, the population ashore declines in numbers. It does not increase again until the ice moves out. Thus, from a nadir of 912 ashore on January 9th, 1948, the numbers increased in five days to 2530 ashore on January 14th. The increment is almost entirely composed of females, rising from about 200 females ashore on January 9th, to "at least 1700" on January 14th (F.I.D.S. Base "H", Seal Log, 1948). This means that cow elephant seals were hauling out at the rate of at least 300 a day on this short stretch of coast. The remarkable size of these figures will be realised when it is stated that at "Hestesletten", South Georgia, at the time when the breeding population was increasing most rapidly, the number of cows hauling out each day was about forty (Table X). Clearly, at Signy Island in 1947 cow elephant seals were prevented from coming ashore in the week prior to January 9th, and when they were able to haul out they did so in correspondingly greater numbers than usual.

These discontinuities in the 1947 curve incidentally serve to confirm the accuracy of the classification of the counts.

Although the presence of pack-ice seems to influence the summer haul-out, it probably has little effect after March because very few seals are hauling out then and the second peak in total numbers has been passed. If ice affects only the arrival of the animals and not their departure, then it should not affect the numbers at this time; nor does it.

As mentioned earlier, the actual freezing of the sea delays the departure of elephant seals, but although the date of final departure varies from year to year according to the ice conditions, it is fixed within narrow limits and approximately coincides with the date of the departure from South Georgia.

At South Georgia the pack-ice is rarely present in summer and then only in small amounts, but brash-ice produced by the calving glaciers appears to have a similar though more restricted effect on the numbers hauled out on certain beaches. The population curves for a given area in South Georgia would probably vary only slightly from year to year if it were not for commercial sealing operations.

3. *Climatic Conditions*

As might be expected, the numbers ashore at each beach throughout the season show considerable fluctuation and correlation with air temperature, solar radiation, sea ice, dew point, relative humidity, hours of snowfall and wind force and direction has been attempted. The effects of tidal variations at Signy Island may be ignored when comparing the different beaches because all counts were carried out at low tide when it was possible to cross the bar at the mouth of Elephant Flats.

In Figure 9, therefore, the curve of total numbers of elephant seals hauled out in Borge Bay during the 1948–49 season is compared with smoothed curves representing wind force, solar radiation, minimum daily air temperatures (at Berntsen Point) and the extent of sea ice. There is reason to believe, however, that the winds recorded at the F.I.D.S. base on Berntsen Point, Signy Island, are not truly representative of the winds experienced over the whole Borge Bay area and the records must therefore be used with caution. Conditions at Drying Point are probably the most closely comparable to those at the base.

The months during which the greatest numbers are hauled out are December, January and February, when nearly all the animals ashore are moulting. During these three months there was open water to the horizon and the air temperature fell below 25°F. only at the beginning of December and for one short period in early February (at a time of low solar radiation and southerly winds up to twenty-five knots from the pack-ice). The daily solar maximum temperatures (black bulb *in vacuo*) remained above 40°F. throughout this period, and as seals are "black bodies" (see below) the effect of the diurnal range of temperature is considerable. During November the strong winds were southerly and easterly and low air temperatures were recorded, but at the end of November föhn winds from Coronation Island raised the minimum air temperature to 28°F. All subsequent minimum daily air temperatures above 30°F. were associated with northerly winds. The low air temperatures experienced in March, April and May were all associated with strong southerly and easterly winds, and from early April onwards, with thick pack-ice. Thus, the maximum numbers were hauled out when air temperatures and solar radiation were high and when the winds tended to be less strong. The final departure is associated with maximum sun temperatures of less than 20°F.

The periodic counts were classified geographically according to the beaches or hauling out grounds frequented (p. 6) and the results of these counts for individual areas have been set out in Figures 10 to 13.

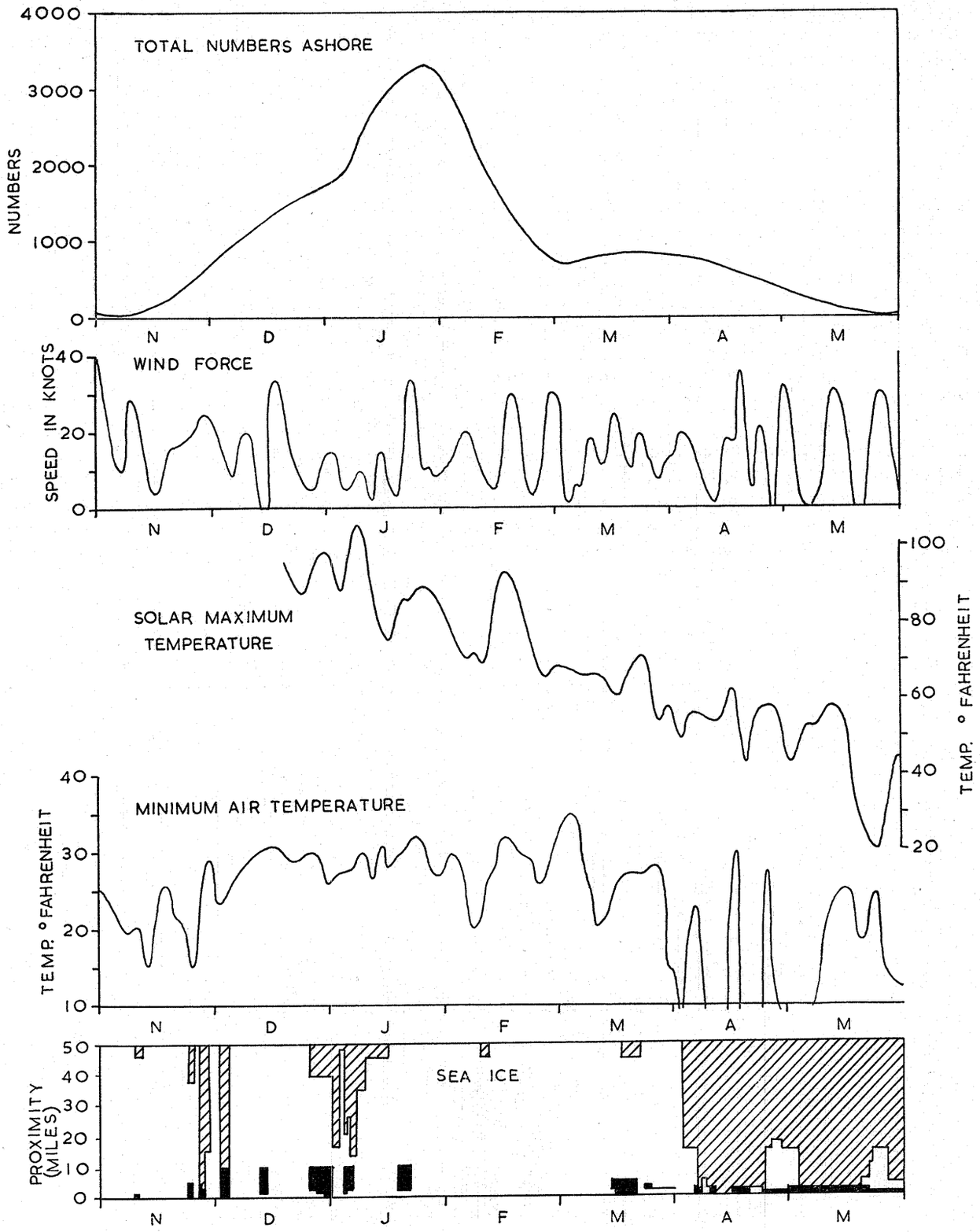


FIGURE 9. Graph showing the total numbers of elephant seals ashore in the Borge Bay area from November 1948 to May 1949, with wind force, solar maximum temperatures, minimum air temperatures, and sea ice conditions set out for comparison.

Although the numerical fluctuations of the entire population have been drawn as smooth curves, these local counts are shown as step diagrams in view of the smaller numbers involved and the discontinuity of the observations.

The *areas* with the most marked fluctuations in numbers were Mirounga Flats, and in the vicinity of Balin Point and Drying Point, all of which are relatively exposed coastal areas. In other parts, such as Elephant Flats (Areas C 1–4), the north-west corner of Mirounga Flats and The Wallows north-west of Balin Point (Area F3), all of which are further from the sea and have larger aggregations of seals, fluctuations in the numbers are less marked.

The curve of the total number hauled out *on all beaches* does not show any marked fluctuations except for those caused by the arrival and departure of the various age classes (see p. 34). Although no counts were made at night, there is circumstantial evidence (p. 17) showing that during the moult cows do not leave the shore; cows are found in "pods" long distances from the sea and marked or distinctive animals are seen in the same position for long periods. If weather conditions do influence the moulting elephant seals, then movements must be local and limited to a selection of habitats on land. The actual temperature of the air can have little effect on these movements since it will be fairly uniform over this small area.

The effect of solar radiation and other climatic factors have now to be considered. The seal is an efficient "black body" and so absorbs a high proportion of the radiant heat from the sun. Records of maximum solar temperatures are available for a period of nine months at Signy Island (discontinued because the instrument was broken). The highest recorded was 140°F. in the first week in January, and from December to March temperatures of about 100°F. were common, but in June and July the solar maximum rose above 50°F. on only one occasion. Thus, on windless days or in sheltered localities solar radiation may considerably modify the effect of air temperature, and absorption of heat may be greater than heat loss. Conversely, on days when the solar radiation is low and more especially at night, the seal will lose heat by "black body" radiation as well as by conduction.

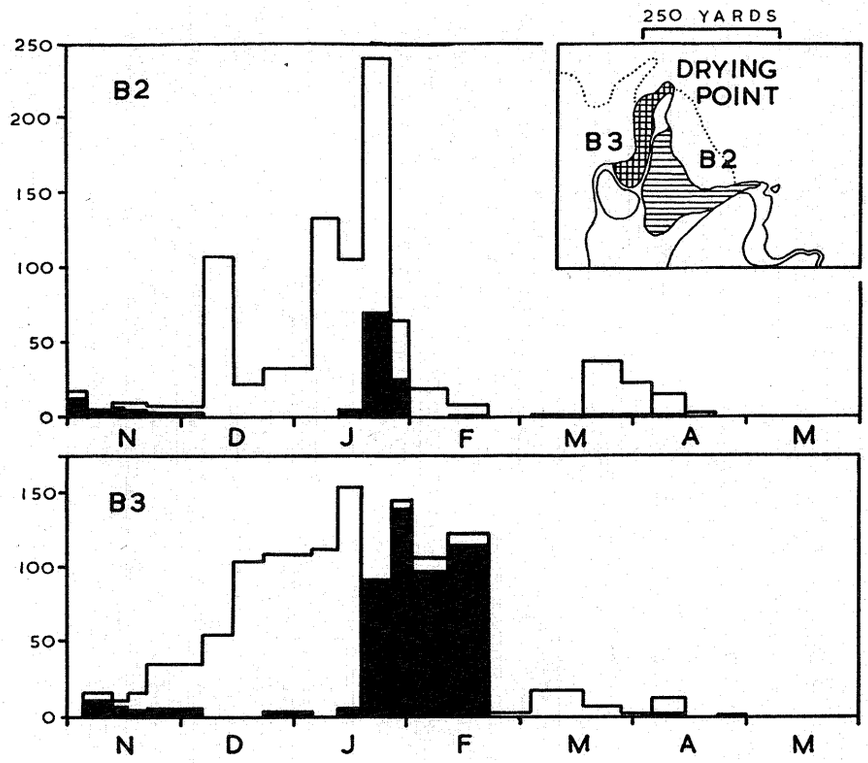


FIGURE 10. Numbers of elephant seals hauled out on beaches B2 and B3, Drying Point, Signy Island, from November 1948 to May 1949. Males—white; females—black. The areas frequented by the animals are shaded.

At South Georgia, in the breeding season, on calm sunny days when solar radiation must have been high (no figures are available) cow elephant seals moved to the water's edge and bulls lay in the water offshore and prevented the cows from leaving. The sand-throwing habit, which is thought to be an indication of unrest or discomfort (see p. 20) was then very prominent.

Observations on two beaches, B2 and B3 at Drying Point (Figure 10), indicated that the numbers of moulting elephant seals ashore on each beach were controlled by wind force and direction. For example, on those occasions during November and December when strong easterly winds were blowing on the exposed beach B2, the numbers ashore there remained low. At these times B3 was sheltered by a low (15 ft.) rocky ridge and its population showed a marked increase. In February, some areas exposed to southerly winds (C3, C4, F3, G*) show a marked decline in numbers. Weather conditions are probably not entirely responsible but they may accelerate the normal departure to sea at this time of year.

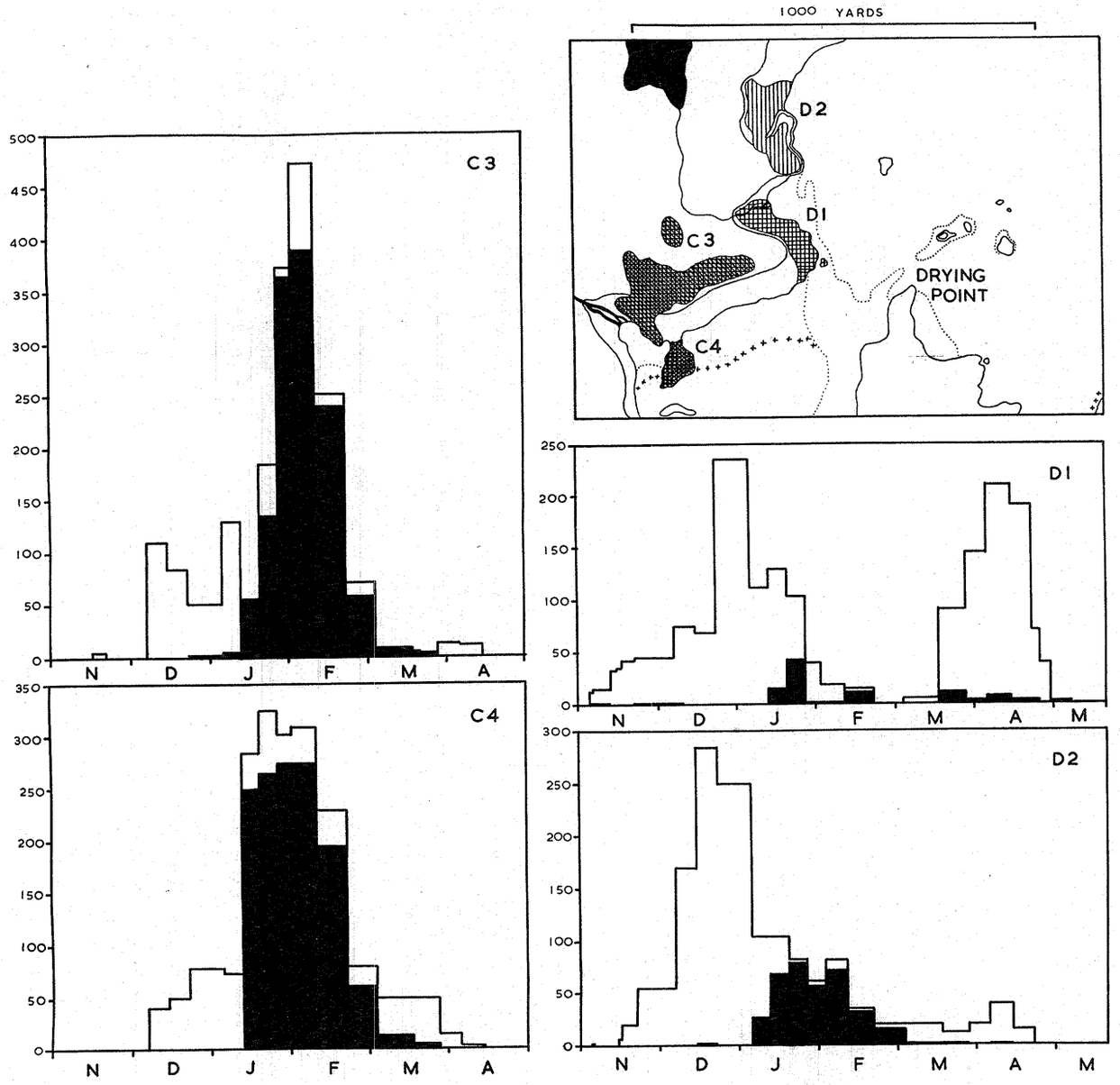


FIGURE 11. Numbers of elephant seals hauled out in areas C3, C4, D1 and D2, Borge Bay, Signy Island, from November 1948 to May 1949. Males—white; females—black. The areas frequented by the animals are shaded.

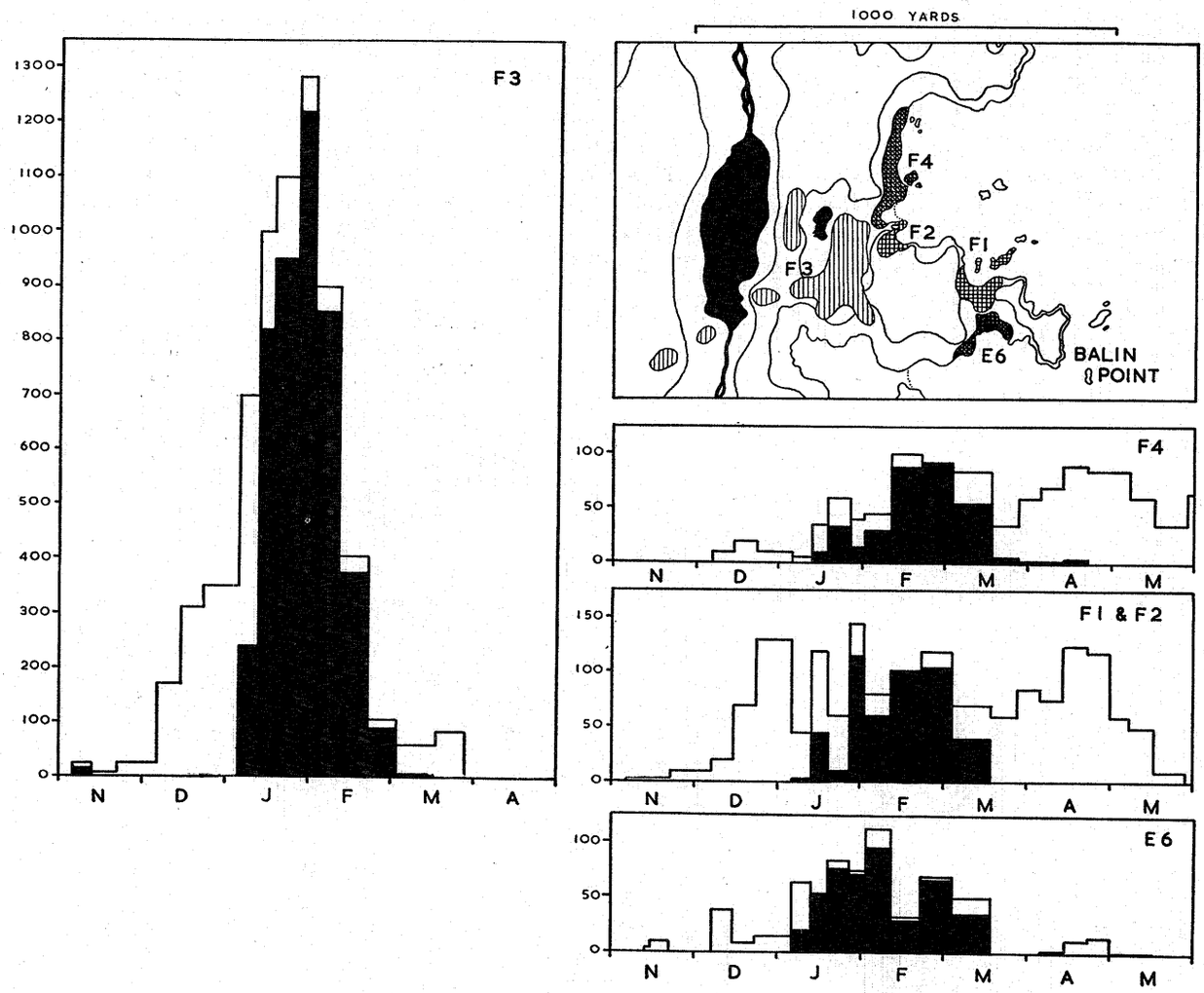


FIGURE 12. Numbers of elephant seals hauled out on beaches E6, F1, F2, F3 and F4, from November 1948 to May 1949. Males—white; females—black. The areas frequented by the animals are shaded.

It appears that moulting elephant seals avoid the water even though they are subject to a considerable diurnal range of temperature, but wind increases the rate of heat loss and causes them to seek sheltered positions. These conclusions were reached by observing the movements of marked animals and animals with distinctive scars, etc. The habitat preference of the females is discussed later.

In the autumn, most of the animals ashore have completed the moult and we get a different picture. At that time the temperature range is greater and it is apparent that the total number hauled out varies. Frequent counts were made in March 1948 on very sheltered beaches in Paal Harbour (the bay south of Borge Bay) where the effect of wind is negligible. At this time the great majority of the seals ashore there were males, and in Figure 14 these counts have been plotted together with the noon air temperatures over the period. There is an apparent correlation between the numbers ashore and the air temperature, so that an increase in the number of seals hauled out generally follows a period of high air temperatures and a decline in numbers is associated with low air temperatures. The extent of the variations in numbers is related to the range of temperature. There is also indirect evidence for diurnal rhythms of activity in the autumn. At night there is no solar radiation and air temperatures are lowest and it has been observed that there is a great increase in activity then. From the numerous tracks on the snow and sea ice it is believed that many animals take to the water at night during this season, though Sapin Jaloustre (1952) concludes from his

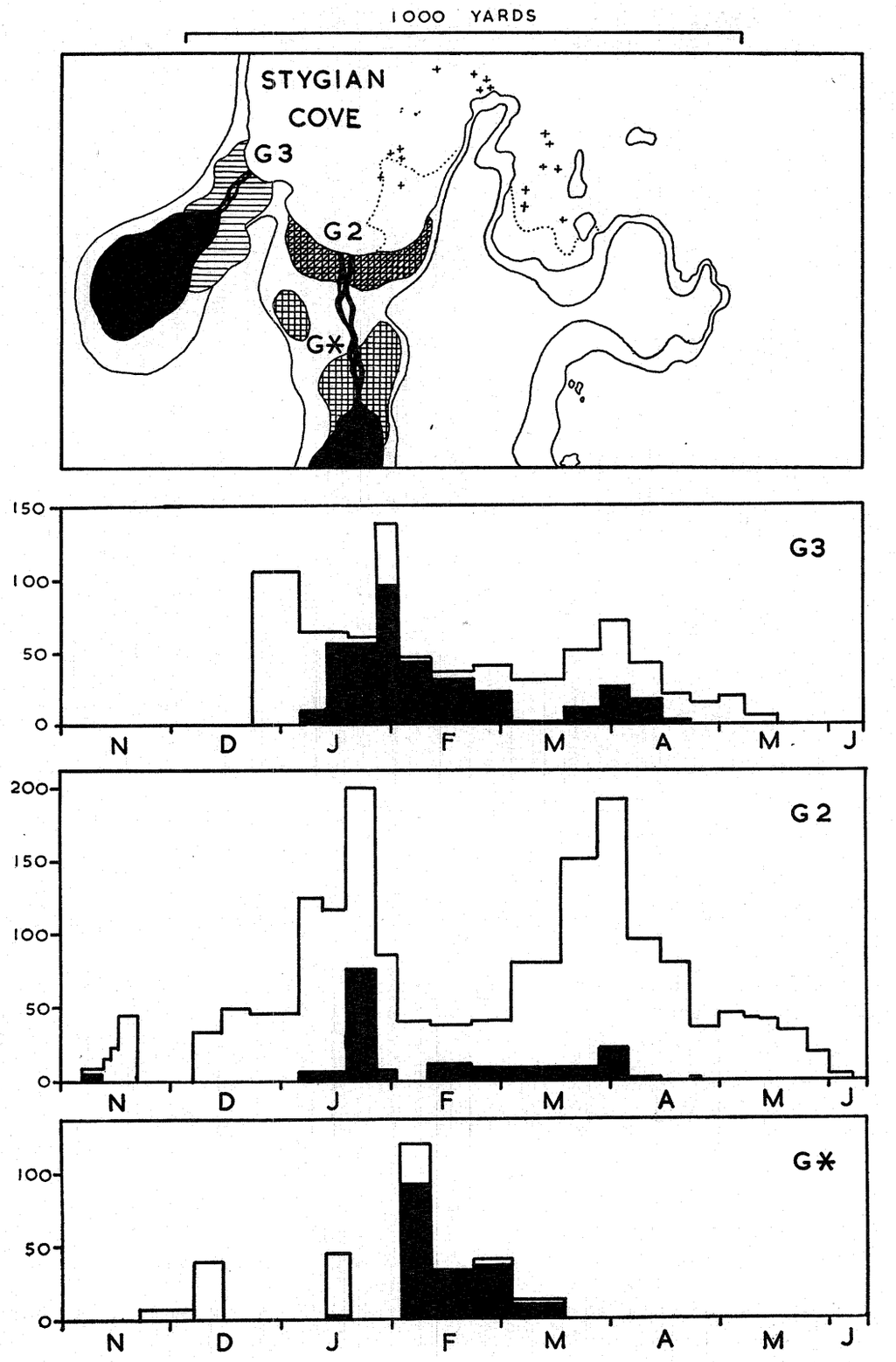


FIGURE 13. Numbers of elephant seals hauled out in areas G*, G2 and G3, from November 1948 to May 1949. Males—white; females—black. The areas frequented by the animals are shaded.

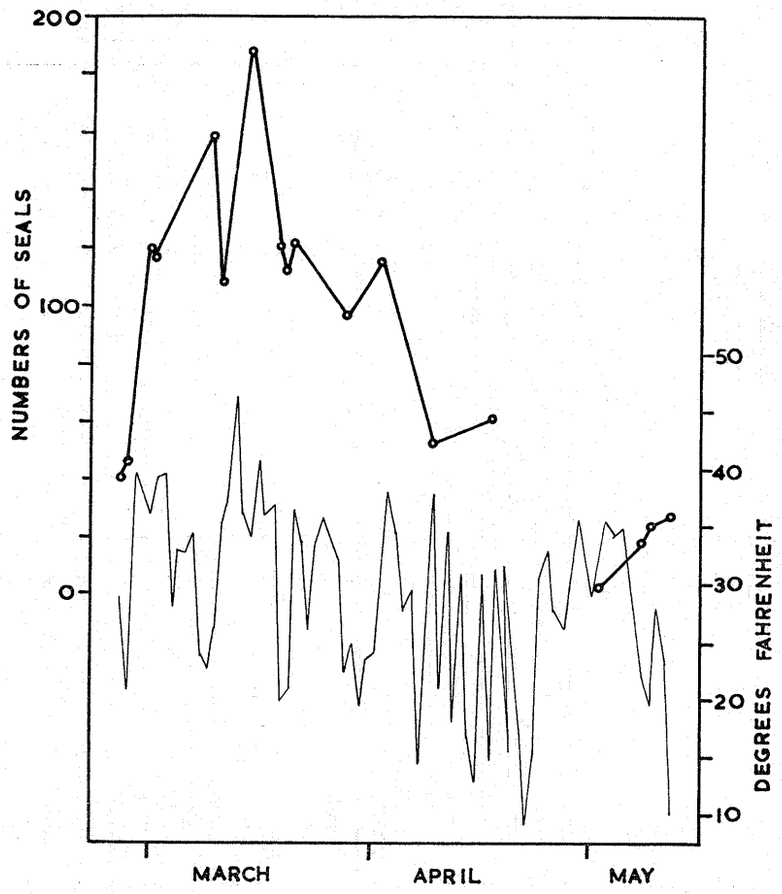


FIGURE 14. Numbers of elephant seals ashore in Paal Harbour, Signy Island, from March to May 1948, compared with daily noon air temperatures over the same period.

work in Terre Adélie that even in the worst weather heat loss is always greater in the water than in the air just above the sea ice.

> He has shown that a body in air at –10°C. (14°F.) in a wind of 60 km./hr. takes twice as long to lose a given number of calories as one in water at –2°C. (28°F.). He also shows that the rate of heat loss of a body in water at –2°C. is exceeded in air at –20°C. only during a "blizzard très dense" of force about 130 km./hr. He further states that in the Weddell seal's microclimate (up to half a metre above the ice) the wind is only a half or a third as strong as the wind recorded by an anemometer on a tower.

However, the seal is not an inanimate body and the heat loss may be compensated by the increased heat production during swimming, though it is unlikely that (as Parry (1949) has suggested for whales) the elephant seal is compelled to swim in order to maintain its body temperature. In any case, the range of sea temperatures in these latitudes is small and for an aquatic mammal like the seal, which is adapted to its environment, these temperatures must be regarded as normal. The sub-epidermal capillaries can probably be controlled and the rate of heat loss varied according to the external physical and internal physiological conditions.

It has already been observed (p. 20) that the rate of heat loss in air is increased during the moult so that the effect of low air temperatures and wind is greatly enhanced at that time.

Another more indefinite effect of rigorous weather conditions is probably to lessen the general "comfort" of the individual. In the summer, the animals cannot take to the water to escape from discomfort (in the form of wind, low temperatures or low humidity acting upon the soft parts, especially the eyes) because the physiology of the moult process results in increased heat loss to water at about 0°C. In the spring they

may enter the sea to escape from discomfort but the cows are then prevented from doing so by the bulls. In the autumn, the males which have completed the moult but are still lying out on land, can and do enter the water to escape from unpleasant weather conditions (Figure 14), but during the moult and even afterwards the gregarious habits and thigmotactic behaviour may serve to minimise the effects of rigorous environment. The refraction effects in the air over a "pod" of elephant seals or the steam arising from them (Plate IIIa) are indications of the effectiveness of this behaviour.

General air T.° (°C.)	Temperature at various distances from animal (°C.)							Body T.°	Direction of measurement
	12 in.	6 in.	3 in.	1 in.	½ in.	¼ in.	skin		
–1.2	—	—	–0.3	+0.2	—	+7.0	+10.8	c.36.0	vertical
+1.2	—	—	—	—	—	—	+14.5	c.36.0	lateral
–6.2	–5.9	–5.8	–5.4	–5.0	–4.7	–0.9	+9.5	c.36.0	lateral

TABLE XIV. Temperature observations on three male elephant seals in still air, April 1949.

With a view to obtaining some quantitive estimate of the temperature gradients involved, *very approximate* measurements were made on three medium sized male elephant seals at Signy Island (Table XIV). A thin-bulbed whirling psychrometer thermometer was fastened to a five foot rod held well away from the observer's body. It will be seen that the temperature of the skin surface is of the order of 12°C. to 16°C. higher than the general air temperature. Thus, animals in the centre of a close-packed "pod" will experience temperatures several degrees above that of the air in general. On cold days in April, May and June, it was noted that aggregations of elephant seals were more closely packed than on warm sunny days. Stonehouse (1953) attributes a similar function to the "huddling" behaviour of emperor penguins (*Aptenodytes forsteri*) though this takes place under much more rigorous environment conditions.

D. DIFFERENCES IN THE BEHAVIOUR OF THE SEXES

The proportions of the sexes hauled out in the non-breeding season in the Borge Bay area have been calculated, allowance being made for the variation in the length of the moult process (p. 35). Of the total summer population 53.4 per cent were females and 46.6 per cent were males. The cows are represented by 11.2 per cent Class I, 41.2 per cent Class II, and one per cent Class III, and the bulls by 3.8 per cent Class I, 32.8 per cent Classes II and III, and 10 per cent Class IV. Thus, the sexes are more or less equally represented with Class II females predominating and Classes II and III males next in importance. The small proportion of Class III females as compared with Class IV males probably reflects a difference in the habits of the sexes during the first two years of life.

There is a marked difference in the distribution of the adults of the two sexes over the area. The females show a definite preference for inland moulting grounds, where muddy wallows are formed, or for broken ground which is well sheltered. The young males show a preference for coastal areas (pebble and sandy beaches) or for irregular ground near the sea. The older males, on the other hand, are almost entirely confined to the beaches and are rarely seen far inland.

In Figure 1 each circle represents the position of a "pod" of predominantly male or female composition, averaging fifty individuals. They were calculated by reference to the percentage composition of the total of all counts made in 1948–49 for each census area, and agree well with general field observations. This distribution map illustrates the fact stated above that the males are concentrated on the beaches whereas the females spend their time ashore inland, usually above the 25 foot contour line. One small "pod" of females was situated on the slopes of Jane Peak at a height of appromixately 200 feet above sea level.

The results of the counts of numbers in several hauling out areas or beaches are shown in Figures 10 to 13. They show that at the beginning of the moulting season the younger males tend to haul out in representative numbers in Areas C3, C4, F3 and E (Mirounga Flats), which are the sites of the very large aggregations of cows during January and February. The younger males haul out in greater numbers than the cows on Beaches B2, D1, D2, and G2, and the sexes are present in approximately equal numbers during the first part of the season in Areas B3, F1, and F2, and G3. In March and April males predominate in all areas, but the major concentrations are at D1, F1, and F2, F4, and G2.

There can be no question of competition for space because, even in the most congested area (F3) there is room for an aggregation twice as large, and by the time the peak of males occurs later in the season, almost all the females have departed. Moreover, the counts for Beaches D1 and D2 show two peaks in the numbers of males and negligible numbers of females.

Nor can the climatic factors be of primary importance because the younger males show a habitat preference in December when the weather conditions are most equable. The snow cover in the area is so reduced by December, when solar radiation is at a maximum, that it cannot be regarded as a deterrent to the seals, but it possibly influences their distribution from April onwards.

It has already been observed (p. 17) that the cows rarely enter the water when moulting but that the coastal distribution of the males is related to the fact that their haul-out is accompanied only by a partial fast, so that the unequal distribution of the sexes when ashore at Signy Island is truly the result of different habits. The cows haul out solely to moult and while doing so (usually at some distance inland) they fast completely, returning to sea immediately the moult process is completed. The males also come ashore to moult but may re-enter the sea for short feeding excursions (probably at night), so that they undergo only a partial fast. This explains their more prosperous condition. Some males also remain ashore after the moult is completed, and the population ashore in April and May consists largely of bulls which have completed the moult. It is difficult to suggest an explanation for the post-moult haul-out because it would seem that at this time the animals should have no ties with the land.

The proportion of the males ashore which had completed the moult, was greatest in March, April and May. Of twelve individuals killed during this period, nine had completed the moult, while in December and January, of the twenty-three males which were killed, five had not begun to moult, thirteen were in process of shedding the hair, and five had completed the moult. General field observations confirm that these proportions of pre-moult, moulting, and post-moult animals in the sample killed, approximate to the proportions in the whole population of males.

The stages of the shedding process shown by the females killed are not representative of the total population because seals were usually killed on the beaches (to reduce the distance large specimens had to be carried) and most of the females killed were approaching or leaving the larger aggregations inland.

Thus, when the numbers of females were at their peak (on January 26th, 1949) 2795 were hauled out in the Borge Bay area. Of these more than three-quarters (2132) were aggregated in Areas C3 and C4, F3 and E4 (the inlet south of F3; Plate VIIc). All of these areas are some distance from the sea and all the cows present in them were moulting. Of these cows killed on the beaches in January and February (their moulting period) two had not begun to moult, twelve were moulting and five had already assumed the new coat. It is known that the two pre-moulting individuals were newly hauled out and still wet from the sea and the five which had completed the moult may have been returning to the sea from inland wallows.

The rapid decline in numbers of females in the inland moulting grounds is not accompanied by a sustained increase in numbers on the beaches, which suggests that cows leaving the wallows when their moult is completed return without delay to the sea (Figures 10 to 13). In view of their emaciated condition this is not surprising.

The conclusions summarised above apply only to the Signy Island herd. There are, as yet, few observations which provide evidence for or against such segregation of the sexes during the moult in other localities. At South Georgia and the Falkland Islands both sexes are found in wallows which form in the tussac grass behind the beaches.

These wallows are much deeper than on Signy Island owing to the difference in climate and to the greater depth of soil. In the Falkland Islands where there is a more luxuriant flora and greater depth of soil than at South Georgia, some of these wallows are very deep. On Arch Island, Falkland Sound, there were some large holes, ". . . about fifteen yards long and ten yards wide, filled with a black oily mud. . . . There were in this

pool several carcases of dead seals, and more in an adjacent pool. The seal . . . by its struggles brought up more carcases and odd bones to the surface. It swam very slowly and the mud was obviously very thick. In the surrounding tussac there were several smaller mud pits." (Field notes, March 4th, 1951). These big wallows were sounded and found to be over seven feet deep at the edge. They originate from small wallows —shallow depressions in the ground between tussac clumps which fill up with rain water and are churned deeper by the movements of the elephant seals and sea-lions (*Otaria byronia*). At South Georgia, the climate is more rigorous and the soil shallow so that really deep wallows are exceptional.

Sorensen (1950, Figure 10) illustrates a mud wallow at Campbell Island. He states that the great majority of elephant seals ashore there are submature males (in contrast to the Signy Island herd) and does not refer to any differences in the habitat of the sexes during the moult. More recently Angot (1954) says that at Kerguelen the segregation of the sexes is complete, each of the various pods being composed of individuals of one of the sexes. His conclusion that the females do not wander so far from the sea is also at variance with the observations put forward in the present paper.

In spite of their preferences for different localities during the moult, the behaviour of the sexes at this time is essentially the same. Both sexes are then much more gregarious than during the breeding season and thigmotactic behaviour is very pronounced. They spend the time lying motionless, apparently asleep, but there are frequent struggles for position. The open mouthed threat (Bartholomew, 1952) is used and no damage inflicted.

IV. REPRODUCTIVE BEHAVIOUR

A. Introduction

AT Signy Island the breeding population is very small and scattered. Breeding was first reported there in 1947 and all the harems were then situated on land (Robin, 1948), but in the years 1948 and 1949 pupping took place on the fast ice and the majority of the harems formed there. It was possible, by marking a large number of seals, to keep individuals under observation from day to day and so to follow their movements and behaviour.

The rookeries at South Georgia were much larger and the animals more closely packed, so that the emphasis of the work was on average rather than on individual behaviour, although some marked individuals were kept under observation over a period of several weeks.

Since the studies of reproductive behaviour were extensive and were the result of observations in two localities which were spread over three seasons, the method of presentation raises difficulties. It will be most convenient to give an introductory account of the breeding colonies at Signy Island and South Georgia and the general behaviour relating to the establishment of the harems. Later, detailed descriptions of the reproductive behaviour of both sexes will be given, illustrated where necessary by extracts from the field notes.

1. *The Occurrence of Twins*

Usually, the elephant seal produces a single pup and twins are rare, but occasionally two pups are seen suckling from one cow: "In Harem 6a I saw two pups suckling from one cow at the same time—one above the other." (Field notes, October 10th, 1951.) However, this is not sufficient evidence for twinning. The occurrence of conjoin twins has already been described and figured in a previous paper (Laws, 1953b, p. 29, Figure 13), and a similar monster was seen and photographed at South Georgia in the 1930–31 season by members of "Discovery Investigations", but only one instance of twin live births has come to the notice of the writer. On October 15th, 1951, "I marked a cow R/n which had just pupped. There were two pups nearby, a male and a female, with umbilical cords still attached to the fresh placentae. No other cows were near so these were probably twins." (Field notes.)

No females represented in the material collected had more than one embryo, but the ovaries of H352, collected on January 1st, each have a *corpus luteum* (average diameters 18.5 mm. and 14.0 mm.) which present the same histological appearance. No embryos were seen, but at this time of year the blastocyst is unattached and difficult to find. These *corpora lutea* may therefore signify potential twins.

Angot (1954) records two pairs of twins, one fraternal, and the other a male and a female. One of the latter pair was slightly abnormal and died, but the two males grew normally although the mother was extremely thin when seen ten days after the first observation.

2. *Sex Ratio at Birth*

It is not difficult to determine the sex ratio by direct counts of weaned and suckling pups before they take to the sea. In Table XV is given the result of sexing 4629 elephant seal pups, which gives a ratio of 82.2 females to every 100 males. Expressed in percentages the relation is 54.9 per cent male and 45.1 per cent female.

Locality	Date	Male	Female
South Orkney Islands	1948–1949	20	18
South Georgia:			
St. Andrews Bay*	28.x.36	229	161
Cumberland East Bay	13.xi.51	183	163
Fortuna Bay	10.xi.51	291	237
Antarctic Bay	11.xi.51	146	111
Possession Bay	11.xi.51	14	24
Beckmann Fjord	12.xi.51	6	10
Sealeopard Fjord	12.xi.51	259	203
"Long Beach"	12.xi.51	159	145
Ample Bay	12.xi.51	102	71
Sunset Fjord	12.xi.51	29	23
Elsehul	19.xi.51	18	7
Undine Harbour	15.xi.51	13	12
Ice Fjord	19.xi.51	291	273
Wilson Harbour	16.xi.51	11	11
Elephant Bay	16.xi.51	28	19
"Langestrand"	16.xi.51	259	200
King Haakon Bay	17.xi.51	234	197
Queen Maud Bay	18.xi.51	248	204
TOTAL		2540	2089

TABLE XV. Sex counts of elephant seal pups. (* Count by Roberts quoted by Bertram (1940)).

3. *The Age at Sexual Maturity*

The age at which the female bears her first pup is three years, so that, as the duration of gestation is about a year, sexual maturity is attained when the female is about two years old.

In the male elephant seal viable sperm are first produced in the testes at an age of about four years. Bulls do not usually play an important part in the breeding rookeries until they are six years old, when as sub-adult bulls they may intercept cows entering or leaving the rookeries. Is it then necessary to distinguish between sexual maturity and breeding maturity in this species? At South Georgia, as a result of sealing operations the younger bulls have come to play an important part because the number of older bulls has been reduced to a low level. Moreover, it is suggested later (p. 66) that the virgin females mate for the first time at sea, in which case the young sexually mature males probably play an important role. It has been shown (p. 34) that males of this age group begin to haul out on land in the second half of November, which does not conflict with such an assumption.

We may say then, that sexual maturity in the female is attained (with rare exceptions) at the age of two years and the first pup is born when the cow is three years old. In the male, however, sexual maturity is not attained until the fourth year, but they do not normally take part in terrestrial mating until their sixth year, although they are probably responsible for the impregnation of the virgin females.

Fuller details substantiating these statements must be left to a later paper.

4. *The Breeding Season*

The breeding season of the elephant seal may be defined as the season of pupping and mating. The term is used to cover the period of the year in which the young are born, and since the females rapidly come into post-partum heat, mating is approximately contemporaneous with pupping.

In Table XVI the dates of the spring haul-out of bulls and cows, and the dates of birth of the first pups, have been summarised for a number of localities. It shows that at Signy Island in 1949, when fast ice remained intact well into the breeding season, the first bulls were seen about ten days later than in the ice-free years 1947 and 1952 (cf. p. 36, the effect of sea ice on the summer haul-out) but in 1948 the "Green" bull was present on September 17th. The date on which the first cows are seen is approximately September 26th (excepting the years 1948 and 1950 for which the information was less complete). The average date of birth of the first pup is October 3rd.

The first bulls hauled out at "Hestesletten", South Georgia, on September 16th, which corresponds with the ice-free seasons at Signy Island, and the first cows were seen about a week earlier than at Signy Island, although the pups were born at about the same time.

The beginning of the season at Dartmouth Point is considerably in advance of the "Hestesletten" rookery and approximates to the season at Campbell Island and at the Iles de Kerguelen although it is later than at Macquarie Island. Reasons are given below for supposing that the difference in the chronology of the breeding season at "Hestesletten" and Dartmouth Point (which is a seal reserve) is connected with commercial sealing operations.

It is less easy to determine the date of the end of the season. It lasts about two months at "Hestesletten", the numbers of cows rising to a peak in the last week of October and then declining rapidly (Figure 8). The haul-out of the much smaller breeding population at Signy Island follows the same order, but in two years during which extensive observations were made (1948 and 1949) the break-up of the fast ice led to the death of large numbers of pups and the premature departure of their mothers. In both localities the breeding season ends at the end of November. At Kergeulen, Angot (1954) gives November 15th as the date of the end of the season.

We may say then, that at Signy Island and probably on the majority of beaches at South Georgia, the breeding season is more or less confined to the last week of September, through October and the greater part of November. At Dartmouth Point and probably in the other seal reserves, the breeding season begins about ten days or a fortnight earlier.

In future discussions of the reproductive cycle the breeding season is taken to be contemporaneous at South Georgia and the South Orkney Islands, although the difference in latitude appears formerly to have resulted in about one month's difference in the date of the season (see p. 59).

Locality	Year	First Observed			Notes
		Bulls	Cows	Pups	
Signy Island	1947°	Sept. 15	Sept. 28	Oct. 5	ice-free
,, ,,	1948	Sept. 17	*c.* Oct. 6	Oct. 8	fast ice
,, ,,	1949	Sept. 23	Sept. 25	Sept. 30	fast ice
,, ,,	1950*	*c.* Sept. 25	*c.* Oct. 5	—	ice-free
,, ,,	1952[m]	Sept. 15	Sept. 25	Sept. 29	ice-free
South Georgia:					
"Hestesletten"	1951	Sept. 16	Sept. 20	Oct. 2	
Dartmouth Point	1951	*c.* Sept. 5	*c.* Sept. 10	Sept. 20	
Campbell Island	1944†	mid-Aug.	Sept. 20	Sept. 24	
Macquarie Island	1949‡	Aug. 2	*c.* Aug. 26	Sept. 4	
Kerguelen	1909[r]	Aug. 28	Sept. 11	Sept. 24	
,,	1952[a]	Aug. 16	Sept. 10	Sept. 19	

TABLE XVI. Comparison of the breeding haul-out of elephant seals in five sub-antarctic and antarctic localities over a number of years. (°, Robin (1948); * communicated by N. Thyer; [m], A. W. Mansfield; †, Sorensen (1950); ‡, Gwynne (1950); [r], Ring (1923); [a], Angot (1954)).

B. Description of the Breeding Colony at Signy Island

1. *The* 1947 *Season*

Robin (1948) gives details of elephant seals hauled out at Signy Island during this season.

In 1947 the fast ice investing the island had broken up before the first elephant seals were seen. On September 15th a pair of males was seen fighting on the pack-ice off the east coast, but it was not until September 26th that any were seen on shore. The first female was observed on September 28th, and on October 2nd there were four in a harem on Drying Point, the first pup being born to one of these on October 5th and the last in this harem on October 30th. The last birth on the island was on November 13th.

There were four harems in the vicinity of Borge Bay and somewhat doubtful evidence (from pups seen there at the end of the breeding season) for two on the west coast. The Borge Bay harems were on Drying Point (corresponding to the Yellow Harem in the following year, p. 50), The Wallows inland from Starfish Cove (corresponding to the Green Harem in 1948, p. 50), the beach north of Elephant Flats, and one at the northern end of Mirounga Flats. One female pupped in Stygian Cove, and a total of seventy-seven pups are known to have been born in the Borge Bay area.

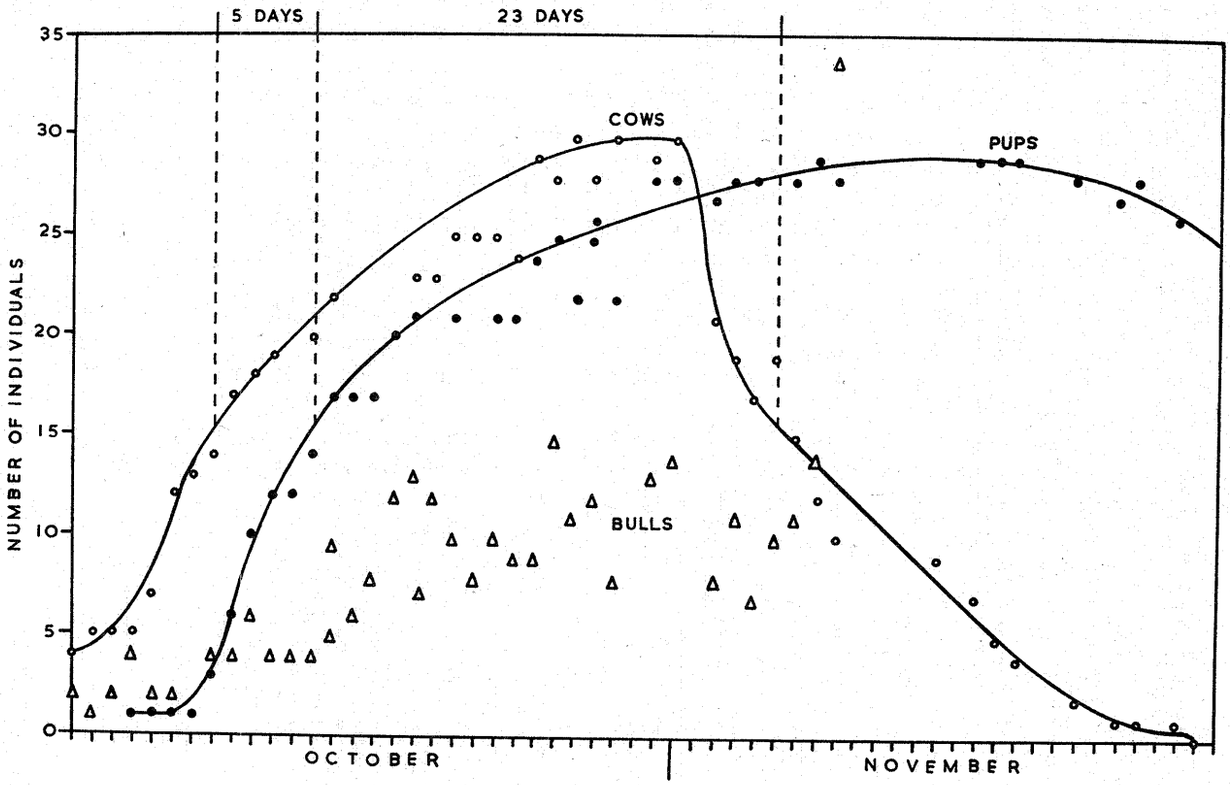


FIGURE 15. Development of a harem at Signy Island.
The birth of the pup occurs five days after the haul-out of the cow and suckling lasts twenty-three days. A steep rise in the number of small bulls occurs after the number of cows begins to decline. (From counts made by F.I.D.S. members in 1947 (Robin, 1948).)

In the vicinity of Drying Point (owing to its proximity to the base hut) members of the F.I.D.S. party were able to carry out daily counts over a long period (Table XIII and Figure 15). These counts demonstrate the formation and decline of an isolated harem in an ice-free year at Signy Island. The figure shows that on average the pups are born five days after the females haul out and that the cows remain in the harem for twenty-eight days before departing to sea when the pup is weaned. It also shows an increase in the number of bulls in the vicinity which reach a maximum at the time when the cows begin to leave. In other words,

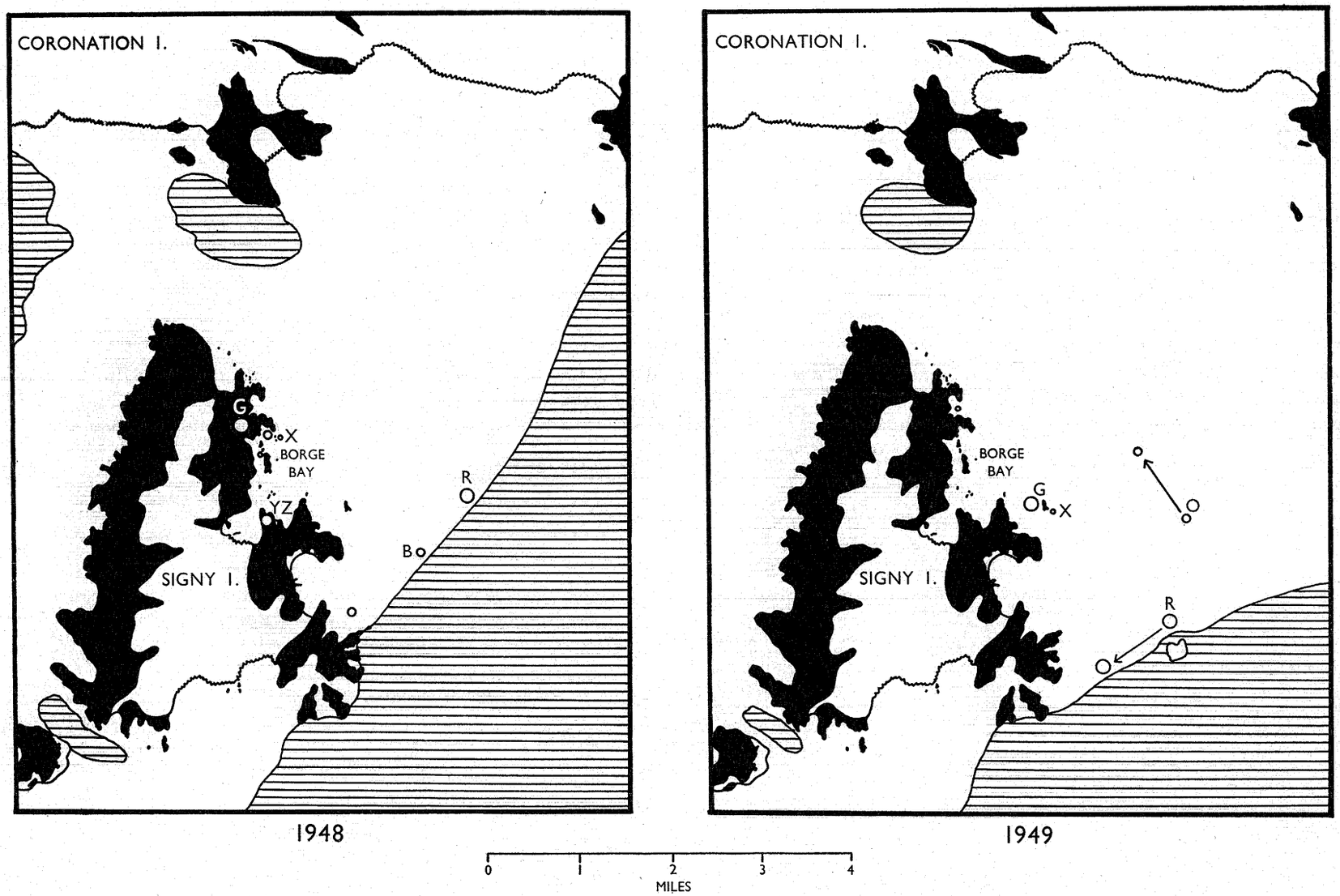


FIGURE 16. Disposition of the harems at Signy Island in 1948 and 1949. Black—land without permanent snow or ice cover; white—land or land-fast ice; lined—open water.

it appears that the greatest number of bulls are present towards the end of lactation when the cows are known to be on heat. It should be pointed out, however, that many of these bulls are younger animals coming ashore for the moult at this time (see p. 34). Further evidence of the nature of the time relations of events during the breeding season is given later (p. 52).

2. *The* 1948 *Season*

In 1948 the fast ice remained intact around the island until the night of October 29th/30th and the average position of the nearest open water during October, is shown in Figure 16.

There was a doubtful record of a bull elephant seal near North Point, Signy Island, on September 3rd, but it was not until September 17th that one was certainly seen. On that day, and again two days later, a large bull (the "Green" bull) was hauled out near Gourlay Point; further out another was seen. On September 26th and 28th the former was present in Stygian Cove but it was not seen again until October 6th when a bull elephant seal crossed the fast ice from the east and was lying near Balin Point in the evening; another five elephant seals were also seen to be heading north-west from the ice edge. This inshore movement continued the following day and on October 8th five cows were hauled out to form two harems in Borge Bay. One of these consisted of two females, a pup and the "Green" bull inland from Balin Point (Area F3), and the other included a large female and a pup between the northernmost of the Thule Islets and the shore and two cows which reached Drying Point at 1030 hours that day.

These individuals formed the nucleus of two harems, painted green and yellow respectively. Several seals were seen near the ice edge and on October 9th a harem was established near a large grounded berg at the ice edge, while three days later another was noted nearby. The individuals in these groups were painted for identification and were known as the Red and Blue Harems. On October 12th the Red Harem consisted of a large bull, twelve cows and six pups, while the Blue Harem was a group of one bull, three cows and two pups. On October 14th a bull, cow and pup were the first indication of a small harem which formed later in the bay north-west of Gourlay Point.

Meanwhile, elephant seals had continued to move inshore from the edge of the fast ice, although the majority remained near the open water. On October 17th a bull and a cow were seen in Stygian Cove and they moved overnight to a position on the sea ice near Balin Point. On October 18th this harem (Orange) contained a bull, three cows and two pups, and an incipient harem of two cows nearby joined it on October 20th. Owing to the apparent instability of the fast ice, which was expected to break up at any moment, the distant harems were not visited after October 19th but binocular observations established that they, as well as the more accessible harems, continued to increase in size.

Thus, when the sea ice broke up there were about fifty cows in six harems. Four of these harems, being situated on the fast ice, were carried out to sea when it broke up. Floes bearing cows and pups of the Orange Harem drifted out past Berntsen Point on the morning of October 30th and cows began to appear on shore during the following two days, six of them being identified from paint marks as coming from the ice harems. They seemed to be rather weak and lay for a long time below the ice foot before attempting to climb above. They joined the harems established on land and formed two more, one between Thule Islets (Mirounga Flats Harem) and one on Drying Point (known as Drying Point Beach Harem; Laws, 1953b, Plate IIIa) near the Yellow Harem.

3. *The* 1949 *Season*

In 1949 the position of the ice edge was futher south and east than in 1948 (Figure 16). The ice remained fairly constant in extent from September 24th until October 15th when it began to break up near the edge, but after October 20th there was little change until the final break-up of the fast ice on November 18th.

On September 23rd a number of large seals were seen to be lying out at the ice edge, and the following day two bulls (Red/A and Red/nose) were fighting near a large grounded iceberg. On September 25th two cows (R/n and R/1) and four bulls were present; a pup was born to one of the cows on September 30th but it was not until October 10th that pups were born in any numbers.

In 1949 all the harems were situated on the fast ice owing to its greater extent and persistence that year. On September 28th an incipient harem formed with the bull R/A and the original two cows. There were seven other bulls in the vicinity and in the following week a few other cows hauled out for short periods. From October 3rd to 7th there was great activity and contests for position amongst the eleven bulls then

present, and the two cows, each with a pup, were undisturbed. Not until October 8th did the harem re-form; it then consisted of bull R/A, the two original cows and a newcomer, R/O, and was south of its former position. The Red Harem continued to grow and when the large "Scarred" bull defeated bull R/A it was in possession of thirteen cows and five pups. Most of the cows hauling out joined the Red Harem but a few managed to elude the waiting bulls and moved inshore. By October 15th there were twenty-nine cows and fifteen pups in the Red Harem and a few scattered cows elsewhere.

The subsequent history of the Red Harem is best described in the form of extracts from the diary.

"15.x.49. I went out to the ice edge at 1500 hours. There is a long swell running and floes are breaking off from the fast ice and moving out to sea. The edge has already been broken back for 100 yards and there is a large bight opposite the harem. It is only 30 yards from open water now and a crack in the fast ice surrounds it. At the south end of this incipient floe the crack is open and the ice rises and falls with the swell. It cannot be long before the whole harem is carried out to sea.

"In the group there are twenty-seven cows and fifteen pups (including one dead pup). Two new cows are heading for the harem from the north-east. The 'Scarred' bull is still in possession and the cows are in more open order today. They are R/1, R/n, R/1/s, R/+, R/A, Y/T, Y/+, Y/n, Y/2, B/r/+, R/r/s, R/11, Y/r/+ (all with pups), R/n/t, Y/F, Y/1/s, Y/1, R/O, Y/8, B/t, B/r/s, 'light cow', and the remainder unmarked.

"16.x.49. The temperature is 37°F. and a gale overnight, continuing this morning, has carried out large areas of the fast ice.

"I went out to the ice edge at 1830 hours. The sea has encroached almost to the rock islet and the harem had evidently been carried out on a floe. It is now re-formed at the ice edge 150 yards to the north of its former position. There are nineteen cows and six pups (two of these new-born). . . . It seems probable that the remaining cows which were in the harem yesterday lost their pups and that those which had not pupped and those whose pups survived the storm hauled out again to form this new harem. This means that twelve pups present yesterday have been carried off (i.e., those of cows R/n, R/1, R/+, R/A, R/1/s, Y/r/s, Y/+, R/r/s, Y/r/+, R/11, Y/n, B/r/+). One unmarked cow has a pup too large to be new-born so it may have survived and acquired a foster mother. . . . The two other surviving pups are with cows R/+ and Y/2. Four of the cows which have presumably lost their pups are lying out again; they are R/A, Y/r/+, R/+, R/r/s. . . .

"17.x.49. At 1800 hours I went to the ice edge. A very strong wind and the frozen surface made it necessary to wear crampons.

"A large crack (four feet wide) now runs northwards from the rock islet. The south-west portion of the ice to seaward of this had gone out, taking the harem with it and the remainder of the ice seaward of the crack was rising and falling about one foot with the swell. The wind whipped up the sea, and waves and spray were driving onto the ice.

"Evidently the harem had been carried out to sea only a short time before. Females in an exhausted condition were hauling out when I arrived. They grouped into two 'pods'. The western 'pod' contained cows R/n/t, R/r/A (with pup), Y/t, Y/F, R/r/s, and three unmarked, one with pup. Both pups are new-born today. Two cows were heading towards the Red Harem having hauled out to the eastwards. They were R/1/s and one unmarked which I painted R/neck. . . .

"Further east, near the crack was a large new bull which I painted R/proboscis. It fought and was defeated by the 'Scarred' bull which rounded up four cows (R/A, R/n, Y/+, and R/neck). Later three of these cows broke away and headed for the other group. The 'Scarred' bull followed and shepherded them all into one big harem. Finally the other cow followed. . . . Yet another was swimming up and down the crack, which was full of sludge ice, trying to haul out.

"18.x.49. The gale continues. . . . I went out to the ice edge at 1800 hours. The harem at the ice edge has moved further east as the piece of ice which held it yesterday has gone out. The 'Scarred' bull lies five yards west of the cows. . . . They are Y/T, Y/r/s, R/r/A, R/A, Y/1, R/r/s, R/n, R/neck, R/F, R/11, Y/2, and four unmarked. There were two pups which appeared to be with the first two cows, and if so were foster-pups. In the crack near the harem was the 'light cow'.

"19.x.49. The harem has moved north-east about 30 yards and more pieces have broken off from the fast ice. On one of these floes the 'light cow' is lying. The 'Scarred' bull has nineteen cows and three pups, one new-born. . . . Cow R/1/s who had lost her pup on October 16th, fought with the unmarked mother of the new-born pup and appropriated it. . . .

"At 1930 hours the ice seaward of the crack moved out as a large floe. . . . Seven elephant seals are visible on the edge of the fast ice near the islet—the others are all on the floe. This break-off coincides with a high tide and a wind of 50 m.p.h. from the north-west."

On October 20th binocular observation from the island showed that there were two harems at the ice edge. One of them, the Red Harem, contained five cows, and the other north-east of the large iceberg (see p. 60) contained six cows. In addition there were seventeen bulls and six cows scattered on the ice near the edge. Most of these cows appeared to have broken away from the harems and were heading to the north-west.

Meanwhile, on October 12th, female G/n had pupped near Outer Islet and with "Scarred-eye" bull, formed the nucleus of what was called the Green Harem.

During the storm other cows began to move away from the ice edge and small harems formed well to the west of the Red Harem, which was still the most important. On October 18th, five cows and the "Scarred-eye" bull (which had been defeated by bull R/A, earlier in the day) lay about a mile and a half north-east of the Red Harem. The following day the bull and three of these cows moved to join the Green Harem. A small harem of three cows and a young bull (Young R/n) was present on October 19th in the bay north-west of Balin Point but later the cows moved south again to join the Green Harem. Thus, on October 20th there were four harems situated on the sea ice, two of them near the edge of the fast ice (the Red Harem in its former position and another one to the north near the large iceberg). Many more cows were moving inshore so that on October 21st the Green Harem contained eight cows and two pups with the bull R/A, and the harems at the ice edge only five and six cows respectively. On October 22nd the Green Harem had thirteen cows and three pups and the Orange Harem ("Scarred-eye" bull) was composed of eleven cows and five pups, while there was a small harem of three cows near Outer Islet (harem "X"). By October 26th the Orange Harem had increased to thirteen cows with nine pups, and the Green Harem to fifteen cows and nine pups, while the size of the harems at the ice edge had decreased.

So far as could be seen there was little more disturbance caused by the fast ice breaking up and by November 15th the Orange Harem was reduced to one cow, and the Green Harem contained only three cows, the others having weaned their pups and departed to sea. When the final break-up occurred and open water reached Outer Islet on November 18th, the "Scarred" bull moved in and took over control of the Green Harem which then numbered only two cows, "and one of these left at 1400 hours. . . . In the evening, the ice under the Green Harem broke up. The pup and cow fell into the water when a crack opened immediately under them. . . ."

The other weaned pups were nearly all lying out on the sea ice and the pup mortality in this year was estimated to be as high as 80 per cent. Only two cows pupped on land in the area. On November 2nd a small cow pupped on a beach near Balin Point, but the heat of the pup's body melted a pit in the snow and it died fourteen days later. The other cow pupped in the small cove east of Stygian Cove on November 21st and, so far as is known, the pup survived.

C. Establishment of Breeding Rookeries at South Georgia

The vicissitudes of the small, recently established breeding colony at Signy Island in 1948 and 1949 have been described, but the structure of the much larger rookeries at South Georgia bears little resemblance to the scattered distribution of the harems at Signy Island. The establishment and maintenance of the harems has been studied in some detail at Dartmouth Point, South Georgia, where a herd of more than 1066 cows hauled out, and when the study began it was thought that it would prove to be typical of a rookery in a natural state, only slightly influenced by man. After the establishment of this rookery has been briefly described it will be compared with other areas in Cumberland Bay and the extent of the influence of man discussed. Then the detailed breeding behaviour of the different sexes and classes of elephant seals will be discussed.

1. *The Dartmouth Point Rookery*

At Dartmouth Point five distinct phases of the re-colonisation of the beaches and the establishment of the breeding organisations were observed. (See Table XI and Figures 17, 18 and 21.)

i. From the end of August to September 10th: Initial colonisation by a few bulls.

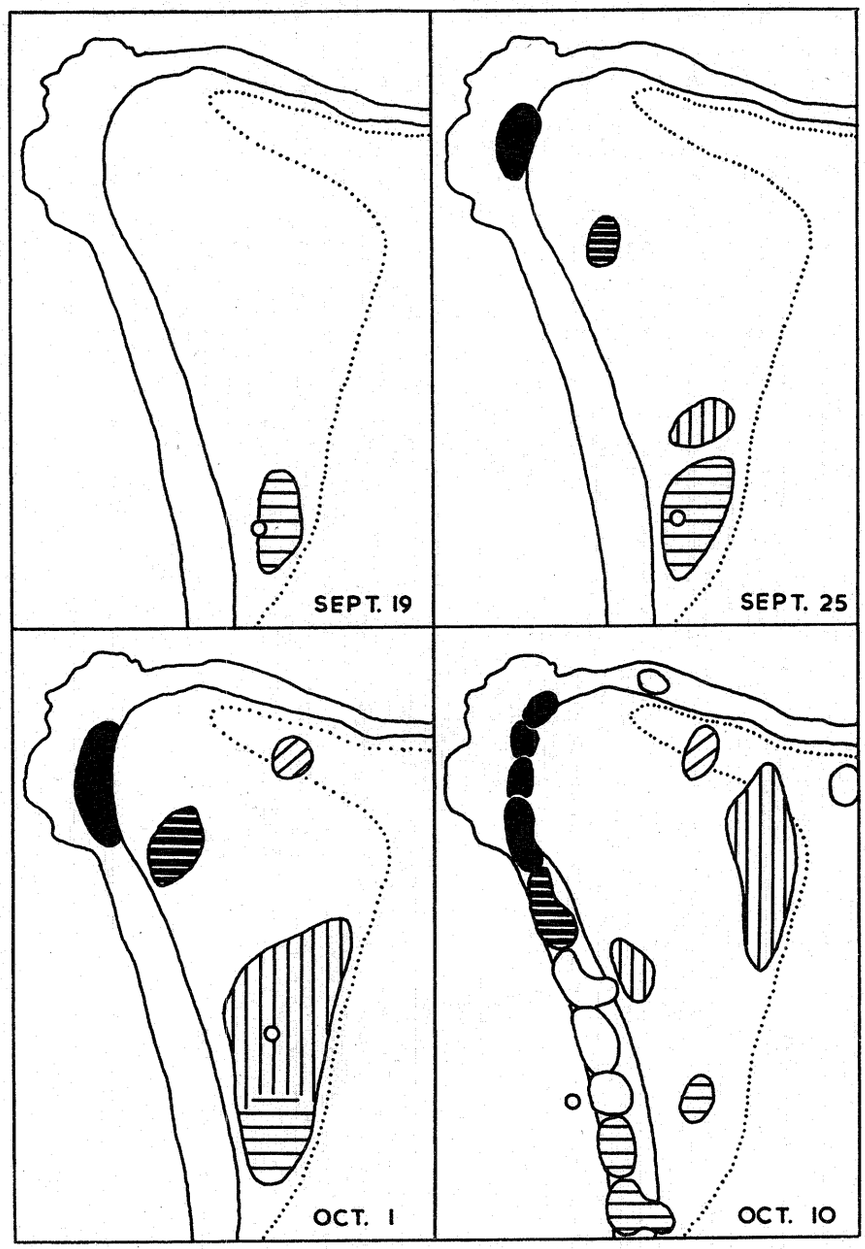


FIGURE 17. Establishment of the rookery on Dartmouth Point, Cumberland East Bay, South Georgia, 1951.
The fifteen foot contour is shown as a dotted line. The origin of the definitive harems was traced by means of marked cows and daily observations; the position of one marked bull is represented by a small circle.

ii. From September 10th to 19th: The cows began to haul out, while the bulls were still increasing in numbers. Some fighting among the bulls.

iii. From September 19th to 30th: a. The first harems formed when the pups were born, averaging five cows per harem. No more bulls appeared and the cows outnumbered the bulls on September 21st and continued to haul out in rapidly increasing numbers.

b. The harems increased in size to average twenty cows each. This was the period of harem expansion.

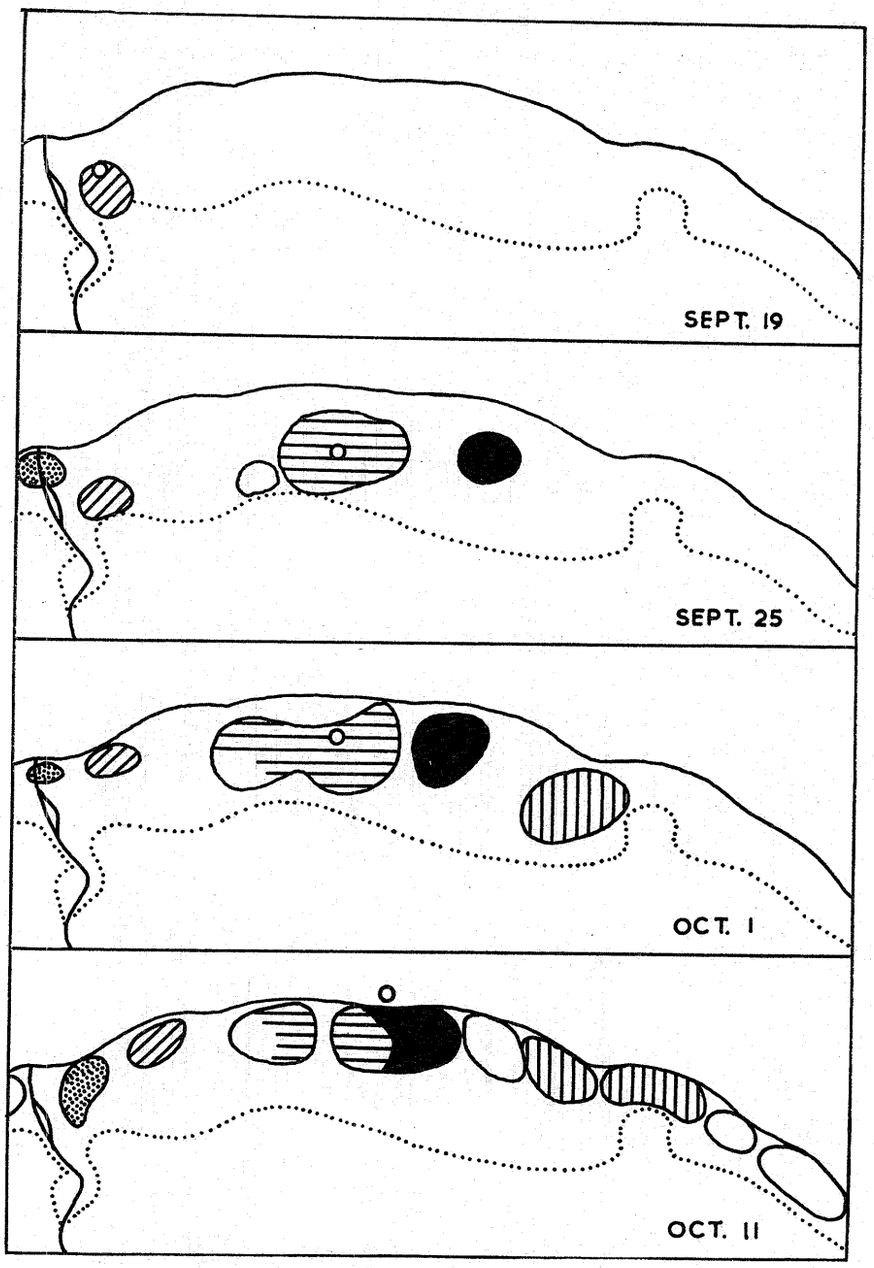


FIGURE 18. Establishment of the rookery at 54°20′ S., 36°25′ W., Cumberland East Bay, South Georgia. The fifteen foot contour is shown as a dotted line. The origin of the definitive harems was traced by means of marked cows and daily observations; the position of one marked bull is represented by a small circle.

iv. From September 30th to October 5th: The harems decreased in density (because of the aggressiveness of cows with pups) and a greater area was covered (see Figure 17). The average number of cows per harem remained stable at about twenty-four, and until the end of this period there were, on average, two bulls per harem (i.e., one dominant and one subordinate).

There was a high pup mortality rate in periods *iii* and early *iv*, largely owing to the thick snow cover.

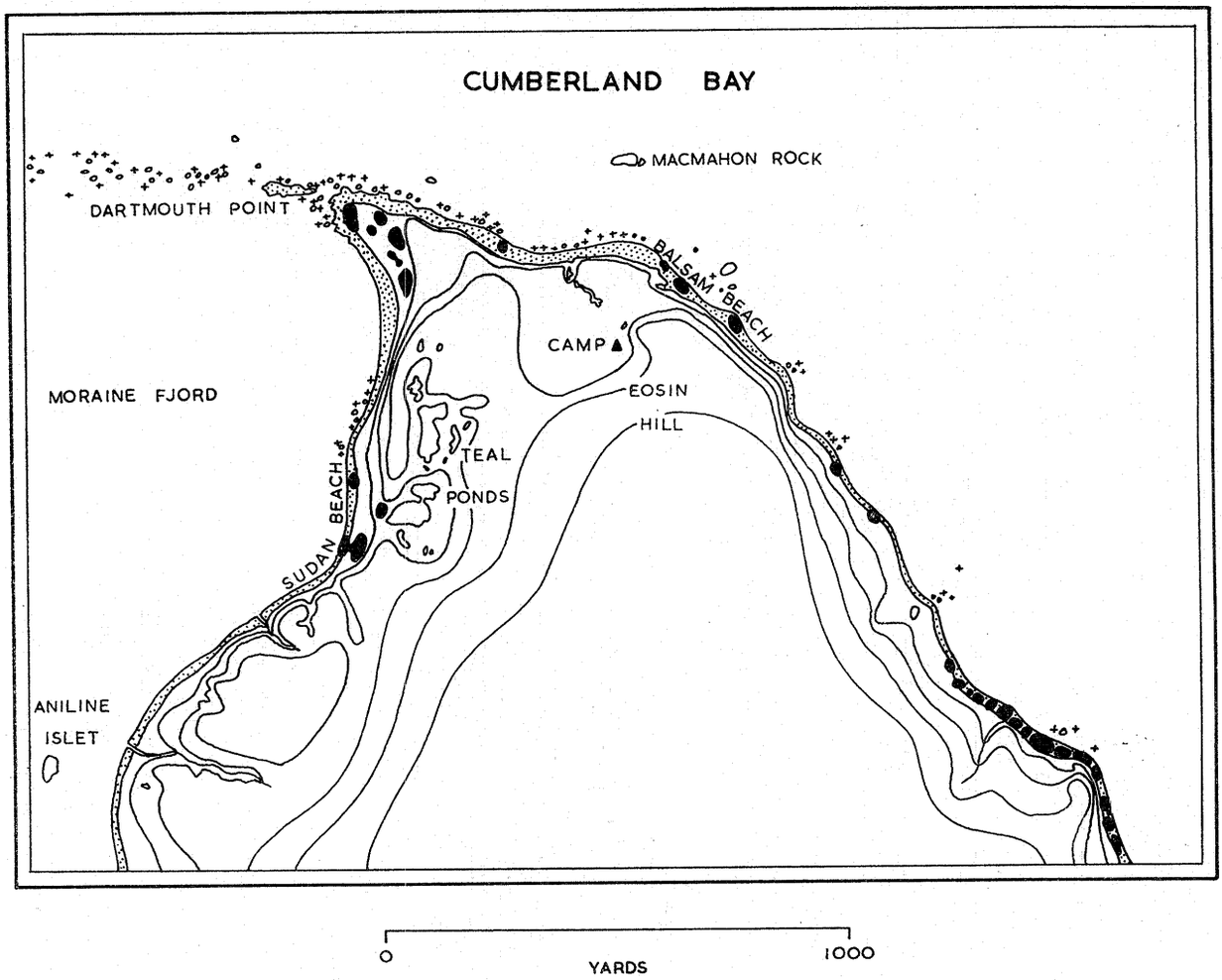


FIGURE 19. Sketch map of the Dartmouth Point area, Cumberland Bay, South Georgia. The position and size of the harems on October 4th, 1951, are shown.

In tussac areas the mortality was as much as 50 per cent. However, at the end of period *iv* only 32 per cent of the cows had pupped.

v. From October 5th onwards: New harems were formed by those already formed splitting up. The cows tended to move down the beach towards the sea, possibly because the snow melts there first. The territory of the bulls decreased and there was a slight increment in their number. At first the newly hauled out cows swelled the numbers of the existing harems on the beaches and then formed new harems, filling in the areas between the initially colonised points. The average number of cows per harem became stable at about nineteen; the average number of cows per bull was twelve. This was the period of rookery expansion.

Observations were discontinued on October 12th, but it was thought possible that as a rapidly increasing number of cows came on heat, greater numbers of bulls would haul out on the beaches.

2. *Other Areas*

Less detailed information over a longer period was obtained for other areas in Cumberland Bay (Figures 21 and 22; Plate IIb). It serves to confirm that the process of rookery establishment is as outlined above, except that the time relations are different and the ratio of cows to bulls is even greater. In Table XVII the

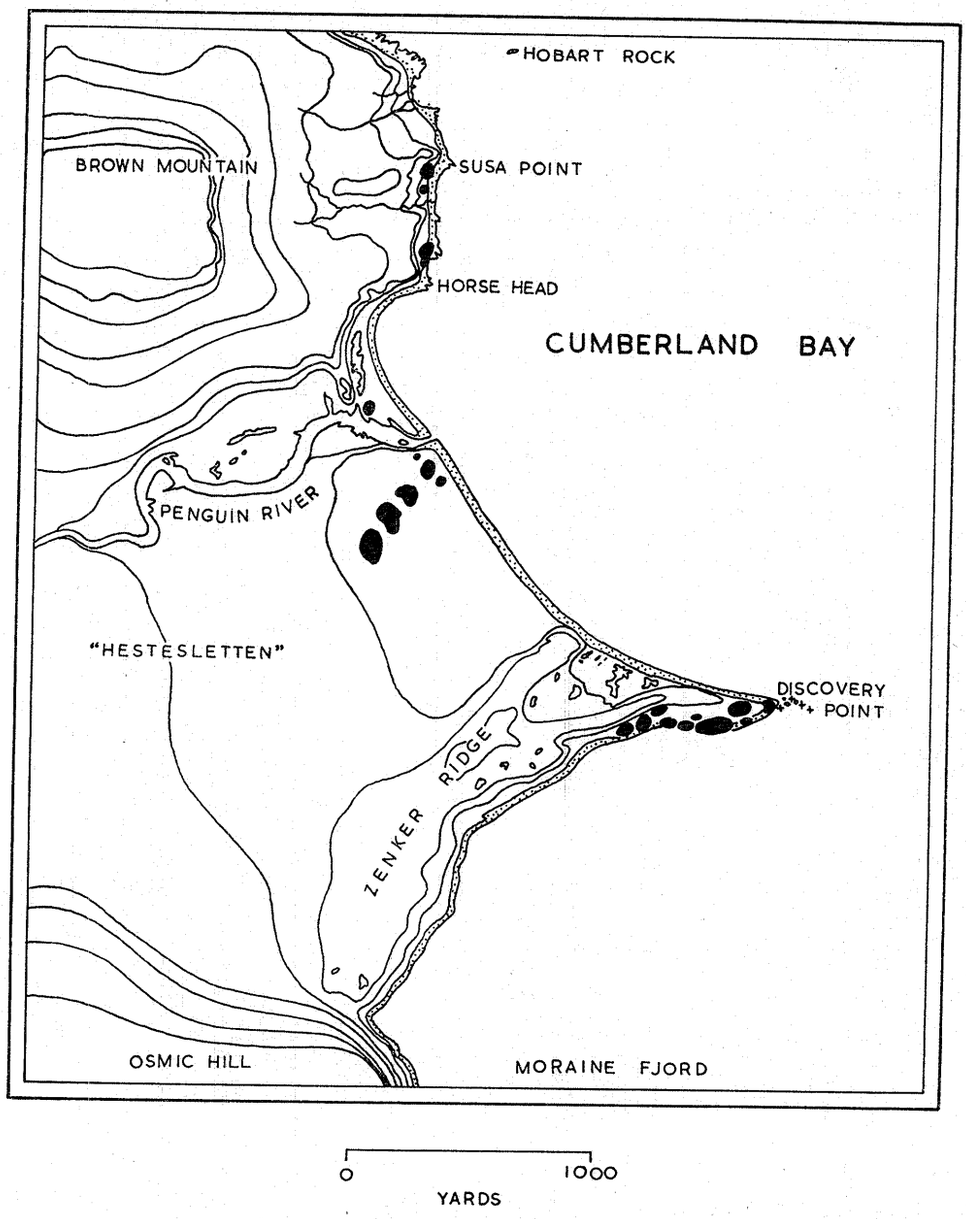


FIGURE 20. Sketch map of the "Hestesletten" area south of Grytviken, Cumberland Bay, South Georgia. The position and size of the harems on October 22nd, 1951, are shown.

Phase	Dartmouth Point	"Hestesletten"	Maiviken
ii.	Sept. 10–19	Sept. 19–22	Sept. 27–Oct. 6
iii.	Sept. 19–30	Sept. 22–Oct. 18	Oct. 6–28
iv.	Sept. 30–Oct. 5	Oct. 18–30	Oct. 28–

TABLE XVII. Relation between the phases of rookery establishment in three areas at South Georgia.

time relations of the three main phases of rookery establishment are set out. The most obvious difference is that the process is retarded and lengthened in the "Hestesletten" (Figures 20 and 22) and Maiviken rookeries relative to the Dartmouth Point Reserve.

The average size of the harems was much greater in these two rookeries. Thus, at Maiviken the average harem size in period *iv* was fifty-two cows, and at "Hestesletten" forty-six, or just about twice as many as in the Dartmouth Point Reserve. The largest single harem at Dartmouth Point (R/face bull) contained 116 cows on September 29th, but by October 1st it had split up and the bull had only eighty-five cows. The size of this harem then remained fairly constant until the cows began to leave several days later.

The largest harem on "Hestesletten" contained over 100 cows but apparently did not split up.

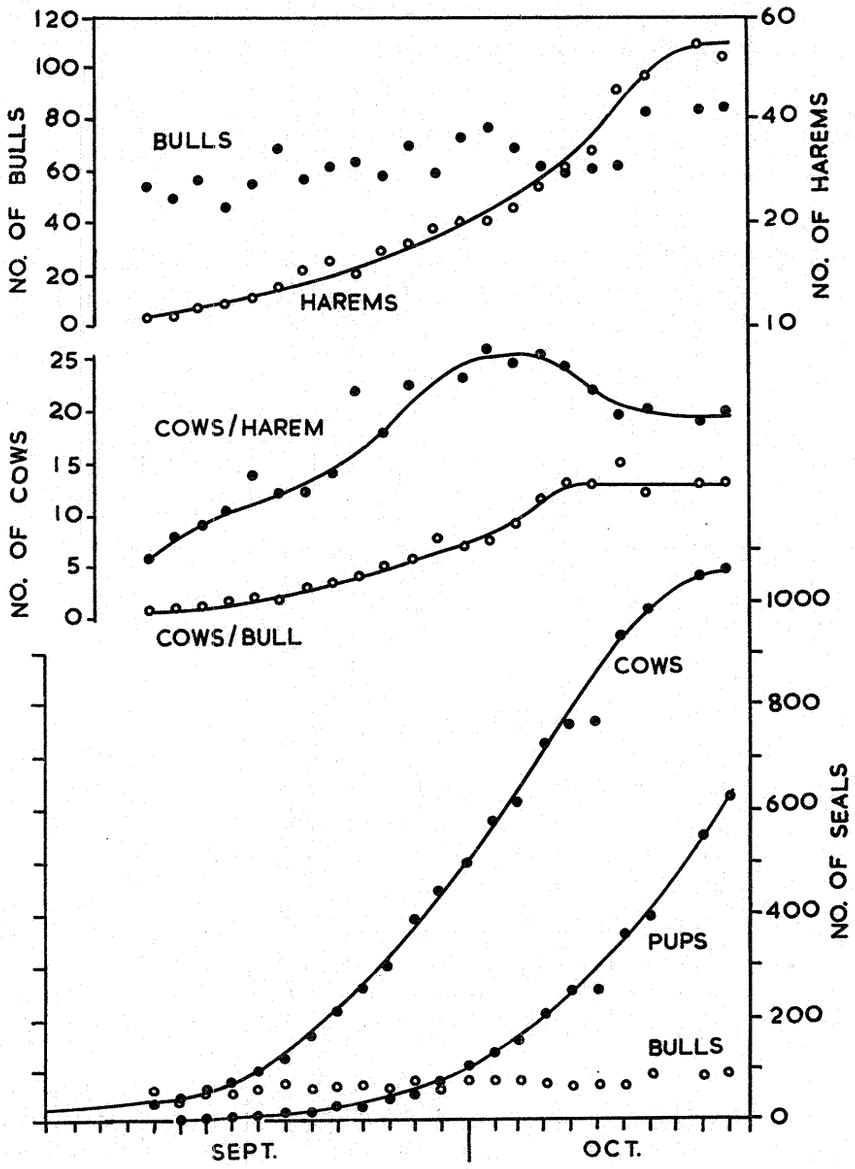


FIGURE 21. Data derived from daily counts of elephant seals in the Dartmouth Point area, September to October 1951.

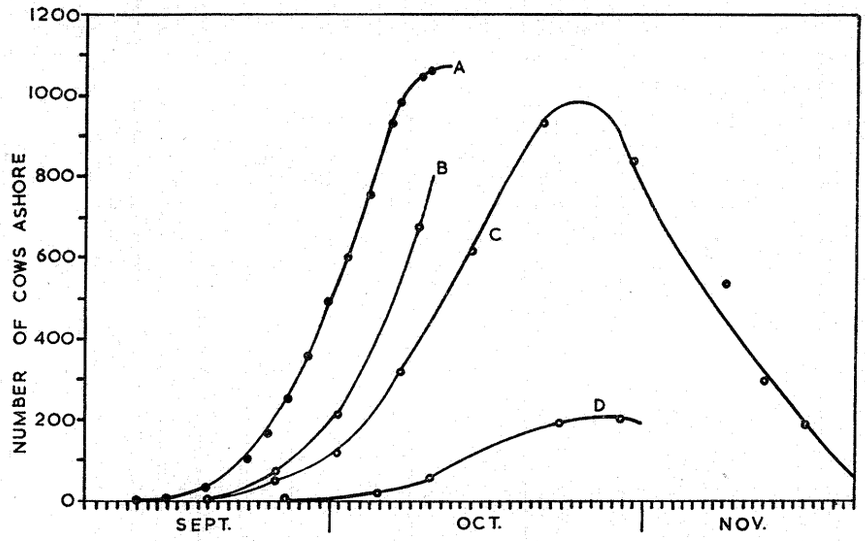


FIGURE 22. Numbers of cows on land during the breeding season in four different localities, South Georgia, 1951. A—Dartmouth Point; B—between 54°20′ S., 36°25′ W., and Nordenskjöld Glacier; C—"Hestesletten"; D—Maiviken.

3. *The Effects of Commercial Sealing Operations upon the Breeding Season at South Georgia*

It seems probable that commercial sealing operations have had two main effects upon the breeding rookeries at South Georgia. Firstly, they have resulted in an extension of the length of the season of reproduction, and in the retardation of its commencement. Secondly, they have greatly altered the natural balance of the sexes.

Cows	Signy Island	South Georgia 1926	Dartmouth Point 1951	Kerguelen 1952	"Hestesletten" 1951	Maiviken 1951
Date of arrival	*c.* Oct. 1	*c.* Aug. 20	Sept. 10	Sept. 10	Sept. 19	—
Maximum numbers	Oct. 22	—	Oct. 11	Oct. 15	Oct. 26	Oct. 28
Effective length of season (days)	38	*c.* 50	60	66*	72	—
Average per harem	12	*c.* 12	24	55(?)	46	52
Maximum per harem	30	30	85	190	100+	—
Number per bull	2	—	13	11.4	28	34
Total number in area studied	*c.* 100	—	1200	—	1100	220

TABLE XVIII. Comparison of breeding rookeries, from analysis of elephant seals at the South Orkneys (1947 to 1949), South Georgia (Matthews, 1929), three beaches in Cumberland Bay, South Georgia (1951) and Kerguelen (Angot, 1954). The columns are arranged from left to right according to the relative extent of disturbance by man. *Paulian (1954) gives the length of the pupping season in 1951 as 43 days.

In Table XVIII, relevant facts about the breeding dynamics of the elephant seal are set out according to the incidence of sealing. At South Georgia from 1910 to 1926 the average annual take by the sealing company was 2799 bulls. During this period the population was apparently increasing, in spite of sealing operations, and approximated to a natural stock. In respect of harem size and the length of the season, the

situation at South Georgia in the nineteen-twenties appears to have been very similar to that obtaining at Signy Island in the years 1947 to 1949. The date of the beginning of the breeding season at South Georgia in the nineteen-twenties appears to have been about a month earlier than the season at Signy Island at the present day, but it now appears to be retarded by one month. It also appears that its duration has increased by almost half. Records of the sealing industry over the years show a change in the date of the catches. The November catch has become progressively larger and the September catch is now very variable. The *average* harem size in the sealing areas (as represented by "Hestesletten" and Maiviken) is now greater than the largest harems seen by Matthews twenty-seven years ago, and the number of subordinate bulls has decreased to less than one per harem.

What is the explanation of these changes? The retardation of the beginning of the season may possibly be explained by the fact that bulls tend not to haul out because of sealing operations. It is then likely that they would remain in condition later in the season and therefore be able to impregnate cows which pup late and would formerly have missed a pregnancy and mated early in the following season (see p. 80). There would also be a tendency for cows not to be impregnated as soon as they come on heat which would also contribute to the extension of the season. However, this hypothesis does not explain why, if they are impregnated at sea (p. 66), the primiparous cows do not haul out earlier.

The numerical alteration in the natural balance of the sexes is more easily explained. The increase in the size of the average harem* and the altered adult sex ratio is an obvious result of the slaughter of bulls during the past thirty years. Although the average annual take by the sealing company prior to 1926 was under three thousand bulls, the average number taken per year over the past decade is over six thousand. In 1951 the catch was the highest since controlled sealing began and totalled 7877 bulls.

At Kerguelen, where sealing operations have not been attempted for many years, the average size of the harems is fifty-five cows (Angot, 1954). The ratio of cows to bulls is 11.4: 1, approximating to the ratio of 13: 1 at Dartmouth Point, but the average number of bulls per harem is about five compared with less than two at Dartmouth Point.

D. Breeding Behaviour of Parous Females

1. *Before Parturition*

The first cows usually haul out several days after the bulls (p. 47) and may undertake extensive wandering before giving birth to the single pup (Tables XIX and XX; Figure 23).

> At Signy Island, in 1949 cow G/n travelled seven miles in three days, mostly over the fast ice, before giving birth to a pup and becoming the nucleus around which the Green Harem developed. Another cow (R/A) travelled four miles in two days, and R/1/s and N travelled three miles in three days. Although the presence of fast ice around Signy island has undoubtedly modified the behaviour of the females, similar movements were observed at South Georgia. These were of smaller range, the cows leaving a beach at one point, and swimming along just offshore before hauling out again.

From observations of marked cows at Signy Island it was established that during 1948 and 1949 parturition followed from one to thirteen days after they hauled out, the average time for forty-four marked cows under observation being five days. The data given in Table XIII and presented graphically in Figure 15 support this conclusion. However, at South Georgia it is known, from records of marked cows and from the curves of population increases at Dartmouth Point (Figure 21) and "Hestesletten" (Figure 8), that the length of the period of lying out before parturition averages eight days. Angot (1954) says that at Kerguelen female elephant seals give birth from four to six days after hauling out. It is possible that the presence of fast ice at Signy Island may delay the haul-out of the cows, or that the long journeys over the ice hasten the onset of parturition, but it must be remembered that the length of time between hauling out and pupping was the same in the ice-free season 1947 as in 1948 and 1949, so that the reason for the differences is probably more fundamental.

In general, during this period the parturient cows are very timid and restless and easily disturbed. Probably the most important factor initiating the formation of a harem is their gregariousness at this time, for there seems to be a desire on the part of those near term for physical contact with, or at least proximity to, others of the same sex.

* Angot's recent work is difficult to reconcile with this.

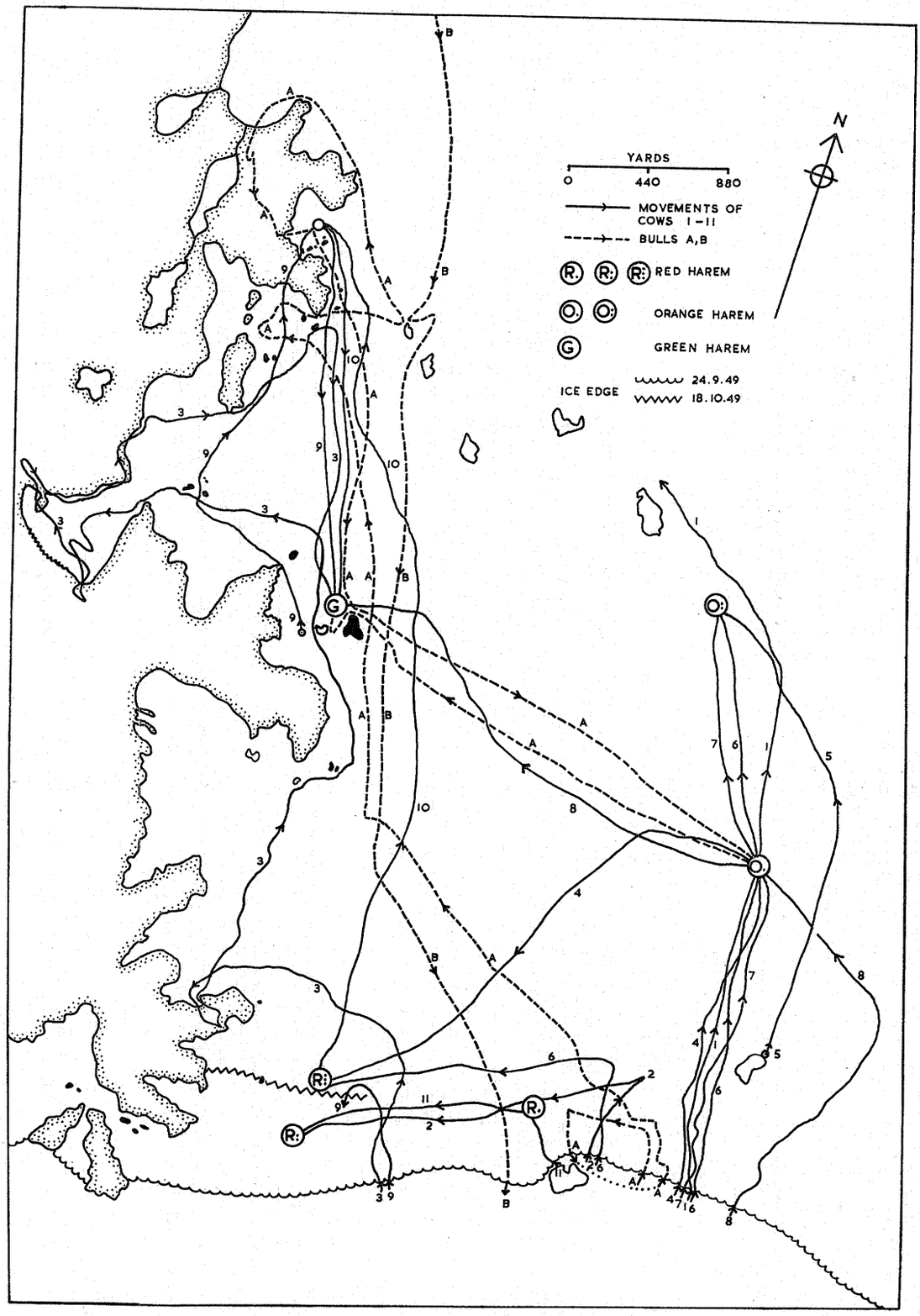


FIGURE 23. Map of the east coast of Signy Island showing the position of the fast ice and ice bergs in 1949, and the movements of eleven marked cows and two marked bulls. Three changes in position of the Red Harem are shown and two positions of the Orange Harems; the Green Harem did not move. Key to numbers: 1=Red-nose cow; 2=Red 1; 3=Green-neck; 4=Yellow^{+}; 5=Red-neck; 6=Blue-right-spot; 7=Blue 1; 8=Red-left-spot-and-nose; 9=Blue-left-spot; 10=Red$-A^{2}$; 11=Red$_{+}$; A=Scarred-eye bull; B=White-nose bull.

BULLS	OCTOBER 8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	NOVEMBER 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Green	G	G	G	G	G	G	–	G	G	Y	Y	O	O	O	O	*R*	*R*	*R*	*R*	*R*	*R*	*R*	G	G	Y	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	–	–	–	left			
Blue	*B*	*B*	*B*	*B*	B	B	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b																											
Red	*R*	*R*	*R*	R	R	R	B	B	B	B	B	B	B	*B*	*B*	*B*	*B*	*B*	*B*	*B*	*B*	*B*																											
Red-yellow						–	–	–	–	O	O	o	o	o	o	O	O	O	o	G	G	G	g	g	g	g	g	g		g			y	y	y	g	g	g		–								
Yellow					Y	Y	Y	Y	Y	y	y	y	y	Y	Y	Y	Y	y	O	O	O	O	g	g	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y	–	–	–				
Yellow-++								–																					o										b									
Yellow-nose																		Y	Y	Y	Y	Y				F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F						
Chinese																				y	y	y	y	y		y	y	y	y	y	y	y	y		y	y		y	y				–	–	–			
Scarred																							Y	Y		F	Y	Y	Y	Y	Z	Y	Y	Y	Y	Y	Z	Y	Y	Y	Y	Z	Z	Z	–	–	–
Yellow-+																												y	y	g	g	f			g			Z	Z	y	y							
Yellow-A																												z	z	z	z	z	z		z	z	z	z	z	z	z	–	–	–	–	–	–
Scarred-eye																													z	z	Z				Z	Z	z			g	g	Z						

COWS	OCTOBER 8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	NOVEMBER 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Green-7	–*	–	–	–	–	–	–	–	–	–	–	G	G	G	G	G	G	G	G	G	G	G	G																									
Green-3	–	G	G	G*	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G																											
Yellow-1	Y*	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y																											
Green-1	G*	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G																									
Green-2	G	G	G	G*	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	G											
Green-4		G	G*	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G		G	G	G	G	G																		
Yellow-2				Y	Y*	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y																										
Yellow-3					R	R	R	R	Y	Y*	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y		Y	Y	Y	Y	Y	Y	Y	Y																
Red-yellow-11								O	O	O	O*	O	O	O	O	O	O	O	O	O	O	O	O†		Y	Y	Y	Y	Y	Y	Y	Y																
Red-yellow-41				R	R	R	R	R	R	O*	O	O	O	O	O	O	O	O	O	O	O	O	O†			G	G	G																			
Red-yellow-12		*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	O*	O	O	O	O	O	O	O	O	O	O	O	O	O†		F	F	F	G	G	G	G	G	G														
Red-yellow-13										O	O	O	O	O	O	O	O	O	O	O	O	O*	O																										
White-1										X*	X	X	O	O	O	O	O	O	O	O	O	O		G	G	G	G																						
Green-0																		*R*	*R*	*R*	*R*	*R*		G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G
Green-5										*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*		G	G	G	G	G	G	G	G	G	G	G	G	G	G	G										
Green-9										*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*		G	G																								
Green-10									*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*		G	G																								
Yellow-X	*R*	*R*	*R*	*R*	R*	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R†				Y	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F						
Yellow-0																							Z	Z	Z	Z*	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z
Yellow-+																							Z	Z	Z	Z	Z	Z	Z	Z	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Z	Z	Z			
Yellow-10																							Z	Z	Y*	Y	Y	Y	Z†	Y	Y	Y	Y	Y	Y												
Yellow-7																		*R*	*R*	*R*	*R*	*R*	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Z	Z	Z
Yellow-8																									Y	Y	Y	Y	Z*	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z
Foul Bay-1																									F	F*	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F				
Large cow																														Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	Z
Yellow-9																									Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y				

TABLE XIX. Movements of 38 marked elephant seals throughout the breeding season, Signy Island, 1948. The break-up of the ice occured on 30th October.

Presence at a harem is indicated by letters: Gg=Green Harem, Bb=Blue Harem, Rr=Red Harem, Yy=Yellow Harem, Oo=Red/Yellow Harem, Xx=incipient Harem near Red/Yellow Harem, Ff=Foul Bay Harem, Zz=Drying Point Beach Harem.

Where a letter is in italic type the record is uncertain. For the bulls capital letters mean dominance (in charge of a harem), small letters signify a subordinate status.

– means observed but not at a harem; * pup born; † pup died.

[*To face p.* 60

BULLS — SEPTEMBER	24	25	26	27	28	29	30
Red-A	–	–	–	–	–	–	–
Red-nose	–	–	–	–	–	–	–
Scarred-eye		–	–	–	–	–	–
Red+		–			–		
Red-spot			–	–	–	–	–
Red-tail			–				
Yellow-X					–		
Yellow-1					–	–	–
Scarred						–	–
Young red-nose							
Red-oblique							
White-nose							
Green-nose							
Yellow-left-spot							

BULLS — OCTOBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Red-A	–	–						R	R	R	r	r	r	–	r	–	–	G	G	G	G	G	G	G	G	G	G	G	G	G	G
Red-nose	–	–	–	–	–	–	–	–	r	r	r	–	r	r			–	g	–	g	g			g							
Scarred-eye	–	–	–	–	–	–	–	–	–	–	–	G	G	G	G	G	G	O	g	g	O	O	O	O	O	O	O	O	O	O	O
Red+									r	r	r	–	–	–	r	–	–	–	r												
Red-spot	–				–	–	–	–	–	r	r	r	r	g	g	–	–	–	–	–	X	X	X	X	X	X	X	X	X	X	X
Red-tail		–	–	–	–	–	–	r	r	–	–	–	g	g	–	–	–		r	*r*	*r*	*r*	*r*	*r*	*r*	g	g	g	g	g	g
Yellow-X	–							r	r	r	r		–	–	–	r		–	r			o	o	o	g	g	g	g	g	g	g
Yellow-1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r	–	r	–	–					x	x	x	x	–	–	–	g
Scarred	–	–	–	–	–	–	–	–	–	–	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	*R*	*R*	*R*	*R*	*R*
Young red-nose	–	–	–	–	–	–	–	–			–		g			–	–	–	–	–	–	–	g	g	o	o	o	o	o	o	
Red-oblique	–	–	–	–		–	–	–	–	r	r	r	r	r				–	–												
White-nose					–		–		–	–	–	–	–		–			r	r												
Green-nose							–	–	–	–	–		–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Yellow-left-spot													–	–		–	–	–	–												

BULLS — NOVEMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Red-A	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	Killed					
Red-nose						g																
Scarred-eye	O	O	O	O	O	O	O	O	O	O	O	O	O	O	–	–	–					
Red+											g	g	g					g				
Red-spot	X	X					X	X	X	X	X	X	X	X	–	–	–	–	–	–	–	–
Red-tail	g	g	g																			
Yellow-X	g	g	g	g																		
Yellow-1	g	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	g	–	–	–	–
Scarred	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	*R*	G	–	–	–	–
Young red-nose																						
Red-oblique																						
White-nose																						
Green-nose	–	–	–	–	–																	
Yellow-left-spot																						

COWS — SEPTEMBER	24	25	26	27	28	29	30
Red-nose		–	–	–	–	–	–
Red-1		–	–	–	–	–	–*

COWS — OCTOBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Red-nose	–	–	–	–	–*	–	–	R	R	R	R	R	R	R	R†			–	–		–	O	O								
Red-1	–	–	–	–	–	–	–	R	R	R	R	R	R	R	R†																
Red-$^+$								–	R	R*	R	R	R	R	R	R†					G	G									
Red-+								–	R		R*	R	R	R	R†	R		R	R		G	O	O	O	O	O	O	O			
Red-A									R	R	R*	R	R	R	R†	R	R	R	R												
Red-left-spot									R	R*	R	R	R	R	R†		R		R												
Green-neck									–	–	–	G*	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G
Yellow-right-spot										R	R	R	R	R	R*	R†		R	R		G	O	O	O	O	O	O	O			
Yellow-1										R	R	R	R	R	R	R*†		R	R												
Yellow-2										R	R	R	R	R*	R	R	†	R	R		–	–	G	G	G	G	G	G	G	G	
Yellow-face										R	R	R	R	R	R	R	R		R												
Yellow-tail										R	R	R	R	R	R	R*	R†	R	R												
Yellow-$^+$										R	R	R	R*	R	R	†	R	O	R												
Red-neck										–	–	–*	–	–	–	–	–	–	–	O	O	O	O	O	O	O	O	O	O	O	
Red-nose/tail												R	R	R	R	R	R	–*	–												
Red-right-spot												R	R	R	R*	†	R	R	R		G	O	O	O	O	O					
Yellow-right-+												R	R	R	R*	R†		–	–												
Red-11													R	R	R*	†		R	R												
Light coloured													–	R	R	R		–	–												
Red-A^2													–	–	–		R	R	–			G	G	G	G*	G	G	G	G	G	G
Blue-right-spot														–	R			–	–		O*	O	O	O	O	O	O	O	O	O	
Blue-tail														–	R							G	G	G	G	G	G	G	G	G	G
Blue-neck														–	R							G	G	G	G	G	G	G	G	G	G
Blue-left-spot														–			G	–	–	G	G*	G	G	G	G	G	G	G	G	G	G
Red-neck^2															R	R	R*	R†	R		G	O	O	O							
Red-B-neck																R	R	–	–		–	X*	X	X	X	X	X	X	X	X	X
Blue-1																		–	–		O	O*	O	O	O	O	O	O	O	O	
Red-left-spot & nose																		–	–		G	G	G*	G	G	G	G	G	G	G	G
Red-right-Z																				–	–	G*	G	G	G	G	G	G	G	G	G

COWS — NOVEMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Green-neck	G	G	G	G	G	left																
Red-A^2	G	G	G	G	G	G	G	G	G	G	G	G	G	G	left							
Blue-tail	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	left						
Blue-neck	G	G	G	G	G	G	G	G	G	G	G	G	G	left								
Blue-left-spot	G	G	G	G	G	G	G	G	G	G	G	G	G	G	left							
Red-B-neck	X	X	X	X	X	X	X	X	X	X	X	X	X	X	left							
Red-left-spot & nose	G	G	G	G	killed																	
Red-right-Z	G	G	G	G	G	G	G	G	G	G	G	G	G	G	left							

TABLE XX. Movements of 43 marked elephant seals throughout the breeding season, Signy Island, 1949. Periods of extensive breaking-up of fast ice, October 15th–20th and final break-up on November 18th.

Presence at a harem is represented by letters: Rr = Red Harem; Gg = Green Harem; Oo = Orange Harem; Xx = small Harem near Green Harem.

Where a letter is in italic type the record is uncertain. For the bulls capital letters mean dominance (in charge of a harem), small letters signify a subordinate status.

– means observed but not at a harem; * pup born; † pup died.

An incident reported in the field notes for October 9th, 1948, illustrates such behaviour: "Female A lies on her belly, occasionally raising the hind part of the body and rocking back and forth, pivotting on the belly. She makes a low, sustained moaning noise. Then she moves over to cow B which is lying some yards away with her pup. Cow A rests her head on the hind flipper of B which tries to move away—A snaps at her. B's pup is yapping and nuzzling for the nipples of its mother. Cow B moves away with her pup and A follows and pivots round so that they are lying head to tail. Cow B then turns on her side for the pup to feed, cow A still making occasional movements."

Later in the season, after the establishment of the first harems, the parturient cows tend to bunch close together, away from the cows which have already pupped. Except for a few early individuals, only four cows out of over 2000 under observation at South Georgia gave birth to the pup solitarily, and then only because bulls prevented them from moving to a harem. At South Georgia it was very obvious that there was a tendency for cows to make for the largest aggregation of females after hauling out, and often when a cow had joined a small harem she would move away and join a larger harem. Thus, at Dartmouth Point in phases *iii* and *iv* of the establishment of rookery organisation (p. 53), the harems increase in size from five to about twenty-four cows before new harems begin to form.

Darling (1938) has drawn attention to the beneficial effects of concentration on the breeding of colonial nesting birds. The mechanisms initiating parturition are little known as yet, and it is possible that the concentration of breeding females may hasten the process, but the parallel with bird colonies is very imperfect.

It has already been pointed out that at Signy Island pupping follows more closely on the haul-out than at South Georgia where the aggregations are larger. This is thought to be the effect of the presence of fast ice.

2. *Parturition*

Owing to the small size of the breeding population at Signy Island, only one birth was observed (through binoculars) but the incident reported above probably indicated the onset of labour in female A. Labour contractions began in a cow which was under close observation at Dartmouth Point about forty-five minutes before the pup was expelled. The following account is taken from field notes for October 10th, 1951:

"The contraction began at 1600 hours, the cow lying on her belly with the neck bent at right angles and the muzzle lying on the stones, the mouth slightly open. Lateral compression of the flanks results in the body moving up and down in spasmodic jerks. The cow raises her head for a short time with eyes closed, the contractions continuing, coupled with a slight rolling motion. The cow then rests her head on the ground and the slight jerks continue, rather like hiccups. At 1620 hours the cow begins to lift the pelvis at each series of contractions, moving the hind part of the body from side to side. The vulval opening gradually enlarges and at 1630 hours the movements become more convulsive, the hind flippers being well raised into the air and the tail elevated. The animal is quite silent all the time, and the eyes are mere slits. At 1635 hours she moves forward a few inches and a slight trickle of amniotic fluid and blood flows from the vagina. The semi-transparent foetal membranes are now visible at each contraction extruded like a balloon, with the black fur of the foetus visible through them. At 1640 hours the movements increase in strength, each one pushing the membranes further out, though they slip in again during the relaxed phase. Then the cow inches forward, facing downhill; the membrane breaks and the pup's head is visible. The cow, moving forward slightly, swings the hind part of the body vigorously from side to side and the pup, divested of membranes, slides out in a rush at 1643 hours.

"The pup starts yapping immediately and the cow makes a slight gargling sound. She is apparently trying to bark; the mouth is open and the throat vibrating, but no sound comes except a very short 'yodel'. The cow nuzzles the pup, starting away at first in surprise when she touches it. At 1645 hours the pup is moving, eyes wide open, and at 1647 hours the cow swings her hindquarters around. The umbilical cord breaks at a weak spot, noticeably redder in colour. The pup begins to search for the nipple and the cow 'bites' it gently on the neck. The after-birth had not occurred ten minutes later."

The actual expulsion of the pup in this case took eight minutes. In two other cows under observation it took ten and four minutes respectively and the pup was expelled tail first. In two other births, for which full observations were not possible, parturition took about four and almost fifteen minutes respectively. Angot (1954, Plate II) gives photographs of the process and states that the young were born tail first in the two cases observed. It seems that this type of presentation is more common than the other. He also states that the size of the young is correlated with the size of the mother, the largest mothers having the largest young, but no evidence for this resulted from the present study. The placenta is either expelled with the pup or up to one hour later.

Cows were invariably silent immediately after giving birth (six cases), the pup's first bark usually occasioning an outburst of "yodelling" (p. 21). Usually the cow begins to make the sand-flipping motions just after parturition, sometimes scooping up the bloody placenta by accident; she does not attempt to clean the pup.

3. *After Parturition*

Attention has been drawn to the extensive wanderings which were carried out by many of the breeding cows at Signy Island before their pup was born and after they had hauled out for the purpose of parturition (p. 59). After parturition the cows move very little and the attachment of the cow to her pup and the latter's inability to move far are an important factor in holding the harems together. Many case histories of females in the small South Orkneys colony prove this point.

Harems occasionally moved as much as fifty yards in the course of several days and in 1948 cow G/7, which pupped in the gap between the northernmost of the Thule Islets and the shore, moved about 300 yards in two days with her ten-day old pup to join the Green Harem. No greater movements are usually made.

> At Dartmouth Point on October 7th, 1951: "I repainted the marked cows in Area 8. They are R/O(2), Y/O, R/OX, R/n(2), R/n and S, R/X, R/r/F and n. All were more or less together in a small group where originally painted, indicating that cows move very little when suckling pups. Those which had moved to the beach, R/O and R/X, were unaccompanied by pups and had probably lost them." (Field notes). The time intervals between these observations were twelve to eighteen days.

The accounts given earlier (p. 51) refer to females hauling out in an exhausted condition after the harems had been carried out to sea. This suggests that the cows had made prolonged attempts to help their pups to keep afloat or to haul out again. It is inconceivable that an animal so at home in the water as the adult elephant seal would be exhausted for any other reason under these circumstances, but only once was a female seen trying to help her pup in the water.

> On November 18th as the ice beneath the Green Harem cracked, a pup fell into the water when a crack opened beneath it. "As the crack widened the pup was seen splashing about, occasionally diving under, the hind flippers out of the water. . . . Occasionally, the pup yapped and the cow kept up a constant moaning bark. . . . It appeared that the pup was unable to get the hind part of the body out of the water, since it lay half out of the water for some time splashing wildly with the hind flippers. The cow bit at the pup as if trying to pull it out and then joined it in the water and appeared to be trying to push it out. The bull re-entered the water and grasped the cow by the neck drawing it away. . . ."

When the cows lost their pups at Signy Island, owing to the break-up of the ice or from other causes, they again undertook extensive wanderings and the bulls were powerless to prevent them.

> Thus, in 1949, cow Y/+ moved two and three-quarter miles in one day, visiting the Orange Harem, and then returning to the Red Harem. Cow Y/r/+, after the death of her pup, left the Red Harem, visited the Green Harem and then moved on to the Orange Harem, where she remained for several days (Table XX and Figure 23); cow $R/_x$ did exactly the same. In 1948 many of those cows which lost pups when the fast ice broke up joined harems on the shore, but were often restless and moved again to other harems.

In general, then, once the pup is born the cow is confined to its vicinity until it is weaned or lost.

Females of many mammalian species tend to become irritable, generally defensive and even positively aggressive during the infancy of their progeny. The elephant seal is no exception and the abrupt and complete change in behaviour which occurs immediately after the birth of the pup is startling. In addition to showing the supposed displacement activities of "yodelling" and sand-throwing (pp. 20 and 21), the formerly timid females become intolerant of disturbance within a very short time of the birth. At this stage the sheathbills (*Chionis alba*) peck at the afterbirth and the pup, and at the swollen vulva of the cow, causing the cows to fight amongst themselves and even to maul their pups. Skuas (*Catharacta skua*), giant petrels (*Macronectes giganteus*) and gulls (*Larus dominicanus*) also persecute the seals in this way but are not so persistent.

> A cow gave birth to a pup in the Green Harem on October 11th, 1948. "Six dominican gulls arrived within a few minutes of the afterbirth and stood in a ring around the seal. Then a giant petrel flew in and landed about a yard behind the cow. It tried to drag the placenta away and took a bite at it. The cow turned, roaring, and snapped at the bird. The giant petrel then galloped around, first on one side and then on the other, with

the cow swinging right and left and making lunges at it. She recovered her normal harsh roar soon after extrusion of the placenta.

"The giant petrel eventually gave up and began to peck at the pup's umbilical cord and finally squatted down a yard or so from the female. She occasionally roused and made a lunge, apparently stimulated by the pup's barks. The birds increased to nine pairs of dominican gulls and two sheathbills. The giant petrel pecked at the pup's back and pulled out some tufts of hair. It then walked away, cleaned its bill in the snow and settled down again. Two skuas arrived and the gulls rose and mobbed them." (Field notes.)

On September 23rd, 1951, on Dartmouth Point: "None of the pups were suckling (1700 hours); only two were with their mothers and the others were wandering around yapping incessantly. They were pecked at by sheathbills and snapped at by other cows. The sheathbills are daring rogues; they peck at the cow's hind-quarters, also the pup's fore and hind flippers. The seals have no effective retaliation, for when they swing around roaring, the cause of the trouble walks off sedately just out of range."

The gregarious habit of the seals affords them some protection from this persecution, because it means that the freedom of movement of the birds is restricted, so that at South Georgia the sprightly sheathbills are the main cause of irritation.

The early period of "hysterical" behaviour ends within one or two hours when the birds have disposed of the afterbirth, but the cows remain very quarrelsome during the remainder of their time ashore. They remain ashore until the pups are weaned (at an average age of twenty-three days) so that they spend an average of twenty-eight days and thirty-one days (at Signy Island and South Georgia respectively) without food. The fact that they also lose probably over 700 pounds in weight when suckling the pup further contributes to their irritation.

In contests for position they usually make the open-mouthed threat (Bartholomew, 1952), and may rear up and lunge forwards to strike with their upper canines. Often they will nip the flanks of a nearby cow when it is not looking. The cows may rear up to look along their backs at the cause of a disturbance, or turn around by swivelling on their bellies, but they cannot remain erect upon the hinder third of the body like the bulls. To a human intruder they react in the same way as to another seal, rearing-up, roaring and giving the open-mouthed threat, and then striking.

As already mentioned, the maternal instinct varies considerably. The cow often snaps at the pup during the first day and does not let it suckle for long. While most cows will attack the cause of any disturbance and defend the pup, others will be indifferent to the pup or desert it. Two cows under observation deserted their pups when separated by the bull, but very occasionally cows will adopt another pup if they lose their own. Only one authentic case was recorded; when two cows fought over a pup and the cow which had lost her own pup won (p. 51, "19.x.49 . . ."). When the pup is trapped in a melt-hole (Laws, 1953b, p. 54) the cow usually remains nearby for several days before leaving. On September 23rd, 1951, at Dartmouth Point, "Cow R/X, after I removed her pup from the hole, repeatedly stared into the hole with goggling eyes and an amazed expression, emitting a throttled bark. The pup crawled towards her, yapping, but she continued to look into the hole. It was as though she had come to associate her pup with the hole but otherwise did not recognise it!" (Field notes.)

4. *Lactation*

The lactation period of thirteen marked cows varied from twenty to twenty-seven days, averaging twenty-three days, which was the actual time for six cows. The nipples are usually two in number, in one case four, and are abdominal in position, being situated one on either side of the umbilicus, 10 to 12 inches apart. Usually they are retracted, but may protrude about one inch above the surface when the pup is feeding. In the blubber beneath each nipple is a small ampulla which serves as a reservoir for milk, and the paired mammary glands, overlain by the blubber and resting on the fascia of the trunk muscles, are situated about two inches lateral to the nipples. During lactation each gland is ellipsoidal in shape, may attain a size of 33 x 10 x 4.5 ins. in a large cow, but in an average sized cow it is about 23 x 8 x 3 ins. when full of milk. Outside the breeding season the dimensions of each gland are about 13 x 5 x 1 ins.

The mammary glands of several marked cows, for which the date of pupping and history was known, were measured and the approximate volume calculated from the formula for a triaxial ellipsoid:

$$V = \frac{4}{3}\pi abc$$

where a = half the long axis, b = half the longest diameter, and c = half the smallest diameter. For

purposes of comparison ten cows were selected, all of standard length about 100 ins. and suckling or about to suckle their first pup. Prior to parturition the gland is very small, with a calculated volume of about 500 ccs., and exhibits little secretory activity (four days before birth of the pup). Within a very short time after the birth of the pup the gland is actively secreting the rich creamy milk (its properties have already been considered, Laws, 1953b, p. 35). During lactation the size of the glands varies greatly, according to the time which has passed since the pup was last fed. The calculated volumes of lactating glands range from 1.97 litres to 5.28 litres. The volume of the glands when the alveoli are empty of milk is probably 550 ccs. Both the pre-parturient gland measured, and one gland of female M143 which had lost her pup and in which secretion had ended, had calculated volumes of this order. Assuming the empty gland to have a volume of 550 ccs., the milk capacity of the largest gland measured (in this sample) was 4.75 litres but the maximum capacity is probably in excess of this, say 5 litres or more.

Towards the end of lactation the young gains weight at the rate of twenty pounds a day (Laws, 1953b), all of which comes indirectly from the blubber of the cow, through the secretion of the mammary gland. Assuming the combined capacity of the two glands to be rather more than 10 litres, they must be completely refilled about once in twenty-four hours to account for the weight increase of the pup. There are long intervals between the suckling periods of the pups and at any moment less than two per cent of the pups are seen to be feeding, so it may well be that there are only one or two suckling periods each day or at night. When the cow loses or finally leaves the pup the mammary glands soon return to the resting state, the milk becoming very thin, yellow and oily before secretion stops.

Lactation probably plays an important part in maintaining the maternal instinct, though it is probably incorrect to regard it as *l'origine de l'amour maternal* (Giar, 1905). Consequently, when the cow ceases to be stimulated by suckling she deserts the pup and weaning may occur in this way.

The young have a very strong instinct to search for the nipples, which operates within a few minutes of birth, but the cow does not usually permit suckling for an hour or more.

The attitudes adopted by the pup and mother during suckling are those common to all phocids. The cow lies on one side and the pup at an angle to her (Laws 1953b, Figure 27). When exploring the mother's side the pup makes a great deal of noise, sucking at the skin and yapping with frustration. The trial and error nature of the search is emphasised by the observation that pups are occasionally seen exploring the side of a bull in this way. The cows were not seen to help the young, except that they occasionally nosed the pup towards the nipple when there was a pressure of milk in the glands. The mother was never heard to invite the young to feed by *un long cri aux accents doux* as Angot (1954) states. When the pup finds the nipple and is actually feeding it makes very little noise. The breasts apparently expel milk when the nipples are stimulated by the pup, for when a pup changes from one to the other a small jet of milk often flows for a few seconds.

5. *Oestrus and Mating*

Observations of the behaviour of marked cows at Signy Island indicated that oestrus began about eighteen days after parturition and lasted for several days, presumably until their departure to sea five days later. Copulation normally occurs on land or fast ice, and for ten cows under observation at Signy Island in 1949 the first successful copulation was recorded thirteen to twenty-four days after parturition, averaging nineteen days. For another six cows in 1948 the latest unsuccessful copulation averaged seventeen days. At Dartmouth Point, South Georgia, of twenty-four cows which were killed at known ages up to twenty-two days after parturition, only three examined, twenty, twenty-one and twenty-two days post-partum, had ovulated. We may say then, that at both Signy Island and South Georgia, oestrus usually begins eighteen days after parturition and lasts for at least five days. Cows which lost their pups came on heat slightly earlier than lactating cows, and remained ashore just over nineteen days (average of fourteen cases) instead of the usual twenty-three days. In all these cases the cows lost their pups in the first half of the lactation period. (Cow Y/X, at Signy Island (1948) lost her pup at seventeen days, when the ice broke up, was not seen for four days, and then joined first the Yellow Harem and later the Mirounga Flats Harem for sixteen days, making thirty-seven days in all. It is possible that here is a cow which escaped impregnation because of the disturbance caused by the break-up of the fast ice, and came on heat for a second time.)

The observations of Angot (1954) also conflict with Matthew's (1929) statement that the cow "will not take the bull until a week or ten days after the birth of the pup". By considering the date of the first birth and the date of the first observed mating at Kerguelen he concluded that mating occurs twenty-one days

post-partum. But we have already seen that there are extensive individual variations. Angot also suggests that oestrus lasts for twelve days, but his figure is based on what appears to be an erroneous estimate of the length of the suckling period, since it is unlikely that there are such great differences between the various localities.

Before the cows come on heat they are indifferent or even aggressive towards the bulls and will not permit mating. Unwilling females keep the hind flippers together and swing the hind part of the body from side to side, effectively frustrating the bull's efforts. When in heat they are sexually receptive to any male, and indeed at one harem on Signy Island they were seen actively to seek out the bull for mating. Usually, however, the male is the aggressive and active member.

Males will attempt to mate with females at any stage of the cycle, often with isolated cows on the sea ice, and sometimes with females which are still gravid. Angot suggests that the males know the females are on heat *par l'intermediare d'effluves quelconques*. No constant tendency of the male to lie on one particular side when pairing was noted.

Bartholomew (1952) has described copulation of the northern elephant seal and as it does not differ materially from that of the southern species, only a passing reference will be made here. When about to pair the bull usually lies with his neck across the back of the cow, pinning her down. He then takes hold by biting her neck, places one fore flipper over the cow's back and with it draws her to him. Then, lying half on his side, he draws his hindquarters up towards the cow's vulva and protrudes the penis. The cow lies on her belly and, if willing, elevates the tail and abducts the hind flippers. Without this co-operation the male never succeeds in inserting the penis into the cow's vulva, and even with the co-operation of the cow the male's first attempts at insertion are often unsuccessful. At the beginning of the pairing time coition lasts for about ten minutes, both animals lying quiescent and then the cow usually moves away, terminating the act. The "peculiar trumpeting call", said occasionally to be made by the bull just before mating (Sorensen, 1950, p. 19) was not heard at any time by the present writer. At the beginning of copulation the bull makes a series of pelvic thrusts and then becomes passive. During the last half of the act the cow often assumes the active role, small undulations pass slowly up the lower part of her body and she flexes and extends the hind flippers. Often the cow raises the fore part of her trunk and mouths the neck of the bull, or makes the "yodelling" vocalisation.

The males are very active sexually and at the height of the pairing period when the majority of cows are on heat, they pair with the receptive cows in rapid succession, the length of the individual act is shortened to three or four minutes, and a bull has been seen to impregnate four females in less than an hour.

Although mating normally occurs on land it has several times been observed taking place in the water. At Signy Island on November 18th, 1949, the fast ice was breaking up under the Green Harem and when a pup fell into the sea the cow went in after it. "The bull re-entered the water, and with his teeth grasped the cow by the neck, drawing her away [from the pup]. There was some commotion and it seemed that the bull was trying to pair with the cow, for his body was under water for some time, the arched back being the only part visible. Presumably the cow was underneath, for this position in the water is unusual, and it is highly probable that copulation occurred. They remained still for about three or four minutes and then broke surface together. The cow appeared to have lost interest in the pup and swam with the bull in one of the leads of open water" (field notes observation at 300 yards with binoculars). This behaviour is almost identical with Angot's (1954) description of aquatic mating and with that of mating in the harp seal (*Phoca groenlandica*) given by Sivertsen (1941, p. 76).

There is little doubt that it was a case of aquatic mating and several other indisputable matings were seen in shallower water, both at Signy Island and South Georgia.

6. *Post-Lactation*

At Signy Island and South Georgia the cows left the harems when the pups were weaned and returned to sea. This necessitated a long journey across the sea ice, in the case of those cows at Signy Island which left their pups before the fast ice broke up. It seems probable that the majority of the females remain at sea for several weeks from the end of lactation until they haul out again for the moult (Figure 8). There is one authentic record of the time relations of breeding and moult, for at Signy Island in 1948 a marked female turned up on the west coast on December 27th at least five weeks after it was marked on the east coast. (This was a yellow mark but owing to weathering was not further identifiable.)

E. Mating of the Virgin Females

So far, only the behaviour of mature female elephant seals has been described. It is influenced by the necessity for bearing their pups on land or ice, and copulation takes place on land because the cows are still suckling their pups at the time when they come on heat.

In the majority of seals the mating act takes place in the water and is rarely seen. In some species it can take place either in or out of the water (Sivertsen, 1941, p. 75) but most of the evidence is in favour of aquatic copulation being normal and terrestrial mating (or pairing on the sea ice) being necessitated by the rapid onset of post-partum heat while the cow is still suckling the pup.

Earlier writers have all stated that, in the case of the elephant seal, the virgin females are impregnated on land several weeks after the pregnant cows haul out, but in the present study only a very few two-year-old females have been seen on land, either at Signy Island or South Georgia. At Signy Island there are only three references, in the field notes, to virgins seen ashore during the breeding season. On October 12th, 1948, "One young silvery-grey cow which looked like a virgin was lying a little way from the main group" of the Red Harem. This later gave birth to a pup and was presumably a precocious breeder, since cows are rarely known to reach sexual maturity when one year old. On November 5th, 1948, four cows which may have been virgins were seen in Stygian Cove and a "possible virgin" the following day on Drying Point Beach. At South Georgia very few females suspected of being virgins were seen during the breeding season, and these cows invariably produced pups a few days after they were first seen. The age group is represented in the collected material by only two individuals, including one precocious female which gave birth to a pup at two years of age.

The evidence of the classified counts at Signy Island suggests that yearling and two-year-old female elephant seals rarely appear on land (earlier, p. 34). Numerically, the younger age groups of any animal are the largest because they have not yet been subjected to the effect of mortality operating over the years. If the virgins mate on land it would have been very obvious to an observer, for they constitute about thirty per cent of the total of adult cows. In fact, practically all of the cows ashore during the breeding season gave birth to pups (Figure 8) and the remainder were mature animals which had aborted or did not mate successfully in the previous season and missed a pregnancy.

In view of this negative evidence, therefore, it is highly probable that females mating for the first time (almost exclusively two years old) are not impregnated on land but in the sea, probably in the usual breeding season of the adult cows. In this connection the following behaviour may be relevant. "A medium bull and a young cow were gambolling in the water offshore. . . . They were striking each other's necks with their chins and the bull placed its fore flipper over the cow several times as in the preliminary to copulation on land. The cow became quiescent and then both began to play again." (Field notes for November 8th, 1948). Mating was not observed.

Recently Angot (1954) has produced similar evidence showing that at Kerguelen the virgin cows are not seen on land during the breeding season. Sorensen (1950, p. 13) also disagrees with Matthews' (1929) statement that virgin cows haul out much later than the mothers and join the harems already formed on the beaches. He says that "occasional virgin cows do join the harems on the beaches during the season; but many also are impregnated by stray bulls elsewhere and at any part of the breeding season". He implies, however, that mating is terrestrial.

There is one other possibility, namely, that the virgin cows are impregnated on land in some remote locality. Darling (1939) found that at North Rona the virgin grey seals mated on outlying skerries. At South Georgia, however, such an occurrence would have been known to the sealers.

We may therefore conclude that although the actual place of the mating of the virgin females is likely to remain a mystery, it probably occurs in inshore waters.

F. Behaviour of the Pup

Although the growth and development of the pup have been described in a previous paper (Laws, 1953b, p. 25–38) it will be convenient to summarise the information already given there, together with that in the present paper.

The young are born at Signy Island in early October, five days after the cows haul-out; at some localities in South Georgia pupping begins rather earlier and the cow hauls out eight days beforehand. At Kerguelen

the season is the same as at South Georgia and the pup is said to be born from four to six days after the haul-out.

At birth the pup bears a black coat of long silky hair which quickly weathers to a woolly brown appearance. It weighs about one hundred pounds and measures about fifty inches from nose to tail. During suckling, which lasts just over three weeks, a thick layer of blubber is deposited, the weight increasing fourfold and the girth being almost doubled. The umbilical cord is shed at eight days. Some three per cent of the pups at Signy Island are born having undergone a pre-natal moult of fur, but usually the moult of the natal fur first becomes obvious at about ten days of age, and is completed at about thirty-four days. The pups first enter the sea voluntarily just after the moult is completed but in abnormal circumstances, such as the break-up of the fast ice around Signy Island, they can swim at a much earlier age.

After weaning at twenty-three days of age the pup exists on the stores of fat laid down during suckling, losing weight at the rate of three to four pounds a day until it begins to be successful in feeding.

These figures are all averages and there is considerable individual variation. Angot's (1954) observations are in moderately close agreement; he gives the time of the beginning of the moult as two weeks, weaning at four weeks to a month, and the end of the moult at five weeks. His figure of two per cent for the pup mortality during this time agrees well with the figure of 2.1 per cent given by Laws (1953b).

1. *Before Weaning*

The birth of the young and the suckling period have already been described in relation to the behaviour of the mother (p. 62) and at the risk of some repetition the behaviour of the pup at this period will now be described.

> It is born with eyes open and within a short time begins to search for the nipples. It proceeds by trial and error, making varied snorts and sucking sounds. "The R/G cow lies on her side and the pup begins to search for the nipples, beginning at the fore flippers and working slowly backwards and up and down over the belly of the cow. It does not find the nipple and the cow rolls over onto her belly. . . . The pup barks incessantly and the cow occasionally raises her head and roars harshly in response." A day later this same pup, "was suckling from the upper nipple of its mother, with lips parted and a good deal of snorting, coughing and swallowing. The cow rolled over once with a bellow, presumably because the pup was too eager and bit with its only two teeth." (Extracts from field notes). Angot (1954) says that as a result of the behaviour described the nipples are often surrounded by an area of raw skin.

The cows squabble among themselves at this time and often bite a strange pup if it comes too close. A hungry pup, on its own, will make for the nearest seal, yapping persistently on a querulous note; it does not appear to be able to recognise its own mother. One which had just been marked with a metal clip on the flipper, went up to the bull, which was lying on his side and began to search for the nipple. The bull roared and reared up, but the youngster was persistent and the bull eventually moved away a few yards to escape its attentions. Three of the females had wounds on the rump, inflicted by this bull.

Usually, the young pups take milk only from the lower breast but the older pups have surprisingly extensile necks when feeding. On one occasion two pups were seen suckling from the same cow, one above the other. It has already been suggested above that there may be only one or two suckling periods each day, because when undisturbed and under observation only a minority of the pups are seen to feed.

> On September 23rd, 1951, in the vicinity of Dartmouth Point: "I sat for about thirty to forty minutes watching the harems in Area 8 from the hill above. None of the pups was suckling; only two were with their mothers and the others were wandering around yapping incessantly. They were pecked at by sheathbills and snapped at by other cows." On October 7th, I sat for an hour at the top of the cliff at the south end of Area 1 watching the general activity of the harems. The bulls were quite motionless on the whole, but the pups yapped and moved continually, causing the cows to move and precipitating squabbles between them. The sheathbills were much less in evidence. Very few cows were engaged in suckling pups and there were three or four pups grouped together in places, having left or been left by their mothers for the time being.

Although the pup does not recognise its mother, the mother is able to recognise her own pup in some way, probably by smell, since in spite of continual separations the marked cows and pups were reunited.

At Signy Island the pups "appear to be unaffected by the severity of the weather. Five were sheltered by their mothers, two were not and one pup was suckling on the windward side of its mother. But all were equally resentful of disturbance. The driven snow and ice covers muzzles and heads in a thick mask of

ice." At South Georgia, on the other hand, the pups appear to suffer from the heat on the warmer days. On one such day "there were several cows with pups in the water owing to the overcrowding of the beach. There was a certain amount of snow- and shingle-flipping. One pup attempted to suckle in the water which was nine inches to a foot deep. On other beaches cows and pups were lying at the water's edge, quite wet from the surf, and I suspect that some pups must be lost in this way."

The pups are very active within a short time of birth and are able to bend their fore flippers in all directions with ease. When the moult begins they are able to scratch all parts of their body to relieve irritation. They can raise their heads so as to look along their own backs in the manner of the adults. Occasionally, they rub the plantar surfaces of the hind flippers together, the digits being spread out so as to stretch the webs (Figure 24b).

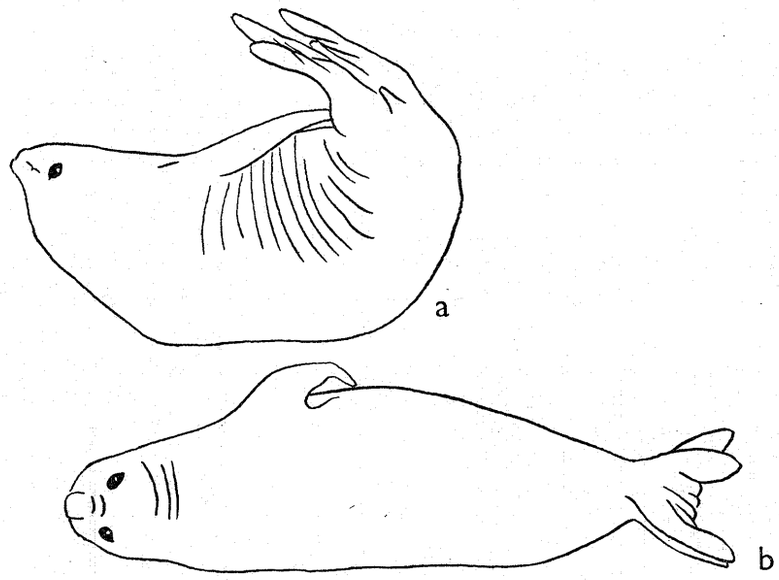


FIGURE 24. Attitudes of young elephant seal pups.
a. scratching with fore flipper.
b. rubbing hind flippers together.

2. *After Weaning*

When weaned, the pups first lie in ones and twos at the fringes of the harem in which they were born and after a day or so move up to the back of the beach and often into the clumps of tussac grass beyond. There, inland of the harems, they aggregate in pods numbering several hundred individuals. It is convenient to call the young at this stage "weaners". There they remain for up to two weeks, sleeping, scratching (Figure 24) and indulging in mock-battles. They then find their way back to the shoreline, where they browse in the pools or shallows before venturing out to sea (Plate VIId).

In parts where the shore is not too precipitous the "weaners" enjoy lying in the freshwater streams and pools, often turning the latter into veritable mud baths filled with a thick, viscous evil-smelling mud, which no doubt hastens the moult process (Angot, 1954, Plate IV). At Signy Island the soil is too deeply frozen to permit the formation of these wallows at that time of year and at South Georgia the soil cover is often relatively thin. It is only at the Falkland Islands and on Kerguelen that the wallows reach considerable dimensions and no doubt some "weaners" are trapped in them, being unable to climb up the slippery sides, just as the younger pups are trapped in the holes they melt in the snow. Other causes of mortality of the young animals have been discussed in an earlier paper.

G. THE MOVEMENTS OF THE MALES

There is a tendency both at Signy Island and South Georgia, for the large bulls to haul out earlier in the season than the smaller ones (Figure 25) and the majority of the breeding bulls have arrived before the

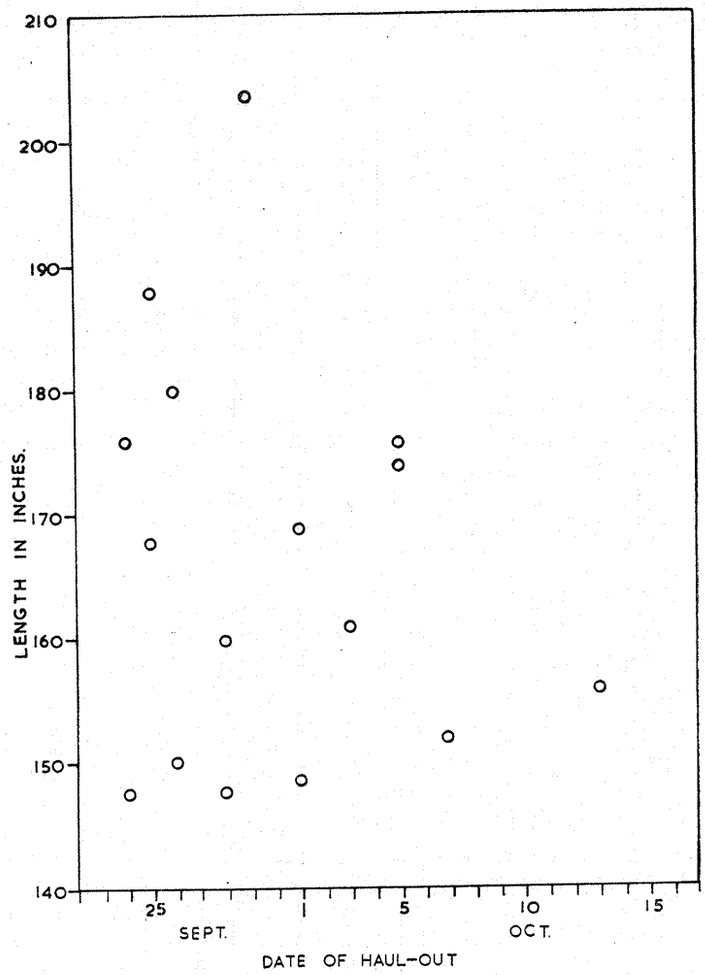


FIGURE 25. The relation between the length (measured photographically) and date of the first haul-out of sixteen bulls at Signy Island in 1949.

peak pupping period and long before the cows are ready to mate. At Signy Island they lie out on the sea ice for several days before the formation of the harems and some re-enter the water at intervals. At South Georgia at this time they frequent the usually snow-covered tussac flats behind the beaches, and at Kerguelen according to Angot (1954), they prefer to remain in the surf.

1. *Movements of Marked Bulls at Signy Island*

In Tables XIX and XX the day to day movements of twenty-six marked bulls which were kept under observation in 1948 and 1949 are set out; the period before the formation of the first harems is not covered by the 1948 data. The only bulls which are known to have been present in both years were the "Scarred-eye" bull and the "Scarred" bull. In 1948 it was believed that the latter and the "Red" bull were one animal, and if this be so, then he took charge of a harem in the same area at approximately the same date each year, and departed at the same time, spending a few days on land after the cows left. In 1948 he remained out of the water for over forty-eight days and in 1949 for fifty-five days (almost eight weeks) without feeding; he was the largest bull actually measured, either on Signy Island or at South Georgia (over-all length in 1949, 20 feet). The largest bull seen at either of these localities (the "Green" bull) was estimated, by comparison with the "Scarred" bull, to be 23 feet long; he probably went without food for at least sixty-five days, from September 17th to November 21st, 1948.

The tables show that, far from remaining with the same harem throughout the season there may be movements involving a distance of several miles on the part of both dominant and subordinate bulls.

For example, the "Green" bull left the Green Harem on October 16th, displaced the "Red-Yellow" bull for the period October 19th to 22nd and probably the "Red" bull (="Scarred" bull) from October 23rd to 29th. The "Green " bull then returned to his own harem (which had remained without a bull until October 27th), stayed there for two days, took over the Yellow Harem from the "Scarred" bull for November 1st, and then returned to the Green Harem until the cows left. Owing to his great size he rarely had to fight for possession; even the "Scarred" bull retreated after a very short battle. The "Green" bull was not present in 1949.

This behaviour is not usual, for the movements of the "Green" bull were voluntary. Usually a bull stayed with a harem until he was displaced by another bull or by the break-up of the fast ice, and then either remained as a subordinate at his former harem or moved to another harem and challenged the dominant bull there. Subordinate bulls may remain in the vicinity of one harem ("Chinese", "Yellow-A", Table XIX) or make extensive journeys ("Red-Yellow", "Yellow+", Table XIX; "Red-tail", "Yellow X", Table XX). At Signy Island there were, on average, five subordinate bulls to each harem and the over-all sex ratio in the breeding season was about two cows to each bull.

The longest recorded journey of this kind is that of "White-nose" which wandered at least fifteen miles under and over the ice (p. 15); "Scarred-eye" travelled ten miles over the ice in 1949 (Figure 23).

2. *Movements of Marked Bulls at South Georgia*

At South Georgia the movements of only eight marked bulls were followed for any length of time, but as the observations support the conclusions already reached and give an impresssion of the complexity of movement, they are summarised below.

Only one marked bull (the large bull R/F) was with the same group of cows for the whole period of observation and his case is similar to that of the "Green" bull at Signy Island in 1948. He was in more or less undisputed command of Area 8 from September 19th until October 11th, when the observations were perforce ended, and it was recorded on September 28th, "Bull R/F now has eighty-five cows with eighteen pups, and six 'bachelor' bulls on the outskirts. The latter fight amongst themselves and one chased another through the edge of the harem. Although this was fifty yards from R/F he rose up and roared, at which the others fled. It leaves no doubt but that R/F controls the whole eighty-five cows." On October 4th, although still in undisputed control, he was seen to have moved from a group of eighty-seven cows in the tussac area to one of twenty-two cows on the beach, presumably because the latter group was more receptive sexually.

This bull was never seen to have recourse to fighting. His aggressive roar was sufficient to deal with all opposition, as on the occasion described above.

Another bull (L/Sc/ff) displaced a large bull (R/n) from Area 1 on September 25th and remained there until observations were discontinued on October 11th. The maximum number of cows in this bull's group at any one time was eighty-eight on September 30th, but it was sometimes difficult to determine his domain owing to the crowded state of the rookeries. Thus, on October 5th, "There are no new harems in Area 1 and the position is complicated. L/Sc/ff still has the largest number of cows (fifty-two cows and twenty-one pups). In the large group of cows there is possibly a break and I attributed the next forty-six cows to another bull lying thirty yards south of L/Sc/ff. It is difficult to be more precise. The bull in the next harem is forty yards south again, with another bull in the same group of cows lying only six yards away. The next dominant male is twenty-five yards away to the south. Very few cows are now lying on the snow. The tendency is to move to the water's edge, and the harems are strung out along the edge of the beach. Area 1 is now quite full and small harems are forming on adjacent beaches. . . ." (Plate VIIb).

Bull R/n which was defeated by L/Sc/ff on September 25th moved to Area 6, near the camp, where there were twelve females and remained in charge of a harem throughout the period of observation. The maximum number of cows in this group was seventy-one on October 5th, when, "he spent half the day in the water chasing cows back to the harem. In the water the cows make little active attempt to escape but are very stubborn. The bull bites their necks and tries to turn them back but is successful with only half." The following day he had "thirty-eight cows and sixteen pups, thirteen cows and four pups having split off the south end of the group to form a new harem with a small male".

Bull Y/n was originally at the small harem in Area 6 but was displaced on September 21st by an unmarked bull (later defeated by R/n). He was seen on September 23rd to be a subordinate at Harem 8a* but was thereafter absent from the area.

* See footnote on p. 6.

On September 24th the bull at Harem 8b was marked R/↑ but the following day it was seen moving south from Harem 8a presumably having been defeated by R/F. From September 26th to 29th it was in charge of Harem 10 but displaced bull R/m/Y/n on September 30th (R/↑ losing his proboscis in the fight!) and took over Harem 12 from this bull. He remained in this area throughout the remainder of the period. The harem numbered fifty-four cows and nine pups when R/↑ moved in but later split into two groups of cows designated 12a and 12b. The former group was in the tussac grass behind the beach; the latter, which was smaller, was located on the beach. Bull R/↑ remained with the group of twenty-four cows on the beach (probably because they were more receptive sexually), and bull Y/T, which had been subordinate to R/M/Y/n later appropriated the forty-one cows comprising Harem 12a. There is no doubt that although he remained with the smaller group of cows, R/↑ was dominant in the area, for on October 6th "Area 12 was again in commotion. This morning R/↑ was on the beach with twenty-seven cows and fourteen pups but later he was rounding up cows from inland [i.e., Harem 12a] and attempting to copulate with them. None of the cows would accept him. The other bulls kept away, so evidently R/↑ controls the whole harem complex when he wishes. His nose is festering badly and looks a glutinous bloody mass. Moreover, he does not appear to have much vitality."

Bull R/m/Y/n, was in charge of Harem 10a on September 24th and 25th before moving to Harem 12a, from which he was driven by R/↑ on the 30th. . . . Bull Y/1/ff and n was at Harem 10b until he fought with R/↑ on September 26th. He was subordinate to R/↑ the following day and moved to Area 8 on September 28th. Later he moved back to Beach 10* where he was in possession of two females on October 3rd. When last noted he was back at Harem 8d but the bull in charge of Harem 8e chased him away after a few blows had been exchanged.

In other words, both at Signy Island and South Georgia, a few large and powerful bulls remained in charge of the same harem for lengthy periods, moving only when they were inclined, and then usually in the direction of the sea. The remainder of the bulls were either dominant for some days at one or two harems before being displaced by a more powerful male, or, never becoming dominant, wandered from one harem to another. Thus, paint-marking has shown that the bull population in the localities studied is continually changing during the breeding season. There is no reason to suppose that this does not hold good for all breeding rookeries. Angot (1954) has figured the "permutations" of four distinctively scarred bulls at Kerguelen over a period of two weeks, but states that from the beginning of October harem bulls remain in charge of the same group of cows.

H. The Breeding Behaviour of the Dominant Males

1. *Relation to the Females*

At South Georgia the first bulls haul out at the end of August and lie among the tussac clumps behind the beaches.

The cows begin to haul out three weeks later and by this time the proportion of aggressive males has increased, but it is not until the first pups are born that any territorial fighting occurs. Perhaps the concentration of breeding cows acts as a sexual stimulus to the bulls. However, the bull does not greatly contribute to the formation of the harems nor to their growth in numbers, which are mainly the result of a gregariousness in the newly hauled-out cows, leading them to seek out others of their kind (p. 59). He does, however, attempt to prevent cows from leaving the area, but is usually ineffective if more than one cow tries to depart at the same time. Owing to his slow speed on land, which is only slightly greater than that of the cows, he can deal with only one at a time and blocks her escape, often by lying across her neck or biting it. He then thumps down on her rump with his neck until she moves, slowly guiding her by pushing her in this way on one side or the other. On one occasion when the cows of the Yellow Harem (Signy Island, 1948) were disturbed and moved in a body towards the sea, the "Scarred" bull followed them and succeeded in driving nine out of twelve back to the harem site. This must be regarded as exceptional, for the high ice-foot at Drying Point beach hindered their escape. It is rare for the cows of a harem to depart in a body and in this case the attempted exodus was the result of human interference. On another occasion when there were ten cows in the Green Harem (November 2nd, 1948) and one cow from the White Harem some distance away, the bull went down the slope and began to push her up. Being unsuccessful he copulated with her.

* See footnote on p. 6.

On hot days at Dartmouth Point the beaches were crowded down to the water's edge. The subordinate bulls were able to swim up and down the length of the beach and take the dominant bulls by surprise with the speed and silence of their approach. When they were confined to land, their slow speed and the commotion they caused among the cows was a handicap. In fact, as Bartholomew (1952) has pointed out, were the bulls not fairly slow and ponderous on land the social structure of the rookeries could not be maintained. On these hot days some dominant bulls lay in the water just offshore, facing the beach and submerged except for the head (Plate IIa) or, if the water was too shallow, they were seen to be constantly flipping water onto their backs. On such days the cows would also try to get into the water to keep cool and it is uncertain whether the bulls' behaviour is directly influenced by the weather or indirectly by its effect upon the behaviour of the cows.

> For example, on October 7th, 1951, at Dartmouth Point: "It was very warm and many of the bulls with harems near the water were in the water preventing cows from straying. The bulls were lying head on to the beach. A new cow joined Harem 1d and the bull, in shallow water, rounded her up. Further along three cows were lying in the surf, sleeping. The bull rounded one up, the cow more or less acquiescent except for occasional bursts of activity. The bull pushed her like a liner at a tug, the cow making little attempt to swim away but occasionally snapping at the bull and diving. Another bull came along in the water but departed when the first looked along his back, arching his head backwards and roaring. Three of the harem bulls in Area 1 were in the water. So was R/F at Area 8 and R/↑ at Area 12. The former lay in the sea just offshore. His back was out of the water because he was in shallows and he splashed water on it from time to time, the action being the same as in flipping sand or stones. . . . I sat for an hour on the top of the cliff at the south end of Area 1 watching the general activity of the rookery. The bulls are quite motionless on the whole; the pups yap and move incessantly and cause the cows to move which precipitates mean little bites by other cows, leading to retaliation, and so on."

In normal weather conditions the bulls usually lay amongst the cows. If a cow then tried to get into the water the bull pursued her, and biting her neck held her under water until she gave up the struggle and returned to the harem. In most cases the cow, if persistent, would escape in time, though only cows which had not yet pupped showed persistance.

In general the cows, with or without pups, do not attempt to escape unless there is some great disturbance. Such disturbances are usually caused by man, and are rarely a result of fights between rival bulls.

The harem bull's main efforts are directed towards impregnating the cows and preventing other bulls from doing so. The harems are therefore much more loosely organised on crowded beaches than in less crowded colonies. Figures 17 and 18 show the way in which the composition of adjacent harems in a crowded rookery was continually changing. As already observed (p. 65), coition is physically impossible without the co-operation of the cow, and after many unsuccessful attempts at the beginning of the season, the dominant bulls attempt to pair with the cows less frequently until they come on heat. The cows will then take any bull and may even compete for the services of a bull.

2. *Relation to Other Males*

Pugnacity. The discrepancies in the size and appearance of the sexes of the elephant seal are presumably the result of sexual selection acting upon the males, and sexual fighting is a feature of the rookeries in the breeding season. Early in the season the bulls are at their peak physical condition and a periodicity in hormone secretion brings about changes in the secondary sexual characters and in behaviour.

The adult proboscis is rather flattened and relaxed in the non-breeding season and approximates to that of a sub-adult (Laws, 1953b, Figure 24); in the breeding season it has a smooth almost semi-circular profile (Plate VIa). The possible function of the proboscis in amplifying the roar has been discussed (p. 21).

It may perhaps be significant that the colour of the inside of the mouth is noticeably redder during the breeding season than at other times.

At South Georgia, when the first bulls haul out at the end of August or early in September, they mostly lie in the same area for several days and tolerate the close presence of other males. Some, however, wander about at this time and are aggressive; they may be in advance of the others in sexual condition.

At Dartmouth Point it was not until September 21st that the bulls in general began to show signs of interest in the cows. "There was much roaring during the night and evidence in the snow this morning of battles. Several bulls have small harems now; the largest is of sixteen cows in Area 8 and the bull was attempting either to collect more or prevent them from leaving."

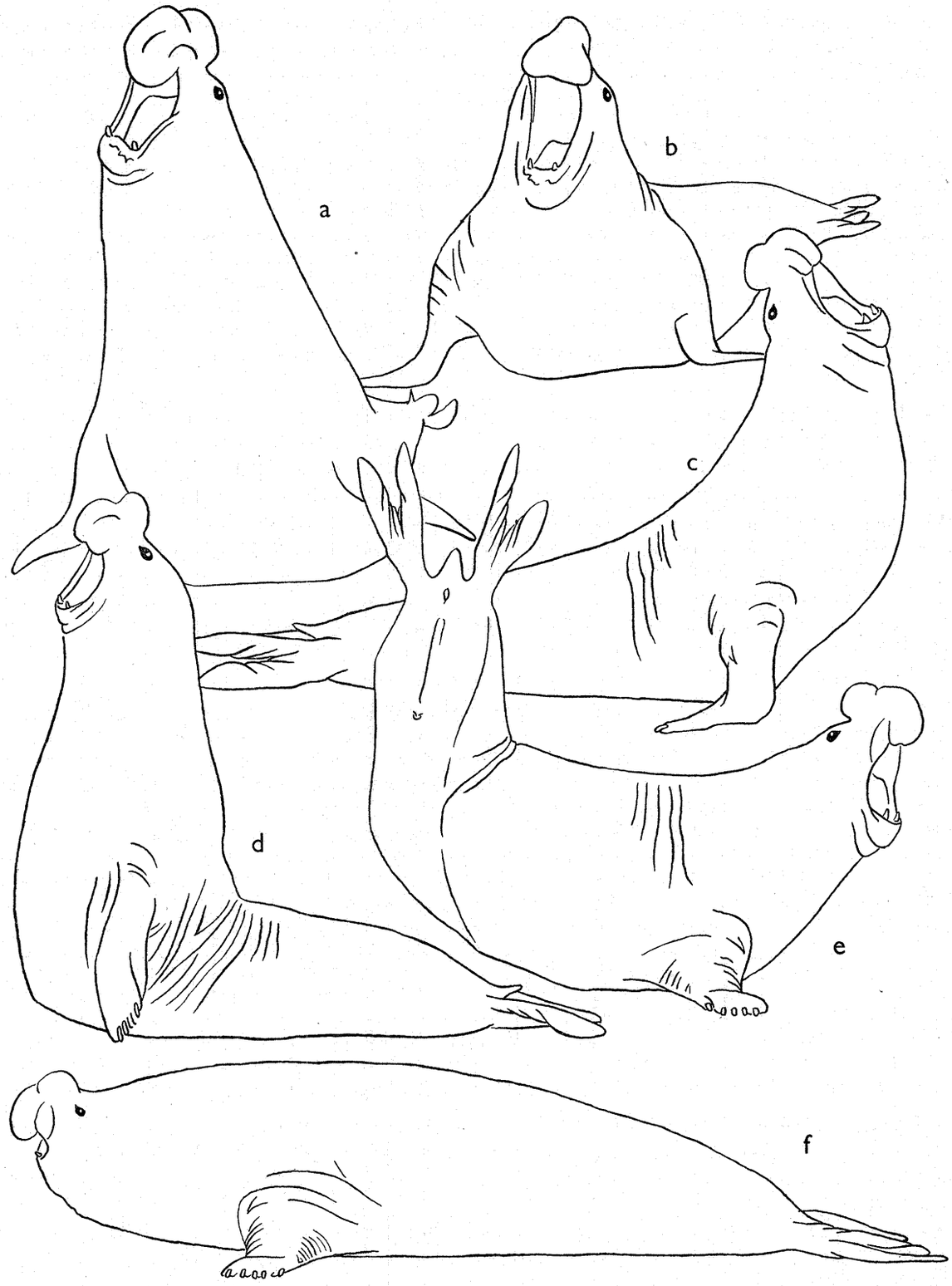


FIGURE 26. Attitudes of the dominant males.

a. Threat—side turning.
b. Roaring at intruder.
c. Looking backwards.
d. Threat—rearing up.
e. Swivelling.
f. Relaxing.

After the initial fights for position at the beginning of the season, the males spend much of their time resting and apparently asleep. Subordinate bulls can therefore invade the harem undetected and often do so (Plate Vd).

> On September 23rd in Area 1, "The bulls of both these harems seem to have no trouble with other bulls which keep at least twenty yards away. . . . Yet, yesterday, subordinate bulls were lying nearer to the harem but were not driven away. Possibly this is because they were quite still and not at all aggressive. . . ." The following day in Area 6, "Another bull which I painted R/X was lying in the centre of the harem, with R/n some distance south near four straggling cows. R/n appeared to tolerate its presence; I thought at first that it had driven off R/n but it is small, hardly moved when I painted it, and then edged further away from R/n. This apparently drew R/n's attention for he roared and the other retreated hurriedly. However, R/X did not go far enough for, with a series of roars, R/n chased him until he was twenty-eight yards away and then returned to his harem." More tolerance was shown by a small bull with a harem of five cows in Area 2. A young male was in the group ". . . attempting to pair with one of the cows, but very inexpertly. The cow was struggling and flipping snow onto her back." Possibly the other bull took the young male for a cow, or was it just disinterested?

Subordinate males are often seen to invade a harem and attempt to pair with a cow, but this usually causes a disturbance amongst the cows and rouses the owner bull. A roar from the latter (Figure 26b) is usually sufficient to send the intruder away. If not, the harem bull gives chase in a straight line regardless of cows and pups. He behaves similarly if any of the encircling subordinate bulls rear up, roar, or move towards the harem. When chasing a rival the owner bull rarely ventures more than ten or twenty yards away from the harem. Wishing to return, he throws his weight onto the fore part of the body, without raising it as in normal locomotion, then in the same motion, he raises the hind parts in the air and swivels round on the belly, pushing with the fore flippers (Figure 26e). If disturbed when asleep he may swing round in this way, but if the disturbance is slight and behind him, he may just raise his head and shoulders so as to look along his own back at the cause of his uneasiness (Figure 26c). As extreme examples the following incidents are quoted.

> On October 6th at Dartmouth Point: "A small bull entering one harem from the sea, raised his head to see the whereabouts of the harem bull; the latter looked around out of the corner of his eye but did not move, whereupon the other departed precipitately." At Signy Island in 1948, the "Green" bull was found on one occasion five hundred yards from his harem having chased another bull before returning. On another occasion (October 17th) the "Green" bull was seen moving towards Drying Point and later "On the way back I heard sounds of battle from Drying Point. I found the 'Yellow' bull lying on the sea ice just off Drying Point, much cut up about the neck and flanks. While I watched, it flipped snow onto its back where there were wounds. . . . It did this twelve times in close succession. From the tracks I was able to make out the course of the struggle. The 'Green' bull had approached from the north up a snow slope some fifteen feet high, at the top of which the harem is situated. The first engagement occurred at the top of this slope, the 'Green' bull defeating the 'Yellow' bull and pursuing him down the slope. Two further battles occurred before the 'Green' bull returned to the harem, after both had fallen through the fast ice at one point! The 'Green' bull was on his way back to the harem when I arrived. . . . It made straight for cow Y/1 on reaching the harem and bit her in the neck as a preliminary to copulation. She was unwilling and escaped." However, a glance at Table XIX shows that the Green Harem was later left without a bull from October 17th to 28th (a period of twelve days). There were other bulls in the vicinity, but one hesitates to conclude that, such was the terror inspired by the "Green" bull, it was not until twelve days had elapsed that other bulls dared to enter his territory!

If it has been necessary to chase away the challenger, the harem bull usually attempts to pair with one of the females on his return and "bachelor" bulls may often invade the harem while the dominant male is pairing. He watches the intruders, if roaring fails to intimidate them, and not until he has finished pairing does he actively drive them away.

A serious challenger always vocalises and postures, sometimes for as long as five minutes before approaching closely and thus never has the advantage of a surprise attack. Only subordinate bulls which are unlikely to defeat the harem bull ever approach quietly. Thus, a dominant male can rest without serious consequences; as soon as the challenge is heard he raises his head and sees the challenger.

There are several possible sequels: The harem bull may turn around and retreat or he may rear up and roar at the challenger (Plate VIb), which may then edge away or roar again in renewed challenge. Only if the challenge is renewed does a fight ensue.

It seems as if there is a grading in strength among the bulls and that most of them are aware of their place in the dominance heirarchy. Sorensen (1950) suggests that mock-fighting between younger non-breeding individuals determines the grading in advance but this seems improbable. More likely, the individual bulls take note of the size of their opponent and the volume of his roar, and in this way are instantly aware of their own superiority or inferiority.

> An interesting example of this appreciation of relative strength was recorded on November 7th, 1948. "A new bull came ashore at the Beach Harem and raised its head to peer over the ice foot. The owner bull ('Scarred-eye') and another bull fled at sight of the newcomer. Only then did he bellow and later took control of the harem." On October 19, 1948, "The 'Red' bull is at the Blue Harem. There are ten cows and four pups. Two other bulls lie 120 yards south and one of these is the 'Blue' bull. It was on an ice ridge and pairing with a solitary cow, which was quite willing—probably she missed impregnation last season. I came up to them and this disturbed the bull which broke off and lay with half his body across the cow's back. Another bull (which I recognised as one of the original two 'bachelors' at the Blue Harem, formerly subordinate to the 'Blue' bull) came up on the 'Blue' bull from behind, moving slowly. When he was still ten yards away the 'Blue' bull heard it and looked around. The other bull lay still, blowing through its proboscis. When the former turned round again the newcomer advanced. The 'Blue' bull then turned, pivotting on its belly, whereupon the other raised itself onto its fore flippers and bellowed. Immediately, the 'Blue' bull turned tail and moved off thirty yards to the north. The newcomer then took over the cow which appeared willing." Bartholomew (1952) gives detailed accounts of similar functions of the vocal threat in the northern elephant seal.

With few exceptions fights occur only between bulls of approximately equal size and strength. There is one further stage in the preliminaries to actual fighting which may eliminate one of the contestants. They rear up facing one another, heads slightly to one side and proboscises erected, and roar with wide open mouth (Figure 26a and d; Plates IIIc and VIb). The weaker may then back away but if not both begin to turn their heads from side to side. They cannot see directly ahead because of the large size of the proboscis and also this movement exposes to view the canine teeth otherwise masked by the proboscis. The movement also presents the red buccal mucosa to the opponent. One is struck by the similarity of this aggressive "display" to that of the grey seal (*Halichoerus grypus*) described by Darling (1939).

On October 24th, 1948, while weighing pups in the harem on Drying Point, an incident occurred which threw some light on the "rearing up" prior to fighting. At that time a stretcher was being used to carry pups from their mothers to the tripod for weighing. The "Yellow" bull was more aggressive than usual, but I found him intimidated by raising the stretcher canvas towards him higher than he could raise himself. If the stretcher was not raised high enough he remained aggressive, but otherwise he backed away slowly, becoming aggressive again as soon as the stretcher was lowered. The bull who can reach the greatest elevation probably has a decided advantage; in any case, since size is usually correlated with fighting ability, this is not surprising.

These preliminaries take a very short time and then, if neither retreats, one lunges forwards and downwards against the other, attempting to lacerate him with the upper canine teeth. All their weight and strength goes into these blows. Fights may last up to ten or fifteen minutes early in the season but later only for one to three minutes or less, terminating after a telling blow has been struck by one of the contestants. Often one will lunge forward and overbalance; the other then strikes with speed and ferocity, sometimes tearing out a large lump of skin and blubber. Once such a blow is struck the fight usually ends, although not invariably so. On September 24th, 1949, the field notes contain the following accounts of a fight between the R/A and R/n bulls from which the former emerged the victor (Plate Ib).

> "As we approached the large divided berg two bull elephants were seen. One approached the other and a fight commenced. Both reared up, dealing slashing blows apparently using the upper canines to inflict gashes on the head and throat of their opponent. As the fight proceeded they remained reared-up, resting against one another and withdrawing their heads so as to make frequent short but powerful thrusts at proboscis, eye and neck. Occasionally, one would be carried away by the force of its blow and fall flat, whereupon, the the other bit at its neck or back. The battle ended after ten minutes with one very fierce downward slash at the neck of the smaller of the two. He backed away for six yards and then turned around and made off. As soon as his back was turned the other followed and was catching up, when the defeated bull which had been eyeing him over his back as he fled, turned around and reared up again. This served to stop his opponent, and then the vanquished turned round again and fled. The other followed for a few yards and then stopped. When fifty yards were between them the defeated bull stopped. . . ." R/n had a much larger proboscis than R/A (Laws, 1953b, Plate IIIb) but was smaller.

Retreat on the part of one of the contestants, even before battle is joined, does not always end the engagement, as in the case of a conflict between "Scarred-eye" and R/T which was recorded on October 9th, 1949.

> " 'Scarred-eye' was moving inshore from the ice edge and went into the bay south of Balin Point, heading for Beach E6. [See Figure 12.] The R/T bull was roaring vociferously, and at 2200 hours 'Scarred-eye' moved in past Balin Rocks. The R/T bull came out forty yards to meet him, then lay still until 'Scarred-eye' came up roaring. R/T backed away before a blow was struck but 'Scarred-eye' came on and there were three short bouts of fighting as R/T backed away. R/T then backed away ten yards, turned and fled, 'Scarred-eye' following for a few yards."

In yet another recorded case the fight was even more one-sided than that described above, as it involved a medium-sized male.

> On October 16th, 1949, the "Scarred" bull was at the Red Harem. "When I arrived it was chasing a medium-sized male. The young male could not move as quickly as the 'Scarred' bull which quickly caught it up. The youngster turned around, reared up, and received several slashes from the 'Scarred' bull without getting in any blows itself. The youngster then turned and was allowed to depart."

It is likely that the "Scarred" bull was an exceptionally aggressive male, and the following account illustrates the less aggressive and more usual reaction to a smaller bull which is not challenging.

> "Cows R/r/A and B/n were lying to the north of the berg bight with bulls Y/X and G/n nearby. Cow B/n looked as if about to pup. Bull R/A appeared and moved towards the cows. Bull G/n saw it and moved away and then up onto a ridge of ice where it stopped and waited for R/A to pass. R/A could easily have attacked G/n but passed by within a few yards of it, while G/n appeared to know that R/A would not attack it. Cow B/n had made for the water but was stopped by bull Y/X trying to pair with it. R/A made for the two and Y/X broke off and approached to within a few yards of R/A, who then roared, and Y/X, as if he had just realised the size of his opponent, hastened to get away.
>
> "R/A tried to pair with cow B/n but she escaped into the water. R/A followed and swam along the ice edge, head and nose breaking the surface, and hauled out again near bulls Y/1/s and 'medium'. R/A approached with a graceful rhythmic motion and Y/1/s, turning, saw him but did not move. Not until R/A was a few yards away did it look again and then suddenly retreated northwards. R/A followed at a slow speed, as if just 'keeping up appearances' and then halted."

These accounts give some idea of the amount of energy expended by the bulls in the breeding season (energy which can be derived solely from their large fat stores) and further evidence is provided by the wounds inflicted. In the fight between R/↑ and R/m/Y/n bulls at Dartmouth Point on September 30th, 1951, the victor (R/↑) lost most of his proboscis. A large chunk torn out during the fight and found the following day measured roughly 8 x 6 x 4 inches. Frequently, wounds of similar severity are inflicted and bulls are usually heavily scarred about the head and neck, so that there is an "integumentary shield" of scar tissue on the chest. It is not as well developed as in *M. angustirostris*. Although lacerations or loss of part of the proboscis occur, the eyes are rarely punctured or torn out, but scratches leading to conjunctivitis are not uncommon.

Once a sufficiently powerful blow is struck the fight ends, the loser backs away, usually unpursued, and then swivels round and hurriedly retreats (Plate Ib). If he does not back far enough before turning round, his opponent may take a bite at his flanks. Incidents have already been described in which the winner pursued his defeated rival, but this only occurs where the harems are widely spaced. More usually the victor roars repeatedly until the other is well outside his territory and then returning to his harem attempts to pair with one of the cows.

After being defeated in full fight bulls were never seen to challenge the victor again, although paint-marked bulls which had been eliminated in the preliminaries to fighting, occasionally challenged and defeated their rival later in the season. The case of the former subordinate of the "Blue" bull has already been quoted (p. 75).

> Similarly, on November 1st, 1948. "When I arrived at the Green Harem it was controlled by the R/Y bull. The 'Red' bull came up the slope but backed away when the R/Y bull reared up. Twenty minutes later the 'Red' bull approached again, both bulls reared up eyeing each other and it was noticeable that R/Y was the smaller. The 'Red' bull lunged, bit R/Y in the neck and shook him twice. R/Y then backed away and fled down the slope on the west side of the ridge."

Territory

The position of isolated harems in open country has been observed to change by as much as 150 yards and changes in position of twenty yards are common. It is, therefore, concluded that dominant bulls do not hold any geographically fixed territory. The territories are instead related to the position of the cows and bull, with a radius which declines progressively throughout the season as the strength of the bull diminishes. As it is determined to some extent by geographical features the radius of territory may vary considerably in different directions, but on the flat sea ice at Signy Island and on "Hestesletten" and the plain north-west of the terminal ice cliffs of the Nordenskjöld Glacier in South Georgia, the territory was approximately circular (Plates IVb, V, VI). In Figure 27 the maximum radius of the territory of dominant males is plotted against the length of time spent ashore. Positions were plotted in the field on large scale maps made for that purpose, and the radius of territory was taken as the nearest *permitted* approach of subordinate bulls. Owing to the changing relationships of the harems throughout the season few marked bulls remained in charge of one particular harem throughout the season and data have been used from only four, three of which are typical.

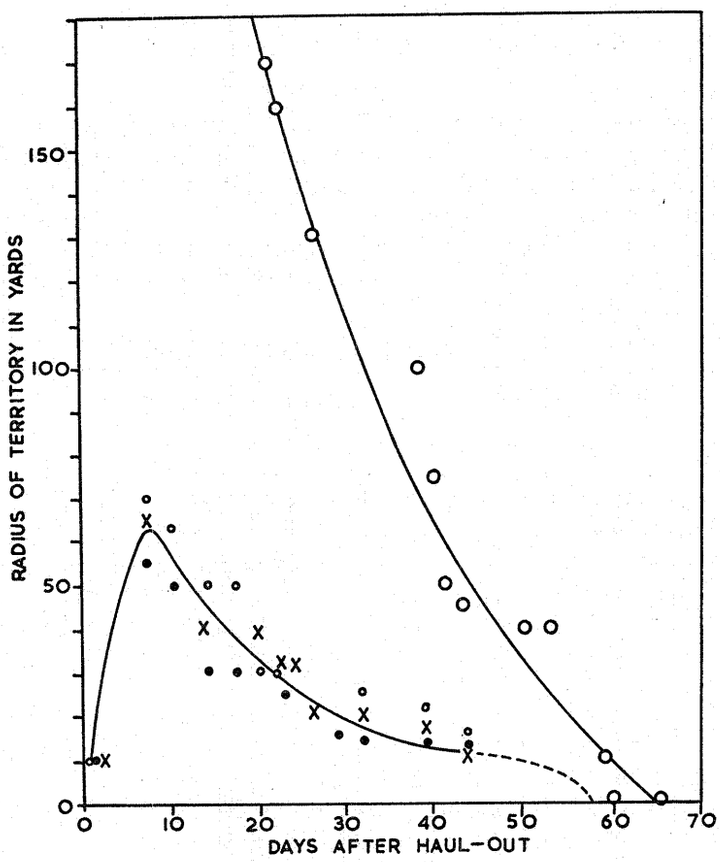


FIGURE 27. Changes in the size of territories according to the length of time since haul-out.
X, o and ● represent three bulls at South Georgia, 1951. O represents the "Green" bull, Signy Island, 1948.

The first series of points is typical of the range of territory at South Georgia. The initial increase in territorial radius corresponds to the second phase in the establishment of the rookery (p. 53). The territory reaches a maximum size of about sixty yards radius at the beginning of the third phase and then declines, rapidly at first, the curve levelling off at about ten yards in phase *v*. At Signy Island where the harems were situated on more open beaches or on the flat sea ice, and where the average size of the bulls was larger, the territorial radius was in most cases slightly greater at first.

The second curve in Figure 27 represents the decline in aggressiveness of the "Green" bull in 1948, which was the largest bull ever seen by the writer. It was very much stronger than the others and wandered about the ten square miles of the breeding area appropriating other harems at will, taking over new harems seven times in six weeks (p. 70 and Table XIX).

On the more crowded beaches at South Georgia this territorial behaviour is modified between adjacent dominant bulls, and applies only to the relation between dominant and subordinate bulls. The boundary between contiguous harems, as evidenced by the pairing relations, is indefinite. Changes of position of marked cows from the centre of one harem into the adjacent harems were observed (Figures 17 and 18), and dominant males during phase *v* of rookery establishment were sometimes only a few yards apart, whereas subordinate bulls were not allowed to approach closer than about ten yards.

At the end of the season when the last cows have left, the aggressiveness of most bulls terminates and they allow sub-adult and other bulls, which begin to haul out for the moult at this time (Figure 8), to lie on the former site of the harems. The paint-marked breeding bulls usually spent several days on land in one of these aggregations before returning to sea. Angot (1954) says that the bull departs three days after the last female has left his harem.

I. Breeding Behaviour of the Subordinate Males

1. *Relation to the Females*

At Signy Island the subordinate males encircle the harem (averaging five per harem) and attempt to pair with arriving or departing cows, or with any cows which become separated from the main body of the harem. It is but rarely that they have the opportunity and at South Georgia, where formerly they must have been responsible for impregnating a proportion of the cows in oestrus, they no longer outnumber the dominant males. Incidents have been described where subordinate males have penetrated the harem unknown to, or tolerated by, the owner bull, but it must be emphasised that this is unusual and successful pairings of this nature must be regarded as very rare.

However, if the virgin females are impregnated in the sea (p. 66) then it seems likely that the subordinate males play an important part. Bartholomew (1952) has pointed out the importance of the matings by subordinate males in maintaining the genetic variability within the population.

2. *Relation to Other Males*

The relations between the subordinate males and the dominant bulls have already been described. There is similarly a dominance heirarchy within the class of subordinate males, which is of considerable importance in conserving the energy of individual dominant males. Thus males, before they can approach the cows or challenge the harem bull, have first to pass through the line of subordinate males which on land, and to a lesser extent in the sea, acts as a "filter" or screen. Fights for position occur among the subordinate males, just as fierce as those between dominant males, but once the heirarchy has been established the threat vocalisation is usually sufficient to maintain it.

The subordinate males probably undergo only partial fasts for they frequently take to the water and their physical condition does not noticeably change as it would if they fasted as rigorously as the dominant bulls. Nevertheless, animals in the latter class, although their strength declines throughout the mating season, are rarely defeated by a subordinate male once they are established. The ability to endure long fasts is essential to the maintenance of a relatively stable breeding rookery.

During the breeding season a few smaller bulls, which are pacific and lie close together, may occasionally be seen on beaches or parts of beaches where there are usually few seals. It was not established whether these were non-breeders but it seems probable.

J. Factors Controlling the Length of the Breeding Season

It has been shown that post-partum heat begins, on average, eighteen days after parturition, and since the cows depart when the pup is twenty-three days old it is probable that oestrus lasts for about five days (see p. 64). The cows pup once a year in the same relatively short period of about two months so that the gestation period must be about a year. If the gestation period plus the parturition-copulation time together totalled one year then individual cows would pup at the same date each year. Also the temporal distribution

of births throughout the season to cows of different ages would tend to be random, and the numerical distribution of births would correspond to the proportions of the different age groups of cows in the population. However, the distribution of births is not random, and is clear that at South Georgia they bear a definite relation to the size and therefore the age of the mother. This pattern can best be explained by assuming that the virgin females are impregnated early in the season and that gestation plus the parturition-copulation period is more than a year, so that the individual cow gives birth some days later each year.

Matthews (1929, p. 236) says that "Most of the late pups are first ones, their mothers having been impregnated for the first time late in the last season". Sorensen (1950) disagrees with this and Roberts at South Georgia (Bertram, 1940, p. 125), Robin (1948) at Signy Island and Angot (1954) have noted a tendency for the largest cows to give birth last. In the present study this was confirmed at South Georgia and it was also established, by means of tooth rings, that among the first cows to pup are the primiparous three-year-old females.

Both at Signy Island and South Georgia it was observed that the bulls began to lose interest in the cows towards mid-November, and it has been established that in the testis material collected and examined histologically, sperm production practically ceases at the end of November (Laws, 1953e). The majority of the breeding bulls are thought to be in anoestrus by November 25th.

Since the post-partum heat occurs eighteen to twenty-three days after parturition it follows that, with few exceptions, the latest date at which a cow may pup and still be served by a bull is about November 7th. Then, in the following year she will pup a few days after November 7th and fail to become pregnant. In fact, few births occur after November 14th at "Hestesletten" (Figure 8) which suggests that the annual retardation of pupping averages about seven days. In three seasons at Signy Island only eleven births were recorded after the main pupping season. The last birth in 1948 occurred seven days later than the last in 1947, and the penultimate birth was six days later in 1948 than in 1947. The date of the last birth in 1949 was seven days later than the date of the penultimate birth in 1948 (Figure 28). It is possible that here the

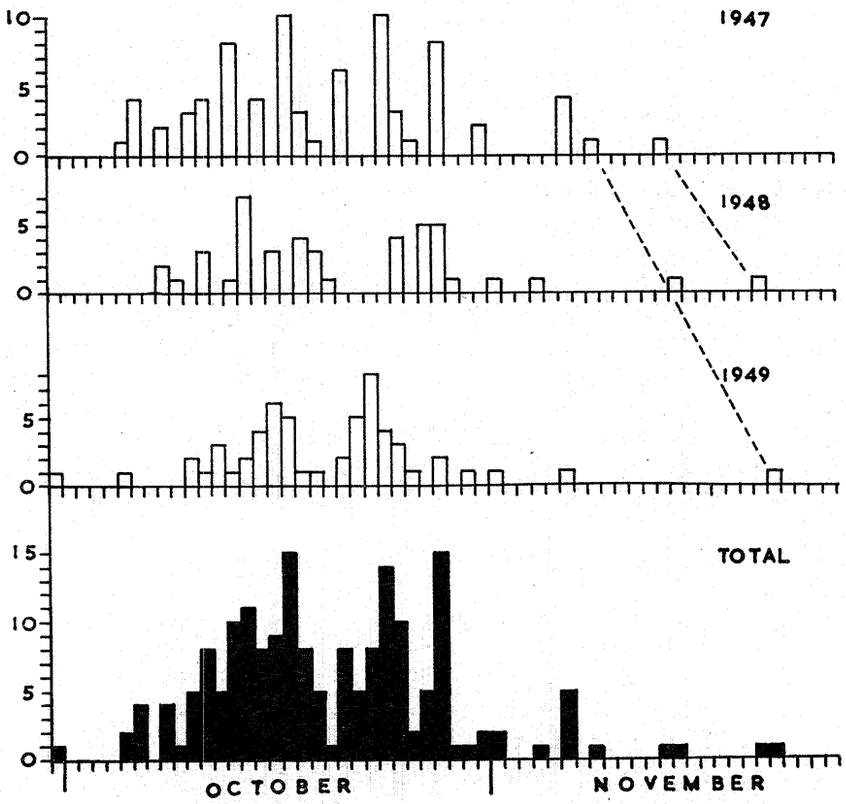


FIGURE 28. Frequency of recorded births, Signy Island, 1947–1949.

annual retardation of two females can be traced. Angot (1954) concludes, from rather doubtful evidence, that the female pups between nine and fifteen days later each year.

The frequency of recorded births at Signy Island has been plotted (Figure 28) and similar data is available for the first weeks of the breeding season at Dartmouth Point, South Georgia, in 1951 (Figure 29). The

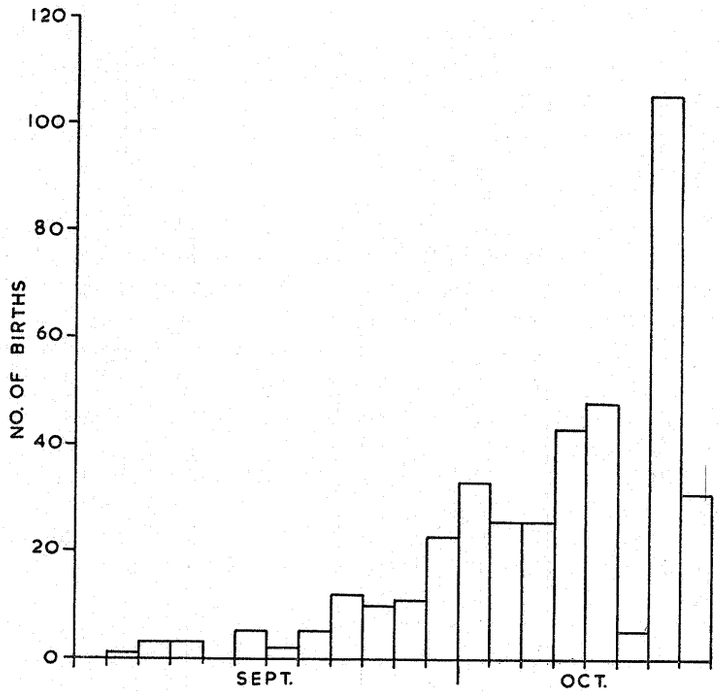


FIGURE 29. Frequency diagram of the incidence of births at Dartmouth Point, South Georgia, in September and October, 1951.

samples are not large enough to show significant peaks in the frequency of occurrence of births. At Dartmouth Point the large number of births on October 7th is associated with particularly calm fine weather. The twenty-four hour periods before the counts on October 6th and 8th were very cold and windy, indicating that the weather conditions, which have been shown to influence the behaviour of seals hauled out in the summer (p. 36), may perhaps slightly influence the time of parturition.

It is reasonable to assume that (at least after the first pregnancy) the length of the gestation period is fixed within fairly narrow limits, and averages one year, plus the annual retardation, minus the parturition-copulation period (that is 365 + 7–18 days) which is about fifty weeks. The primiparous females (mainly three-year-old but some two years and four years) give birth to their pups in September and early October, and then pup a week later each year so that there comes a season when some of them are not impregnated. They miss a pregnancy and probably mate early in the following season at the same time and place as the virgin cows.

From the post-mortem examination of mature female elephant seals certain conclusions have been drawn about the frequency of "missed" pregnancies. In the significant material, there is only one non-pregnant female from the first four years of sexual maturity. In the fifth and sixth years after the attainment of sexual maturity there are three "missed" pregnancies out of fourteen. The next occur in the tenth year of maturity when there are two out of twelve. It is postulated that, subject to individual variations, "missed" pregnancies first become frequent in the fifth or sixth annual breeding cycles, owing to the cow pupping too late in the season to ensure impregnation. (Abortions were recorded from the fifth and eleventh pregnancies.) Elsewhere (Laws, 1953b), it has been stated that the average expectation of life of the female elephant seal after the first pregnancy is of the order of a further seven years. Thus, each cow which has safely completed the first, probably misses, on average, one pregnancy (in the seventh or eighth year of age)

and therefore bears seven pups during her lifetime. If this be correct then approximately one-eighth or 12.5 per cent of the mature cows will fail to become pregnant each year. From the significant material collected, six out of forty-three cows were non-pregnant, a proportion of 13.9 per cent which, allowing for the smallness of the sample, is in close agreement with the theoretical figure. Only one senile female elephant seal has been collected and in the author's opinion the majority of cows continue to produce pups annually with infrequent "missed" pregnancies until they die.

Thus, owing to the individual variations in the time of mating of the virgin cows, "missed" pregnancies, and abortions during pregnancy, cows of almost any age group may give birth on a particular day, although the general rule outlined above holds good.

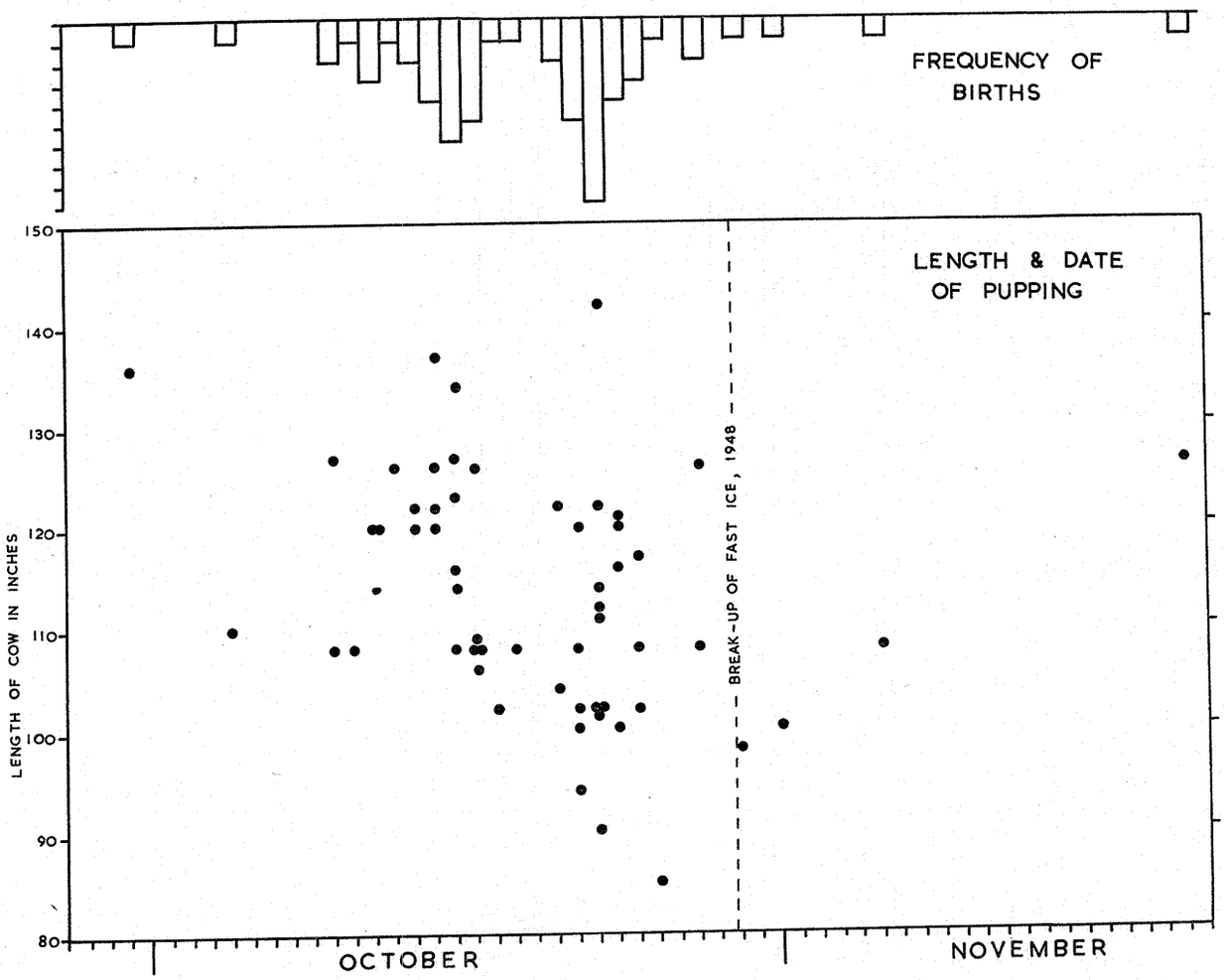


FIGURE 30. Frequency of recorded births at Signy Island throughout the 1949 breeding season. The lengths (measured photographically) and dates of parturition for fifty-eight breeding cows in this season are also shown.

At Signy Island, length measurements (photographic) of fifty-eight breeding cows and their dates of parturition in 1949 are known (Figure 30). The relation between their size and date of pupping is the reverse of that established at South Georgia, and the average size decreases throughout the season. This may be explained by assuming, for the following reasons, that the abnormal ice conditions occurring at the South Orkneys Islands in recent years had altered the usual pattern. Firstly, the presence of fast ice in some years may be expected to delay the mating of the virgin females; secondly, if a cow loses her pup she will come on heat sooner than when suckling and will not lose condition to the same extent, so that the gestation period (that is the period of delay in implantation) may be shorter; thirdly, and probably most important, many

cows fail to be impregnated owing to the disorganisation of the social structure caused by the break-up of the fast ice.

To summarise, the length of the breeding season is controlled in two ways:

1. The beginning depends on the date at which the first cows produce their pups, which, assuming a gestation period of fixed length, is itself dependent upon the time at which the virgin females and females which had missed a pregnancy were impregnated by the bulls in the previous season.
2. The end of the season is controlled by the date at which the bulls cease to produce sperm in sufficient quantity to ensure fertile mating.

It may well be that the bulls alone are responsible for maintaining the constancy and duration of the season of reproduction, for the time of impregnation of the virgin females is naturally dependent upon the presence of the males.

V. DISCUSSION

THE male elephant seal becomes sexually mature at about four years of age and the female at two years; at this time the virgin females and the young sexually mature males probably mate aquatically. By comparison with old females, it seems likely that the primiparous females haul out about forty-nine weeks after their impregnation and give birth to their pups on land eight days later. They are re-impregnated from nineteen to twenty-three days later, their pups being weaned within a few days, and during the breeding season they fast for about twenty-eight to thirty-one days.

The bulls do not normally participate in the terrestrial breeding organisation until they are from five to seven years old. They begin to haul out early in September before the first cows appear and the larger males remain ashore during their rut for over eight weeks, without feeding. Then, towards the end of November, they cease to produce sperm and lose interest in the cows.

The individual females give birth to their single pup about a week later each year, since the gestation period plus the parturition-copulation interval total more than a year. After a number of years the cow pups so late in the season that the chances of males being present in breeding condition are slight. Cows which miss pregnancy in this way probably mate aquatically at the beginning of the next breeding season together with the virgin cows since neither group is seen on land in representative numbers. The following pregnancies are again retarded by about a week in successive years, and then, after producing about seven pups, the average mature female dies during her twelfth year.

Conversely, the males appear to haul out earlier each year, after attaining sexual maturity, so that they spend progressively more time on land and take an increasingly active part in terrestrial breeding.

The seals are not as aquatically adapted as the whales, and have to come on land in order to give birth to their pups. In some species, such as *Phoca vitulina*, the young frequently have to swim within a few hours of birth, but in the elephant seal, although the pups can swim within a very short time of birth, they do not normally leave their parent until they are twenty-three days old and spend at least another two weeks on land before entering the water. In consequence of the need for terrestrial parturition, the elephant seal population, which is spread over the Southern Ocean (probably just outside the northern limit of the pack-ice) during the winter, concentrates in spring on the few suitable beaches of the breeding islands and forms vast rookeries.

Each rookery is formed of a number of loose impermanent social units known as harems, which comprise a mature bull and, according to the size and strength of the bull, a variable number of cows from one or two to over a hundred.

The gregarious instinct of the cows is the primary factor responsible for the formation of the harems; then after the birth of the pup the maternal instincts of the cow make it restless and aggressive towards other seals, but owing to the ties which keep her with the pup she does not seek to leave until it is weaned. During the suckling period she does not feed and loses weight at the rate of approximately thirty pounds a day.

The length of the period of recuperation after lactation is probably fairly constant, so that the time of the moult is progressively delayed (because of the annual retardation of the breeding haul-out) and is confined within much narrower limits than the moulting season of the males. The moult completed, the cow must feed relatively much more intensively that the larger male because she has to provide for a rapidly growing

foetus, and to lay down fat reserves for the post-natal growth of her pup during the next spring, as well as having to maintain her own general health at an optimum level.

During the breeding season the bulls are concerned only with maintaining their position among the cows for sexual gratification. They attempt to mate with the females in their vicinity, unsuccessfully at first, because the females do not come on heat until about three to four weeks after they join the harems, and will not permit mating until they are ready. The conspicuous secondary sexual characters of the bulls (their great size and strength, the proboscis, and their ability to undergo prolonged fasts) have all developed in relation to the need for maintaining their position among the cows if they are to breed successfully. The function of the roar as a substitute for actual fighting and the consequent saving of energy effected, is of great importance.

Bertram (1940) in his excellent comparative study of pinniped behaviour stresses that the polygynous species always mate on land, but there is now strong evidence that the female elephant seal mates aquatically when she has not recently given birth to a pup. Thus, Bertram's statement that the elephant seal is the only truly polygynous phocid and the only one which always copulates on land rather than in the water, is open to doubt. It is also known that the grey seal (*Halichoerus grypus*), which has a polygynous breeding organisation, can copulate either on land or in the water, and even the most highly social otariids can copulate aquatically. The chances of observing copulation in the water are very small and it is probably of much more constant occurrence than has been assumed. All other phocids apparently mate aquatically because copulation elsewhere has rarely been observed; indeed, all species of seals are much more at home in the water than on land and there can be little doubt that copulation is much more easily accomplished in the water than on land.

Therefore, it is apparent that although aquatic copulation is more common among the phocid species than terrestrial mating, in the elephant seal the reverse is found to be true. It is suggested that terrestrial mating is the common condition in the elephant seal, not because it is the only type possible, but because the majority of females in the breeding season have given birth to a pup and their maternal instincts keep them in the vicinity of their pup, and therefore on land, at this time. The female elephant seal, as we have seen, enters oestrus towards the end of lactation. Terrestrial mating is therefore a secondary condition, in this species, resulting from the temporal relations of oestrus and lactation.

It seems probable that the degree of specialisation of the breeding organisation will depend upon the rapidity of the onset of post-partum heat and the length of the lactation period. Lactation in the otariids lasts for up to six months; the females do not of course fast all this time and are impregnated by the bulls before being permitted to return to the sea for the first time early in lactation. Probably owing to the need for greater activity on the part of the males which this entails, the disparity in size between the sexes of otariids is much greater than that between the phocid species which are polygynous or nearly so.

The usual condition among the phocids is for oestrus to occur after weaning (correlated with the shortening of the lactation period, relative to that of the otariids), although the parturition-copulation interval is often less in the otariids. It may well be that in those species such as the grey seal (*H. grypus*) and the hooded seal (*Cystophora cristata*) in which polygyny is not very well developed, the overlap between lactation and oestrus is very slight, or variable.

Clearly, in those species in which oestrus occurs after the weaning of the pup, and the female is no longer kept in one particular area by maternal ties, there would be no evolutionary or genetic advantage in the maintenance of harems and the consequent evolution of disparity in size between the sexes and the ability to endure long fasts.

Thus, Bertram's concept of polygyny as occurring only in those species in which terrestrial copulation is the rule can be extended: terrestrial mating is seen to be a consequence of the reduction of the interval between parturition and oestrus, so that the females come on heat when still tied to the land by their maternal instincts.

An attempt has been made, by employing histological techniques, to determine the nature of the physiological changes in the reproductive tract during the annual cycle, and especially those connected with the phenomenon of implantation of the blastocyst which has been shown to be delayed for about four months. This work has been described (Laws, 1953e) and will be published shortly.

We must now consider the part played by delayed implantation in the reproductive cycle of the elephant seal and its influence on the reproductive behaviour and especially polygyny.

In the southern elephant seal the duration of the gestation period is fifty weeks or about eleven and a half

months; implantation of the blastocyst is delayed for four months so that the period of active development of the embryo is reduced to seven and a half months. When curves based on published information (Bertram, 1940; Hamilton, 1939) and personal observations were drawn up showing the rate of embryonic growth of the Weddell seal (*Leptonychotes weddelli*), crabeater seal (*Lobodon carcinophaga*) and leopard seal (*Hydrurga leptonyx*), it was apparent that in these three species the duration of pregnancy varied from eight to ten months, as compared with eleven and a half months in the elephant seal. Since in all species the pupping season is confined to a relatively short period in the spring, it follows that oestrus occurs in the leopard seal about four months after parturition, three months after parturition in the crabeater seal, and two months in the Weddell; in the elephant seal it begins nineteen days after parturition. In the southern elephant seal, crabeater and leopard, the period of active embryonic growth appears to be seven and a half months, and in the Weddell seal about eight and a half to nine months. The hooded seal (*Cystophora cristata*), the only other extant genus placed with *Mirounga* in the sub-family *Cystophorinae*, has a period of delay in implantation of the blastocyst of about three to four months and the length of the active development is about seven and a half to eight and a half months. Oestrus in this species occurs at about the same time after pupping as in the elephant seal (Høst, unpublished, about fourteen days), at about the same time as weaning occurs (Nansen (1925), two to three weeks after pupping). They are found in units of a bull, cow and pup, on the pack-ice (Olds, 1950). Thus, it seems that in the phocids the length of the period of active growth of the embryo (from implantation of the blastocyst to parturition) is fixed at about seven and a half to eight and a half months as a rule, but the length of the period of delay in implantation is variable.

Now, if we consider the reproductive cycle, taking the time of oestrus and mating as the starting point it seems that the length of the free blastocyst stage is determined by certain physiological and environmental factors which we do not yet understand. The pup is born within the same short season each year, at a time which will allow it the maximum opportunity to gain nutritional independence and to prepare to face the following winter. This is the theory put forward by Fries (1880) to explain delayed implantation, but since discredited on the grounds that the Roe deer bears its young too late in the season and the bear too early to benefit by delayed implantation. Furthermore, it is difficult to reconcile it with the tropical armadillo.

If, on the other hand, we place emphasis on the time of *implantation* as the fixed point in the cycle, then the delay in implantation may be a mechanism which, by advancing the season of oestrus, ensures that mating occurs when the female seals are concentrated in a comparatively small area (during or just after lactation) and not spread out over a large area of the ocean. The fact that the length of the period of active embryonic growth is so nearly equal in the species considered while the length of period of delay is so variable, lends support to this view.

It is significant that in the species under discussion, the elephant seal which has the longest period of delay, with oestrus occurring very soon after parturition, is highly polygynous and has a complex social organisation during the breeding season. The Weddell seal, which has the next longest period of delay aggregates in *pupping* rookeries, but does not form into harems. Little is known about this stage of the annual cycle in the crabeater owing to its inaccessibility, while the leopard seal which mates about four months after parturition and has no long free blastocyst stage, is one of the most solitary of all seals. Insufficient is known about the reproductive cycle of the hooded seal to determine whether mating occurs before lactation is finished or after, but even if its cycle was identical with that of the southern elephant seal, the nature of its habitat would preclude the maintenance of a complex harem system.

Finally, a possibly significant observation, connecting delayed implantation with the moult season of female elephant seals, deserves mention. In the females examined it was noticed that no implanted embryos or blastocysts were found until after the moult process was completed. It has been shown that the cows undergo a very rigorous fast at this time, and it is suggested that the result of the low nutritive level and general ill-health associated with moulting might be to bring about abortion if the embryo developed normally from the time of conception. In other words, the type of moult undergone by the elephant seal may only be possible because of delayed implantation, or alternatively, the length of the delay in implantation may be determined by the moult. Wright (1942) has shown that a correlation exists between the moult and the sexual cycle in the weasel. However, although the moult may be connected in some way with the mechanism determining the end of the free blastocyst stage, the fundamental causes of delayed implantation remain uncertain.

VI. SUMMARY

1. The behaviour of elephant seals in the small colony at Signy Island, South Orkney Islands, was studied during several antarctic seasons. These observations have been extended by work in the larger rookeries at South Georgia during one season.

2. In this paper the past and present distribution of *Mirounga leonina* Linn. is discussed and evidence of pelagic dispersal and migrations considered. It is concluded that the pelagic movements are in the nature of a general dispersal rather than a true migration, although there may be a small scale migration in the Falkland Islands Dependencies. The most southerly record of the species is from latitude 77°40′ S.

3. The general behaviour and attributes of the species are discussed, including locomotion, aquatic behaviour, the relation of the species to sea ice in the southern part of its range, feeding habits, fasting periods, the occurrence of sand and stones in the stomach, the moult, the displacement activity of sand-throwing, vocalisation, hearing and vision, and mock-fighting.

4. The behaviour of the southern elephant seal in relation to man and other animals is described.

5. From data furnished by weekly counts of the animals ashore, a detailed anaylsis of the population dynamics of the Signy Island herd in the non-breeding season is attempted, and factors influencing the summer haul-out are discussed. The need for moulting on land is probably the primary cause, but the presence or absence of pack-ice and fast ice and varying climatic conditions are also important.

6. The observed differences in the behaviour of the sexes during the moult period are discussed.

7. Observations relating to the occurrence of twins, the sex ratio at birth (based on the sexing of 4629 pups) and the age at sexual maturity are presented.

8. The chronology of the breeding season in several localities is discussed and it is concluded that the season is now approximately contemporaneous at South Georgia and the South Orkney Islands, although at one time the season at South Georgia may have occurred a month earlier.

9. The condition of the small breeding colony at Signy Island in 1947, 1948 and 1949 is described. In 1948 and 1949 a high proportion of the pups were born on fast ice up to two miles from land and the break-up of the ice resulted in a high rate of mortality

10. From observations at Signy Island and South Georgia the seasonal establishment and build-up of the breeding rookeries at South Georgia are described and the effects of commercial sealing operations on the breeding behaviour are considered. It is suggested that the beginning of the breeding season has been retarded and its duration lengthened; the *average* harem size is now nearly twice the size of the largest harems existing twenty-seven years ago. The initial formation of the harems and the selection of the sites are largely due to the gregarious behaviour of the parturient cows, but later the dominant males assist their growth and maintain them as undisturbed units by resisting the challenge of other males and by preventing the cows from straying.

11. The breeding behaviour of the two sexes and several age groups is considered separately in some detail.

The female hauls out on land a week before giving birth to the pup and then spends an average of twenty-three days in lactation, coming on heat on the nineteenth day. During these four weeks she remains ashore and does not feed.

12. Strong circumstantial evidence suggests that the virgin females are impregnated by the younger males at sea in the vicinity of the breeding area. This aquatic pairing probably takes place at the same time as the mating of the parous females on shore.

13. The behaviour of the pup from birth until its departure to sea five or six weeks later is outlined briefly. In the latter half of this period it lives on the fat reserves laid down during suckling.

14. The results of short term paint-marking experiments at Signy Island and South Georgia, are presented and discussed. They show that the female can undertake long journeys before the birth of the pup and is then more or less sedentary until the pup is weaned, when she returns to sea to recuperate. If the pup dies or is lost, the cow may again wander about the breeding area but does not usually leave until she has been impregnated by a bull. Similarly, the males may undertake long journeys by sea, land, or over the fast ice at all times of the breeding season. Once a powerful bull has established his position among the cows

he does not usually leave until they have all departed. Owing to the continual competition between the bulls the ownership of the harems often changes.

15. The aggressive behaviour of the males and the important role played by the roar as a substitute for fighting are described. The nature of the territory and the relation of its area to the power of the bull, and its decrease as the breeding season progresses, are also discussed.

16. The nature of the annual reproductive cycle in both sexes is correlated with the behaviour of the seals. The average size of the females giving birth increases during the breeding season, and the beginning of the season is determined by the time at which the primiparous females give birth. Each season the individual female hauls out about a week later and there comes a time when she gives birth too late in the season to be successfully impregnated by a bull, for the males have a well-defined rut lasting from September to late November. She then misses a pregnancy and probably mates aquatically at the same time as the virgin females early next season. By this mechanism the breeding season is confined to a relatively short period of the year.

17. Lastly, the known facts of the reproductive cycle of both sexes are summarised and a new hypothesis which attempts to explain the phenomenon of polygyny in the pinnipedia is put forward. This emphasises the importance of terrestrial mating in the development of the complex social organisation of the breeding season, and shows that terrestrial mating results from the shortening of the interval between parturition and oestrus so that pairing occurs before the pup is weaned.

The phenomenon of delayed implantation is reviewed in relation to the shortening of the parturition-copulation interval, and the suggestion made that it is a mechanism enabling the mating to take place shortly after pupping when the females are still concentrated in a relatively small area.

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VIII. REFERENCES

ADMIRALTY, Hydrographic Department. 1948. *Antarctic Pilot*. London.

ANGOT, M. 1954. Observations sur les mammifères marins de l'Archipel de Kerguelen, avec une étude detaillée de l'éléphant de mer, *Mirounga leonina* (L.). *Mammalia*, **15**, 1, 1–111.

ARETAS, R. 1951. L'éléphant de mer (*Mirounga leonina* (Linn.)). Etude biologique de l'espèce dans les possessions françaises Australes (Archip. des Kerguelen). *Mammalia*, **15**, 4, 105–17.

BAGSHAWE, T. W. 1939. *Two Men in the Antarctic*. Cambridge.

BARROW, K. M. 1910. *Three Years on Tristan da Cunha*. London.

BARTHOLOMEW, G. A. Jr. 1952. Reproductive and social behaviour of the northern elephant seal. *Univ. Calif. Publ. Zool.*, **47**, 15, 369–472.

BEACH, F. A. 1948. *Hormones and Behaviour*. New York.

BERTRAM, G. C. L. 1940. The biology of the Weddell and crabeater seals: with a study of the comparative behaviour of the Pinnipedia. *Sci. Rep. Brit. Graham Land Exped.*, 1934–7, **1**, 1–139.

BOULENGER, E. G. 1937. *World Natural History*. London.

CARRARA, I. S. 1952, Lobos marinos, pinguinos y guaneras de las costas del litoral maritimo e islas adjacentes de la Republica Argentina. *Spec. Publ. Fac. Cienc. Vet., Univ. Nac. La Plata*, 191–9.

CHRISTENSEN, L. 1942. *Such is the Antarctic*. London.

DARLING, F. F. 1938. *Bird Flocks and the Breeding Cycle*. Cambridge.

————. 1939. *A Naturalist on Rona*. Oxford.

DAVIES, J. L. 1949. Observations on the grey seal (Halichoerus grypus) at Ramsey Island, Pembrokeshire. *Proc. Zool. Soc. Lond.*, **119,** 673–92.

————. 1953. Colony size and reproduction in the grey seal. *Proc. Zool. Soc. Lond.*, **123,** 327–32.

DORAN, A. H. G. 1878. Morphology of the mammalian ossicula auditus. *Trans. Linn. Soc. Lond.* (*Zool.*), **1,** VII, 371–498.

DOUTT, J. K. 1942. A review of the genus Phoca. *Ann. Carnegie Mus.*, **XXIX,** 61–125.

ENDERS, R. K., O. P. PEARSON & H. K. PEARSON. 1946. On certain aspects of reproduction in the fur seal. *Anat. Rec.*, **94,** 213–26.

FRASER, F. C. 1935. Zoological notes from the voyage of Peter Mundy 1655–56, (b). Sea elephant on St. Helena. *Proc. Linn. Soc. Lond.*, **147,** 33–5.

GIAR, A. 1905. Les origines de l'amour maternel. *Bull. Inst. gén. psychol.*, **4,** 387–401.

GIBBNEY, L. 1953. Delayed implantation in the elephant seal. *Nature, Lond.*, **172,** 590.

GWYNNE, A. M. (Unpublished.) Macquarie Island—Natural History. Monthly summaries, April, 1949–April, 1950.

HAMILTON, J. E. 1933. The southern sea lion, *Otaria byronia* (De Blainville). "*Discovery*" *Rep.*, **VIII,** 269–318.

————. 1939a. The leopard seal, *Hydrurga leptonyx* (De Blainville). "*Discovery*" *Rep.*, **XVIII,** 239–64.

————. 1939b. A second report on the southern sea lion *Otaria byronia* (De Blainville). "*Discovery*" *Rep.*, **XIX,** 121–64.

————. 1940. On the history of the elephant seal, *Mirounga leonina* (Linn.). *Proc. Linn. Soc. Lond.*, **152,** 1, 33–37.

————. 1947. On the present status of the elephant seal in South Georgia. *Proc. Zool. Soc. Lond.*, **117,** 1, 272–5.

HAMLETT, G. W. D. 1935. Delayed implantation and discontinuous development in mammals. *Quart. Rev. Biol.*, **10,** 432–37.

HAVINGA, B. 1933. Der seehund (*Phoca vitulina* Linn.) in den Hollandischen gewassern. *Tijdschr. ned. dierk. Vereen.*, 3, III, 79–111.

HUEY, L. M. 1930a. Past and present status of the northern elephant seal with a note on the Guadeloupe fur seal. *J. Mammal.*, **11,** 188–94.

————. 1930b. Capture of an elephant seal off San Diego, California, with notes on stomach contents. *J. Mammal.*, **11,** 229–31.

JOHANSEN, F. 1910. Observations on seals (Pinnipedia) and whales (Cetacea) made on the Danmark expedition, 1906–8. *Medd. Grønland.*, **45,** 201–24.

KERMACK, K. A. (Unpublished). Report on biological observations made in Fl.F. *Empire Victory*, Season 1945–6.

KETTLEWELL, H. B. D. & R. Rand. 1955. Elephant seal cow and pup on South African coast. *Nature, Lond.*, **175,** 1000–1001.

KITCHING, G. C. 1936. The manatee of St. Helena. *Nature, Lond.*, **138,** 33–4.

LAWS, R. M. 1952a. Seal marking methods. *Polar Record*, **6,** No. 43, 359–61.

————. 1952b. A new method of age determination for mammals. *Nature, Lond.*, **169,** 972.

————. 1953a. A new method of age determination for mammals with special reference to the elephant seal (*Mirounga leonina*, Linn.). *Falkland Islands Dependencies Survey Scientific Reports* No. 2, 11 pp.

————. 1953b. The elephant seal (*Mirounga leonina*, Linn.). I. Growth and age. *Falkland Islands Dependencies Survey Scientific Reports*, No. 8, pp. 62.

————. 1953c. The seals of the Falkland Islands and Dependencies *Oryx*, **2,** No. 2, 87–97.

————. 1953d. The elephant seal industry at South Georgia. *Polar Record*, **6,** No. 46, 746–54.

————. 1953e (Unpublished). *The Reproduction of the Southern Elephant Seal*. Ph.D. Dissertation, University of Cambridge. 199 pp.

LONNBERG, E. 1906. Contributions to the fauna of South Georgia. *K. svenska Vetensk Akad. Handl.*, **XL,** 5, 3–21.

————. 1921. *The natural history of Juan Fernandez and Easter Island*, **3,** Zoology. Uppsala.

LYDEKKER, R., 1909. On the skull-characters in the southern sea elephant. *Proc. zool. Soc. Lond.*, 1909, 600–6.

MACGILLIVRAY, J. (Unpublished Admiralty MS.). Private journal of the voyage of H.M.S. *Herald*, 1854.

MARR, J. W. S. (Unpublished). Fourth voyage of *Discovery II*. Notes on Antarctic islands (South Shetlands and South Orkneys), 1933.

————. 1935. The South Orkney Islands. "*Discovery*" *Rep.*, **X,** 285–382.

MARSHALL, E. H. 1930. Report on a visit to the Ross Dependency. *Geogr. J.*, **75,** 251.

MATTHEWS, L. H. 1929. The natural history of the elephant seal, with notes on other seals found at South Georgia. "*Discovery*" *Rep.*, **I,** 233–56.

MAWSON, SIR D. 1915. *The Home of the Blizzard*. London.

MOLINA, G. 1782. *Saggio sulla Storia Naturale del Chili*. Bologna.

MORTENSEN, T. 1934. The manatee of St. Helena. *Nature, Lond.*, **133,** 417.

MOSELEY, H. N. 1892. *Notes by a Naturalist on* H.M.S. *Challenger*. London.

MURPHY, R. C. 1936. *Oceanic Birds of South America*. Amer. Mus. Nat. Hist., New York.

————. 1914. Notes on the sea elephant, *Mirounga leonina*, Linn. *Bull Amer. Mus. Nat. Hist.*, **33,** 63–79.

MURRAY, A. 1866. *The Geographical Distribution of Mammals.* London.

NANSEN, F. 1925. *Hunting and Adventure in the Arctic.* London.

OLDS, J. M. 1950. Notes on the hood seal (*Cystophora cristata*). *J. Mammal.*, **31,** 450–2.

OSBURN, R. C. 1911. California elephant seals at the New York aquarium. *Bull. N.Y. Zool. Soc.*, **45,** 759–62.

OSGOOD, W. H., E. A. PREEBLE & G. H. PARKER. 1914. The fur seals and other life of the Pribilof Islands, Alaska, in 1914. *Bull. U.S. Bur. Fish.*, **34,** 1–172.

PARRY, D. A. 1949. The structure of whale blubber and a discussion of its thermal properties. *Quart. J. micr. Sci.*, **90,** 13–25.

PAULIAN, P. 1954. Sur quelques variations de la date de mise bas de l'éléphant de mer (*Mirounga leonina*). *Mammalia*, **18,** 375–9.

PERON, F. 1816. *Voyage de Découvertes aux Terres Australes.* Paris.

RING. T. P. A. 1923. The elephant seals of Kerguelen Land. *Proc. Zool. Soc. Lond.*, 1923, 431–43.

ROBERTS, A. 1951. *The mammals of South Africa.* Cape Town.

ROBIN, G. DE Q. (Unpublished). Biological Report. Falkland Islands Dependencies Survey, Base "H", Annual Report, 1947.

SAPIN-JALOUSTRE, J. 1952. Les phoques de Terre Adélie. *Mammalia*, **XVI,** 4, 179–212.

SCHEFFER, V. B. & J. W. SLIPP. 1944. The harbor seal in Washington State. *Amer. Midl. Nat.*, **32,** 373–416.

SCHOLANDER, P. F. 1940. Experimental investigations on the respiratory function of diving mammals and birds. *Hvalrådets Skrifter*, **22,** 1–131.

SCHROEDER, C. R. & H. M. WEGEFORTH. 1935. The occurrence of gastric ulcers in sea mammals of the Californian coast, aêtiology and pathology. *J. Amer. vet. med. Ass.*, **87,** 333–42.

SHAW, G. 1801. *General Zoology.* London.

SIVERTSEN, E. 1941. On the biology of the harp seal, *Phoca groenlandica* Erxl. *Hvalrådets Skrifter*, **26,** 1–166.

SKOTTSBERG, C. 1912. The vegetation in South Georgia. *Wiss. Ergebn. schwed. Sudpolarexped.*, 1901–3, Bd. IV, 12.

SORENSEN, J. H. 1950. Elephant seals of Campbell Island. *Cape Exped. Series, Bull.* No. 6.

STONEHOUSE, B. 1953. The emperor penguin (*Aptenodytes forsteri* Gray) I. Breeding behaviour and development. *Falkland Islands Dependencies Survey Scientific Reports* No. 6, 33 pp.

TROLL, B. 1928. Der haarwechsel des see-elephanten. *Anat. Anz.*, **65,** 327–33.

WILKES, C. 1845. *Narrative of the exploring expedition, by authority of Congress, during the years* 1838–42.

WILSON, E. A. 1907a. Mammalia (Whales and Seals). *British National Antarctic Expedition*, 1901–4, *Nat. Hist.*, **2,** 1–69.

————. 1907b. Aves. *British National Antartic Expedition Reports*, 1901–4, *Nat. Hist.*, **2,** 1–31.

WRIGHT, P. L. 1942. A correlation between the spring moult and spring changes in the sexual cycle of the weasel. *J. exp. Zool.*, **91,** 103–10.

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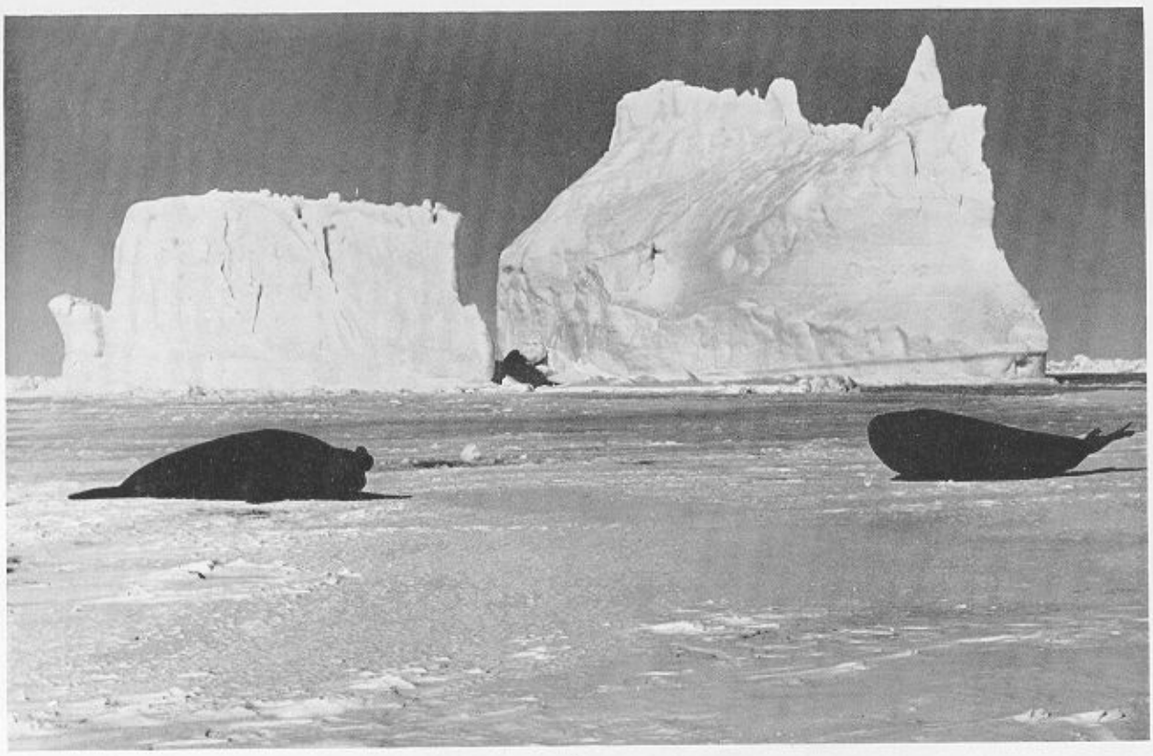
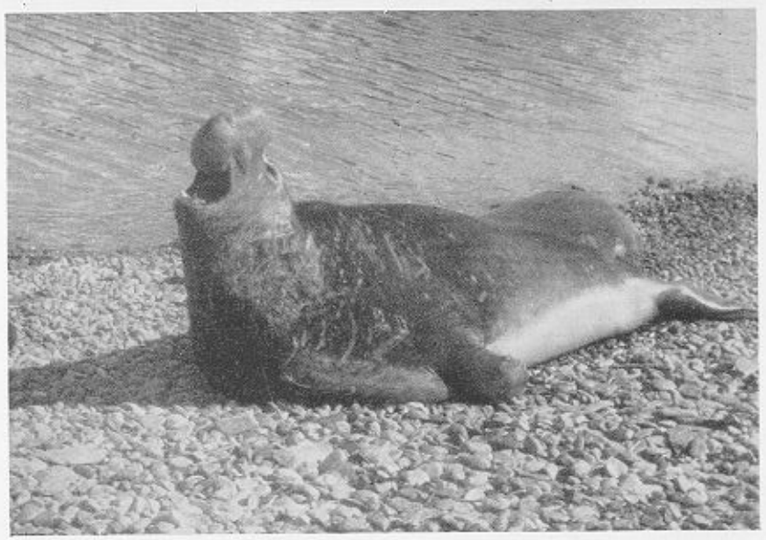


b

(a) Signy Island from Coronation Island. Note unbroken fast ice to the east. Borge Bay is slightly to the left of the centre of the picture. (*Photo: F. L. Johnson.*)

(b) End of fight between bull elephant seals Red/A and Red/nose near large berg at edge of fast ice, Signy Island, September 24th, 1949. Red/nose is backing away defeated.



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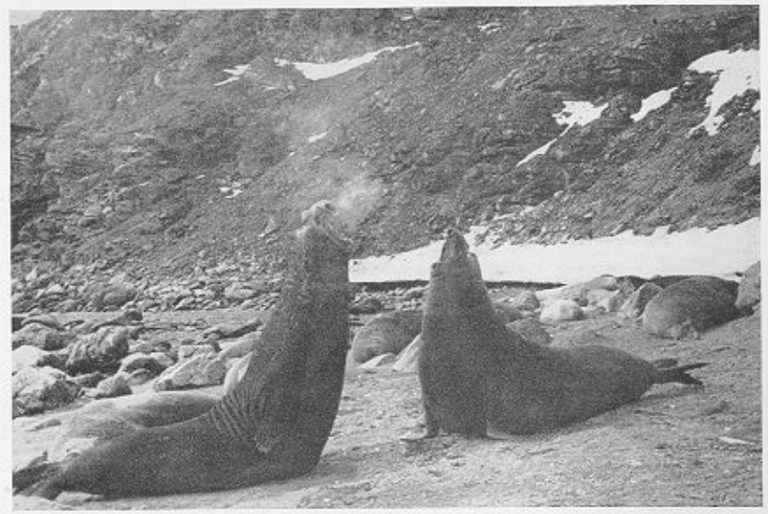

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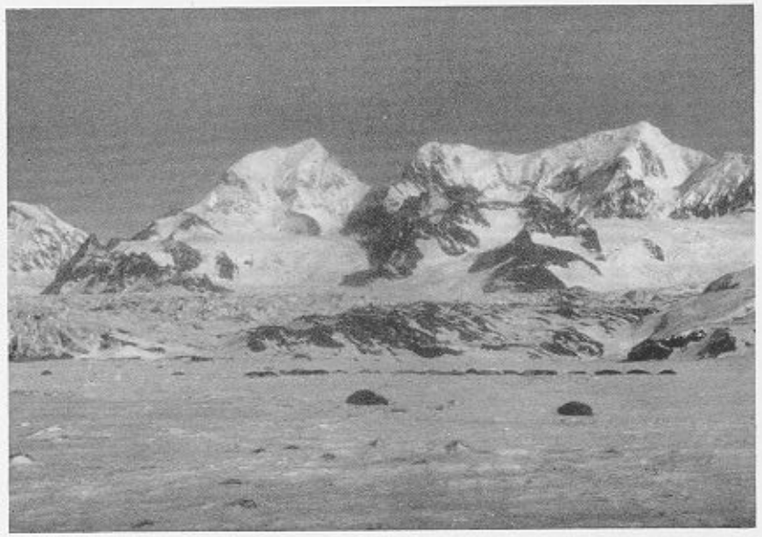

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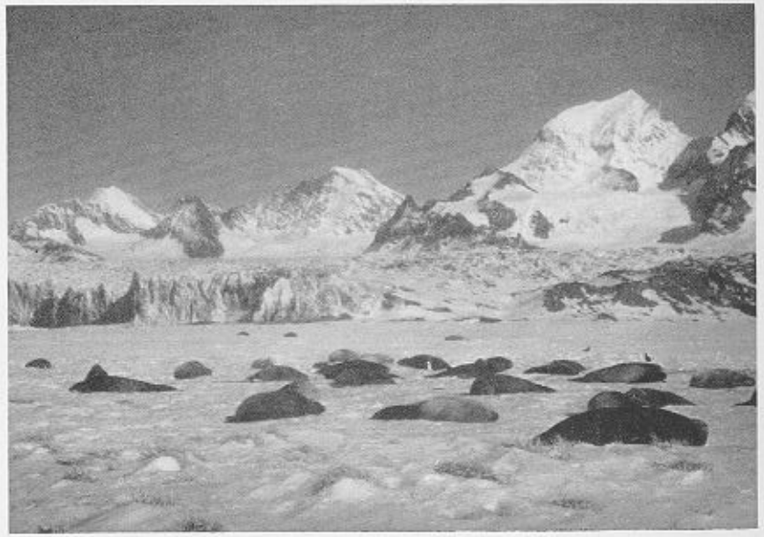


d

(a) Dominant male making vocal challenge, Discovery Point, South Georgia.

(b) Actions preliminary to fighting. Large bull rearing up and roaring; younger male backing away. No blows were struck.

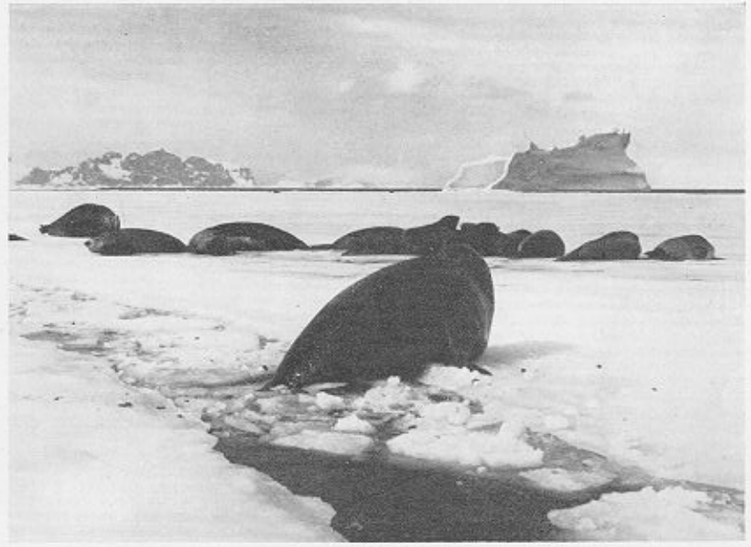
(c) Large harem on flat plain near west side of Nordenskjöld Glacier, South Georgia. Several subordinate bulls are lying at the edge of the dominant bull's territory which in this instance is circular.

(d) A nearer view of the harem shown in VIc. Note spacing of cows and subordinate bulls behind.

a

b

c



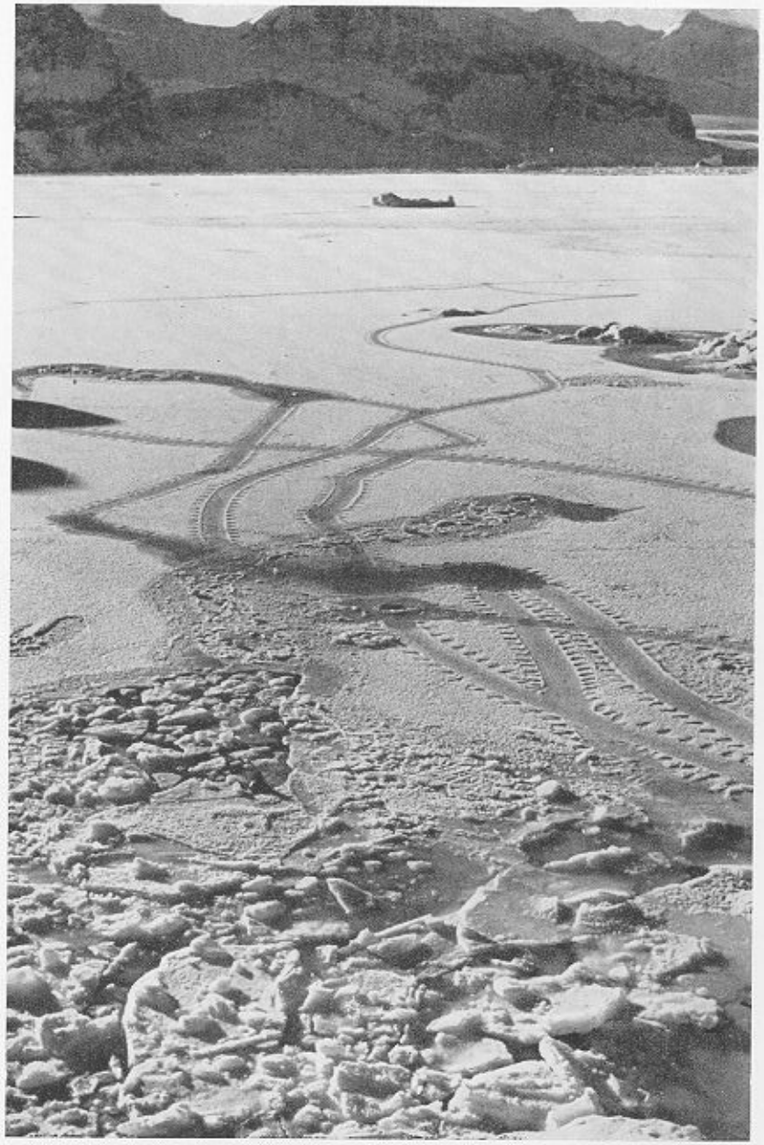
d

(a) Female elephant seal in pack-ice, South Orkney Islands.

(b) Looking west to Red Harem. Signy Island, October 1949. The harem is situated at the seaward side of a large crack in the fast ice.

(c) Red harem on fast ice, Signy Island, 1948. Coronation Island to the north.

(d) October 19th, 1949. Subordinate bull (Red/tail) hauling out of crack shown in Vb. Dominant bull ("Scarred" bull), left centre, about to charge. (Note large grounded iceberg seen in Plates Ib and IVc, and Figure 23.)



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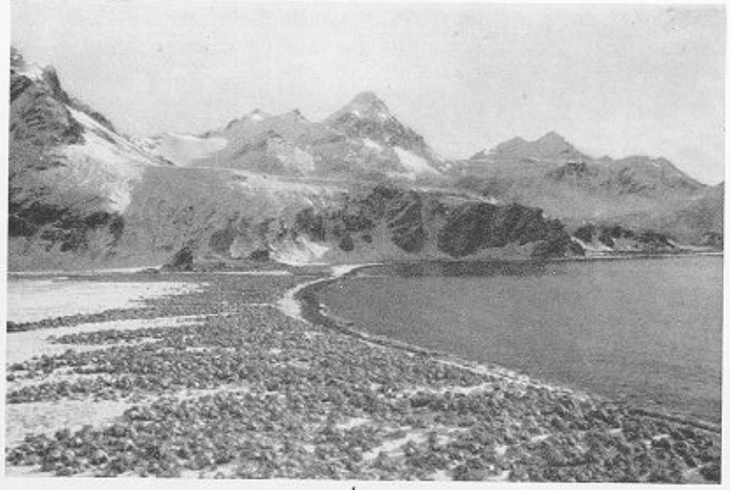


b

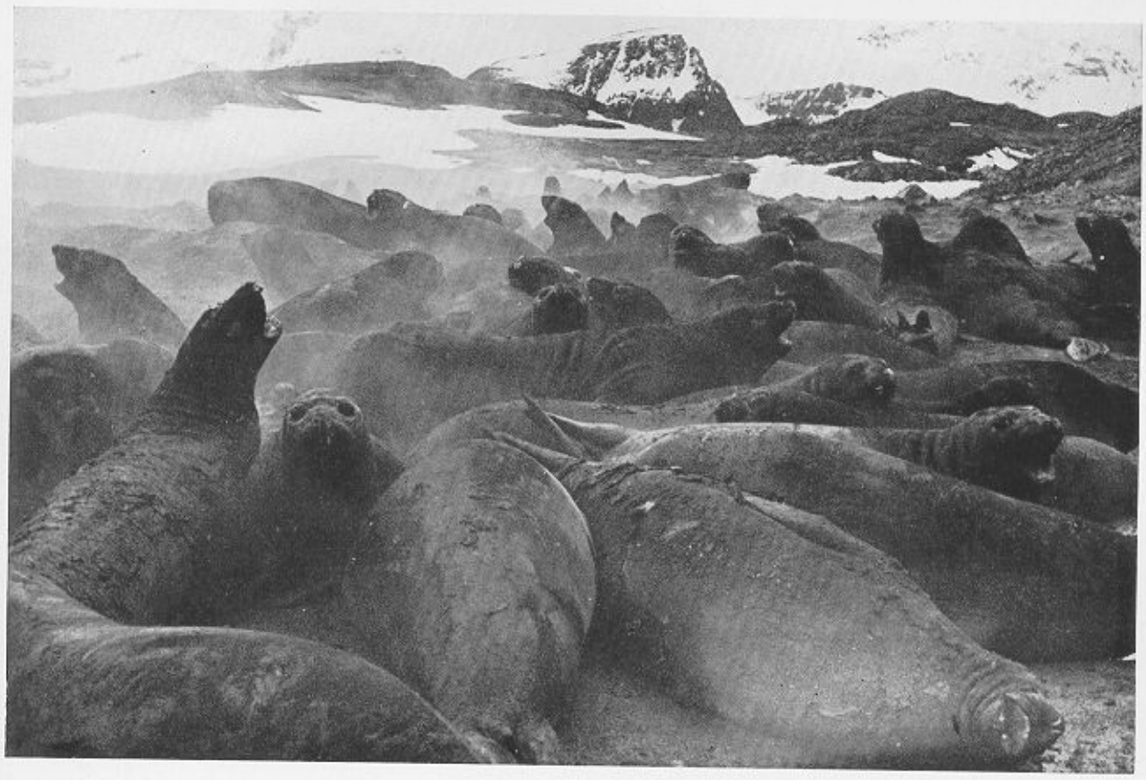
c

(a) Near Berry Head, Signy Island, looking northwards. The head of an elephant seal is visible above the ice in the left foreground, and tracks and breathing holes can be seen on the recently formed ice.

(b) "Hestesletten" from Zenker Ridge, South Georgia. There is a seaward fringe of tussock grass.

(c) Marking a large bull elephant seal (Red/A) at the ice edge Signy Island. Paint brush held in left hand. (*Photo: C. J. Skilling.*)

PLATE IV



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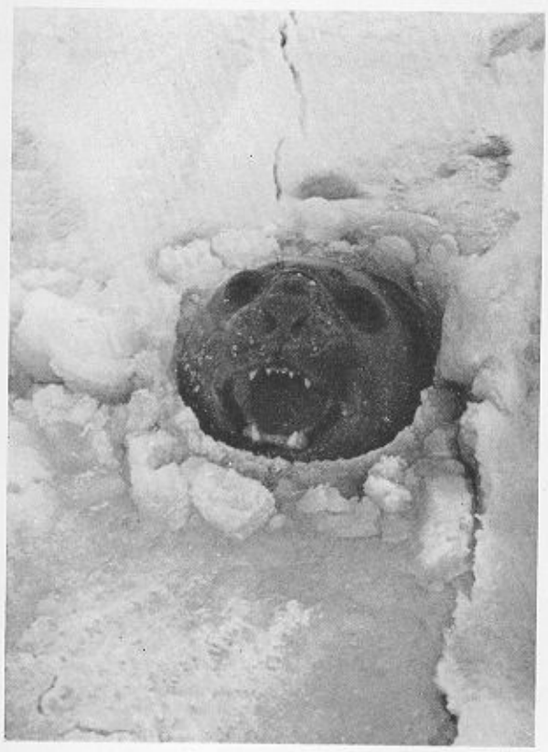

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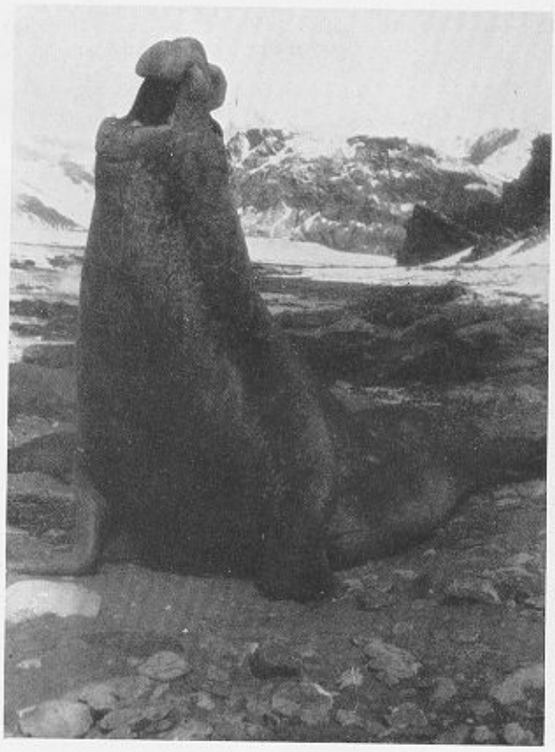


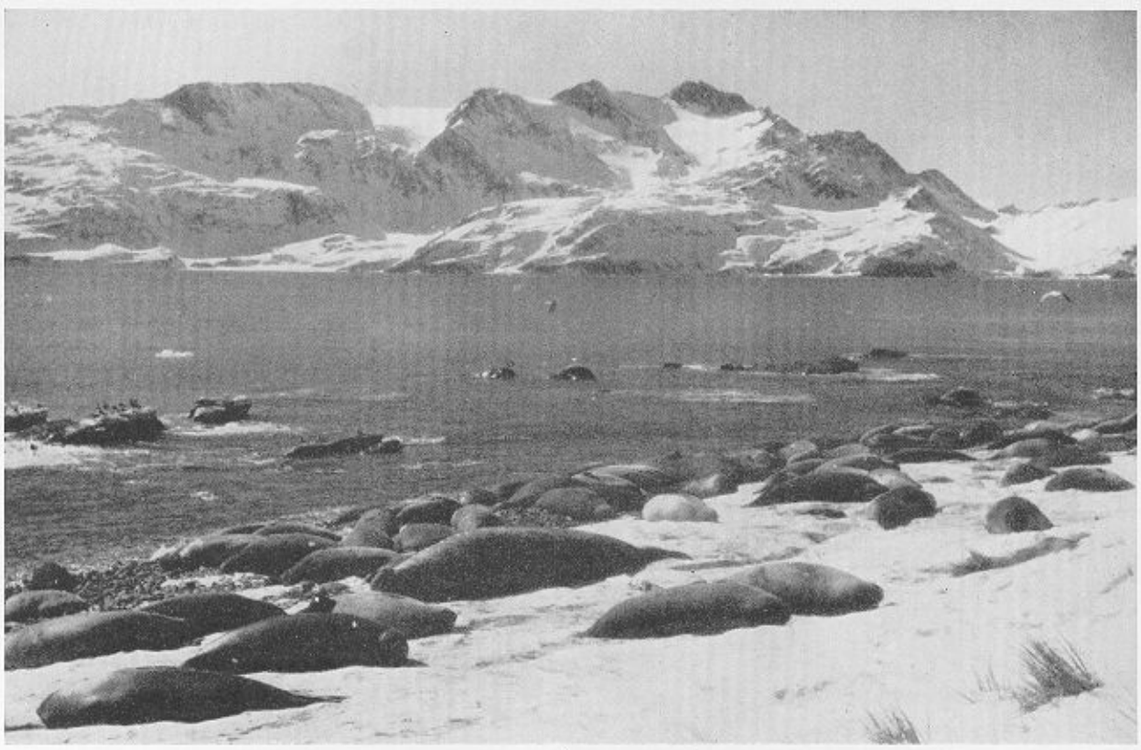
c

(a) Part of a large "pod" of female elephant seals at The Wallows, Signy Island. Ragged moulted patches of hair and epidermis can be seen.

(b) Young male elephant seal at newly made breathing hole in sea ice, Signy Island.

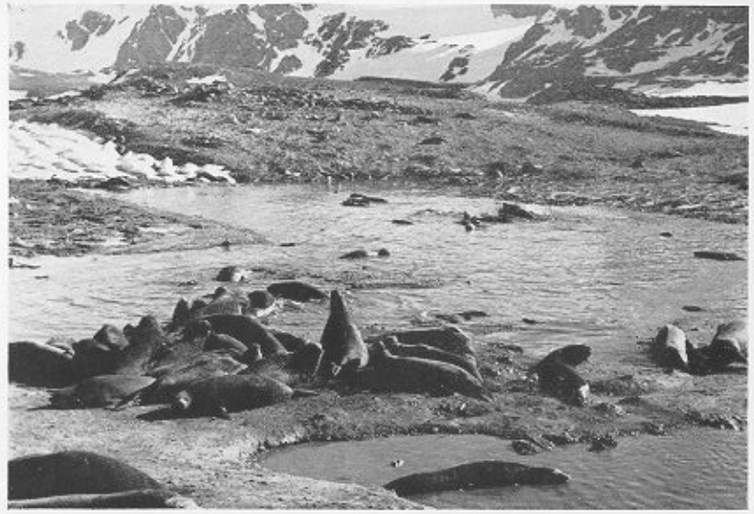
(c) Dominant bull elephant seal making vocal challenge, Susa Point, South Georgia.

a



b

(a) Part of rookery on Dartmouth Point, South Georgia, looking towards King Edward Cove. Note harem bull in water.
(b) Part of rookery at Lat. 54°20′ S., Long. 36°25′ W., Cumberland East Bay, South Georgia. A dominant bull lies in the centre foreground.



a

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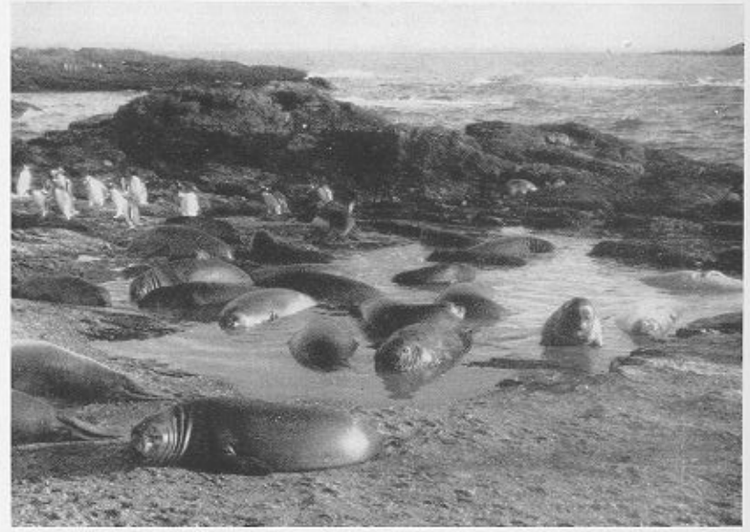

d

(a) Moulting elephant seals at The Wallows, Signy Island. Some animals are in freshwater pond and others on slopes behind.
(b) Harem at Lat. 54°20′ S., Long. 36°25′ W., Cumberland East Bay, South Georgia, seen from above. The bull is in the water just offshore, and has just prevented a cow from leaving.
(c) Large "pod" of closely packed, moulting, female elephant seals, near The Wallows, Signy Island.
(d) Young weaned pups in rock pool, King Haakon Bay, South Georgia.