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THE FUR SEAL OF SOUTH GEORGIA

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Natural Environment Research Council, London



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ABSTRACT

AN account is given of the general biology and status of the fur seal, *Arctocephalus tropicalis gazella* (Peters, 1875), in South Georgia.

The external characters and the structure of the pelage are described. An epizoic pedunculate barnacle, *Lepas australis* Darwin, is noted as infesting some seals.

The position of the South Georgia seals is considered in relation to other members of the genus. An account is given of the present distribution of *Arctocephalus* species and of the known history of exploitation of this species at South Georgia and elsewhere.

The fur seals' habitat and the beaches at present colonized in South Georgia are described in detail. It is concluded that the breeding stations of fur seals on the various islands of the Scotia Ridge enjoy a similar summer climate of cool, overcast days without extremes of temperature and with high relative humidity. An investigation of interspecific relationships of the fur seals are considered. It is thought that an increasing fur seal stock might be in competition with elephant seals, *Mirounga leonina* (Linn.), for breeding sites.

The general and sexual behaviour of the seals are described. It is found that the seals in South Georgia feed on *Euphausia superba*, fish and cephalopods, and it is concluded that the first of these is the staple diet. The vocalizations of the seals are described and their sensory equipment commented on. A brief account is given of grooming and the moult.

The establishment of breeding aggregations of fur seals and their sexual behaviour are described. Cows haul out about 2½ days before the birth of their young and come into oestrus about 8 days after parturition. The peak of cow haul-out is at the end of November. An analysis of the milk and an account of the early growth of the pup are given; the lactation period is thought to be about 100 days. Harem bulls first arrive at about the beginning of November and by the middle of January the break-up of harem structure is apparent.

Annual censuses were made at Bird Island between 1957 and 1962. Between these dates the number of pups born increased from 5,350 to 10,200. Comments are made on the progress of fresh colonization on the islands of the Scotia Ridge. It is concluded that the residual Antarctic fur seal stocks are undergoing a phase of expansion.

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I. INTRODUCTION

THE field work which forms the basis of this study of the biology of the South Georgia fur seal, *Arctocephalus tropicalis gazella* (Peters, 1875), was carried out while the author was employed by the Government of the Falkland Islands as biologist and sealing inspector in South Georgia.

The main breeding colony of fur seals in South Georgia, which is on Bird Island, was visited on at least one occasion in all the breeding seasons from 1956–57 to 1961–62, inclusive; a total of 135 days or parts of days was spent observing the seals. Observations were made by the author, sometimes with the assistance of various helpers, in January, March, May, September, November and December, and on his behalf in February and April. Casual observations have also been provided by a United States Antarctic Research Program party led by W. L. N. Tickell, which wintered at Bird Island in 1962–64.

The behaviour of the seals was studied by direct observation. Field glasses of medium power were found useful for detailed studies of individuals or when working from a vantage point at some distance, but seals can usually be approached sufficiently closely to render visual aids unnecessary. The observer generally equipped himself with a light metal tube or bamboo pole, about 6 ft. long and about 1.5 in. in diameter at its thicker end, with which to ward off any seal which became too aggressive. Female and juvenile seals could easily be kept at bay with such a pole and large bulls could be deterred from aggressive advances by tapping them lightly on the snout at the base of the whiskers (p. 51).

Individual fur seals were recognized either by physical characteristics (most useful in the case of scarred specimens, white-coated seals or those infested with barnacles) or by paint marks. Cellulose lacquer was found suitable for marking but probably any brightly coloured paint would do. A brush with short stiffish bristles, tied to a bamboo pole, was used to apply the paint, and the marks were renewed as necessary.

Animals taken as specimens were killed with a 0.22 rifle firing long rifle cartridges. The skulls of fur seals are quite fragile and, to avoid complete disintegration of the calvarium of the more juvenile specimens, a practice was made of removing the bullets from the cartridges, pouring out about half of the charge, replacing the bullets and cutting them down to within a millimetre or so of the neck of the case. Such reduced charge rounds would kill a seal instantly if fired into the skull at close range. The largest bulls (like all seals) could easily be killed with the high velocity cartridge.

Standard measurements were taken from dead specimens with a surveyor's linen tape marked in centimetres. Weights up to 180 lb. (82 kg.) were recorded direct with a Salter spring balance suspended from a bamboo tripod, but above this limit a pulley system was used with a consequent reduction in accuracy. Young seals and pups were weighed with a balance calibrated up to 30 lb. (13.6 kg.).

The reproductive tract was preserved from all specimens killed, and other samples of organs and tissues were removed and preserved whenever possible. Fixation was usually in 4 per cent formaldehyde buffered with borax, but special fixatives were used where appropriate.

A large number of the skulls collected have been deposited in the British Museum (Natural History), together with some other skeletal material and skins.

It is hoped that a further paper on aspects of the reproductive system of the fur seals will be published in due course.

II. THE FUR SEAL OF SOUTH GEORGIA

A. GENERAL DESCRIPTION

The otariid seals in their general structure demonstrate a compromise between the terrestrial and aquatic modes of life. Although they retain considerably more of the characteristics of the primitive terrestrial stock than do the phocids, they show many specializations of both anatomy and behaviour. The most significant of these is the ability to rotate the hind limbs forward under the body, thus permitting a gressi-grade manner of locomotion on land. It is frequently stated that the Otariidae are not so highly specialized for an aquatic existence as the Phocidae, but although this is true it should not be taken as meaning that the otariids are less successful in their own environment. Where otariid and phocid species have occurred sympatrically there appears to be no tendency for the phocids to oust the otariids, though in all too many

cases the otariid population has been exterminated by man. The otariid seals inhabit predominantly the cool temperate and sub-temperate waters; they have failed to exploit the polar waters in the same manner as the phocids, eleven of whose eighteen species are to be found in association with sea ice. Scheffer (1958) attempted to estimate the numbers of the various pinnipede species, and came to the conclusion that there were between 2·9 and 4·2 million otariid individuals and between 10·9 and 22·1 million phocids. To some extent the disparity in the totals reflects the very intensive hunting to which the various otariid species have been subjected in the last 200 years.

The Otariidae are divided into two sub-families; the Otariinae (sea lions) comprising four genera and five species and the Arctocephalinae (fur seals) comprising two genera and eight species. All the members of the family resemble one another, and the seven species of the genus *Arctocephalus* present as similar a series of forms as can be found in a mammalian genus. A general description of the species inhabiting South Georgia (shown later to be *Arctocephalus tropicalis gazella*) cannot hope to be absolutely distinctive, and as few accurate descriptions of other members of the genus exist, it is not possible to say which, if any, of the characters are specific.

As in all the polygynous pinnipeds, there is a great disparity in size between the sexes. In the South Georgia fur seal males reach a weight of 150–160 kg. (330–353 lb.) and a nose–tail length of about 1·95 m. (6·4 ft.); females rarely exceed 50 kg. (110 lb.) weight or a nose–tail length of 1·4 m. (4·6 ft.) (see Appendix). The weights of both sexes fluctuate considerably throughout the year, the male building up a ponderous layer of blubber during the winter which is utilized during the subsequent breeding season, and the females varying with the growth of their foetuses and mammary glands. In general, however, the adult male is about 3·5 times as heavy as the post-partum female. Similar figures are given for *A. tropicalis tropicalis* by Rand (1956a) and Paulian (1964). For *A. pusillus*, Rand (1959) gave weights of males as 450–800 lb. (204–373 kg.) and females 200–300 lb. (91–136 kg.); these were from a large sample of animals taken throughout the year and, no doubt, similar fluctuations occur in the South Georgia fur seal. In the northern fur seal (*Callorhinus ursinus*), the adult male is 7–8 ft. (2·1–2·4 m.) long and weighs up to 600 lb. (272 kg.), whilst the adult female is 5–5·5 ft. (1·5–1·7 m.) long and weighs up to 130 lb. (59 kg.) (Kenyon and Scheffer, 1955). In the latter species, in which the social structure and polygynism are more highly developed than in any other otariid, the sexual size disparity is considerably more marked than in *Arctocephalus* (Plate 1a–c).

The adult female, or cow (the term “clapmatch” which was often used by the early sealers is now obsolete), presents the most generalized form, the bull (or “wig” of the sealers) differing mainly by its much greater size, the development of neck musculature and the dense and shaggy mane. The trunk of the seal in both sexes is evenly cigar-shaped, having its greatest diameter slightly anterior to the middle where the fore flippers are inserted; the hind flippers and the greatly reduced tail together form the posterior termination to the body. The fore flippers can be folded flat against the body to produce a stream-lined outline; presumably the trailing hind flippers do not cause turbulence when the seal is moving through the water. The body is invested in a dense pelage of dual structure (described in detail below) which covers all but the extremities; the rhinarium, the tips of the ears and the palmar surfaces of the flippers are naked. The upper surfaces of the flippers are haired in part, the hair limit on the fore flipper forming a sinuous curve over the wrist, while on the hind flipper the digits are haired almost to the claws though the interdigital webs are naked (Fig. 1). The exposed skin is pigmented intensely black, a factor which may be connected with temperature regulation. The flippers differ from the normal mammalian limb in the great reduction in length of the upper limb bones, which are contained within the general contour of the body, and by the extension of the digits, which are connected by dense pads of connective tissue in the manus and by webs of skin in the pes. In eight adult cows the length of the fore flipper (the mean of the two measurements from the anterior and posterior insertions of the flipper to its tip) averaged 33·80 cm. (13·35 in.) or 27·85 per cent of the total nose–tail length; in seven adult bulls the average was 49·07 cm. (27·30 in.) or 27·07 per cent of total length. Both fore and hind flippers are used for locomotion and weight-bearing on land as well as for locomotion in the water, and thickened skin is present on both though particularly well developed on the palmar surface of the fore flipper. Nails are rudimentary on the manus though present on all five digits; they appear to be non-functional. On the pes the nails of the three middle digits are well developed and used for grooming the pelage. They grow to a length of about 2·5 cm. (1·0 in.) in males and 2 cm. (0·80 in.) in females, and about one-third consists of a free edge overhanging the nail-bed. The nails of the first and fifth digits are only one-third of the length of those on the other

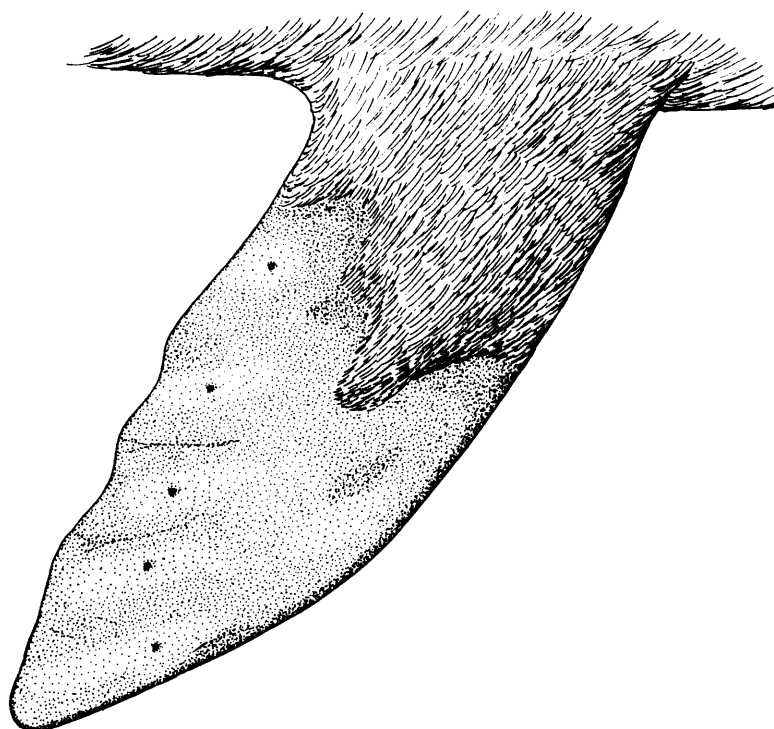


FIGURE 1

Right fore flipper of an adult fur seal, showing rudimentary nails and hair limit.

three and, like the non-functional nails of the manus, do not possess a free edge. The two outer nails tend to point inwards while the middle one is directed along the phalanx. The peculiar wear noted by Rand (1956*b*, p. 15) in the Cape fur seal, which results in one nail pointing in a different direction from the other two, was not seen in the South Georgia seals. As in other members of the genus, the two outer digits of the pes of the South Georgia seals are longer than the middle ones, which are sub-equal, the middle digit being slightly shorter than the others. The tail is connected to the hind flippers by a small fold of skin, scarcely deserving the name of a web.

In males a scrotum is developed, though even after puberty the testes are not permanently descended and can be withdrawn into the inguinal canal when the animal moves. The penial aperture lies slightly more than half-way along from the anus to the umbilicus. In the female the vulva is extended dorsally so that the urethral, vaginal and anal orifices are enclosed in a common furrow. There are four abdominal nipples in both sexes.

The fore quarters of the seals appear large owing to the insertion of the flippers rather far back along the body (the posterior border of the axilla lying approximately half-way along the body length). The neck is long and very flexible; there is no reduction in either number or size of the cervical vertebrae as seen in some other aquatic mammals. In adult bulls there is great muscular development of the neck, and the growth of the mane adds still further to the heavy appearance of this region of the body. The head is relatively small and the snout pointed though not elongated. Several field observers have commented on a resemblance to the head of a dog or an otter, though the similarity is not apparent to all. An abundant moustache of laterally placed mystacial vibrissae is developed in both sexes and reaches its maximum luxuriance in the bulls in which an individual whisker may measure up to 48 cm. (19 in.) in length. The rhinarium is, as mentioned above, naked; it is not normally moist. The eyes are large and have dark-brown irides (smoky blue at birth); as in some other pinnipeds, the iris relaxes immediately after death to reveal an iridescent green tapetum. The pelage below the eye is kept moist by the overflowing tears from the orbit, the lachrymonasal duct being absent. The ear pinnae are small, measuring about 6 cm. (2.35 in.) in length in the male and 4.5 cm. (1.76 in.) in the female, and form an elongated scroll. The aperture of the scroll can be closed by muscular action, and presumably when submerged the pressure of the water on the edges of the scroll forms a water-tight seal. The pinnae are capable of limited movement.

Various body measurements of the South Georgia fur seal are set out in Appendix I and II, and body weights are plotted against nose-tail lengths in Fig. 2. Rand (1956*b*) has discussed in detail the age groups of the Cape fur seal. The number of specimens killed in South Georgia was not sufficient for this form of treatment, but the general pattern of development is similar to that described by Rand.

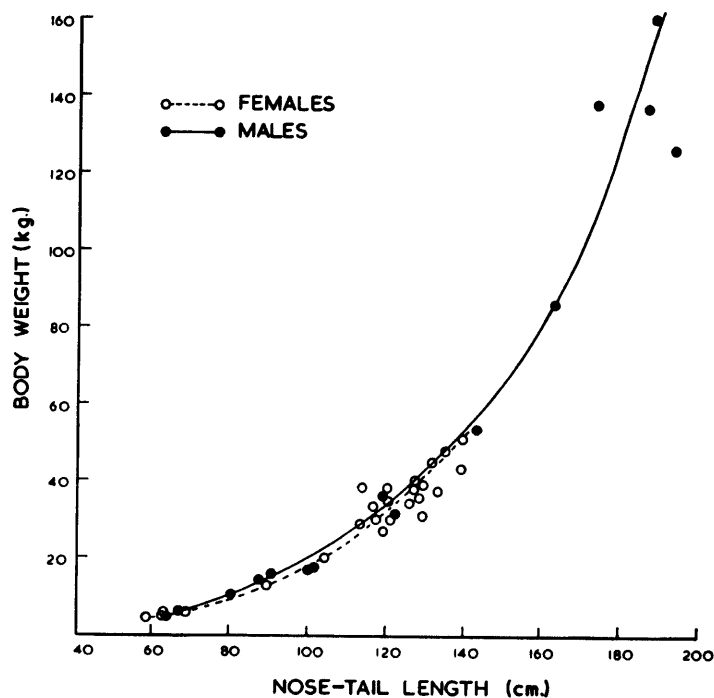


FIGURE 2

Body weight of *Arctocephalus tropicalis gazella* plotted against nose-tail length.

B. COLORATION

The paucity of descriptions of the coloration of fur seals reflects the difficulty of describing the coat colour of these creatures. Except when freshly moulted, or newly arrived on land after the winter feeding period, staining always affects the colours of the hairs to some extent. In addition, the colours vary with the dampness of the coat and also appear to change according to the direction in which it is viewed, so that it is difficult to give a final and recognizable description. The following description of the South Georgia seals is based on field observation supplemented by examination of prepared skins. Of the four skins from South Georgia in the collection of the British Museum, one, a yearling (registered number 1918.10.31), is merely rough-salted and is useless for descriptive purposes. The three others (registered numbers 58.485, 58.486 and 58.487), have preserved the original colours excellently; fat staining, so often a scourge of prepared pinnipede skins, seems entirely absent and there is little rookery stain, this presumably having been washed out in the dressing process. The major differences in appearance between the prepared skins and the living animals (in so far as this can be judged from memory) is the coarser texture of the former, due partly to the lack of natural grooming and partly to the very dry nature of the preserved skins which causes the hairs to be rather more recurved than is common in nature. An attempt has been made to identify these colours by using Ridgway's (1912) Color Standards and the Color Atlas of Villalobos-Dominguez and Villalobos (1947) and the results are given below. In the descriptions the terms used by these authors are italicized and are distinguished by the letters R and V, respectively. The colour names not italicized are not standard colour terms and are merely descriptive. I am indebted to Miss J. E. King of the British Museum for assistance in the colour-matching of the three skins in the collection there.

1. *The cow*

The dorsal and latero-dorsal surfaces vary from grey (*Neutral Grey* R; *Grey* 6 V) to a slightly brownish tinge, almost to russet, depending on the length of time the animal has been ashore. (This tendency to brownness exists in all classes of seal and will not be referred to further.) The dorsal coloration extends under the chin but the throat and breast are creamy (*Light Antimony Yellow* R; *O O Y* 16-6' V) and this colour forms a narrow lateral stripe posterior to the insertion of the flippers. The cream is often stained in specimens which have been long ashore but becomes brownish, never orange. The breast coloration is continued backwards to the level of the insertion of the fore flippers; it then shades into a dark gingery colour (*Cinnamon Buff* R or *Pinkish Cinnamon* R; *O*. 14-9' V) which extends over the belly, being separated from the dorsal grey by the cream stripe mentioned above. Around the insertion of the flippers the hair colour darkens to a rich chestnut (*Chestnut Brown* R; *SO* 2-6' V), and this tone darkens distally on the flippers to almost black; the naked skin of the extremities and soles is black. Bordering the lips and around the eyes the short hairs are brownish; a slightly lighter area extends from the upper lips just posterior to the vibrissae to between the rhinarium and the eyes. The rhinarium is very dark brown or black, sometimes grey (the latter probably being due to desquamation of the superficial epithelial cells). The ears are naked at their tips, where they are black; the middle third is lighter than the general coat colour. The underfur on the back (not visible in the field) is dark fawn colour (approximating to *Vinaceous Cinnamon* R); it is slightly darker on the belly.

2. *The bull*

The general coloration of the bull is essentially similar to that of the cow though the development of the mane, the greater length of the individual hairs and the development of two types of guard hair combine to give a very different appearance. Dorsally the bull presents a much more grizzled appearance than the cow, the heavy mane in particular showing many white hairs. This mane extends over the neck, shoulders and breast down to the level of the insertion of the fore flippers so that the entire "front" of the bull when in the alert position (see p. 52) is covered by the mane. There is no variation in colour between the chest and the back of the neck. A darker yoke extends upwards from the insertion of the fore flippers over the shoulders, posterior to the mane. This is easily seen in young animals but is often obscured in aged bulls. Ventrally, the colour pattern (with the exception of the chest) is similar to that of the cow though the colours are generally darker. The region between the fore flippers is the same rich chestnut as the axillae of the cow, and this shades on the belly to a slightly lighter hue (*Brussels Brown* R; *O O S* 6-6' V). The underfur, which is often visible in the mane region, is darker than that of the cow and is of a reddish colour (*Cinnamon* R; *O O S* 12-6' V).

3. *The pup*

The newly born young of both sexes are very dark brown or black dorsally, with a grey-brown belly which may be a full russet colour when the pup is a few days old. The head is grizzled by the presence of white-tipped guard hairs which become progressively more common and give rise to the condition of "white-face" in pups from about the age of three weeks (Plate Ic). The lips and sides of the chin are russet, tending to cream around the insertion of the vibrissae. The rhinarium is occasionally covered with short grey hairs and is always bordered posteriorly by lighter hair. The underfur is smoky grey (*Pale Neutral Grey* R; *O O S* 11-2' V). The guard hairs are extremely shiny when clean.

The yearling coat of both sexes is dorsally a beautiful silvery grey and its ventral coloration is lighter than that of the adult cow. The underfur is intermediate between the smoky grey of the pup and the dark fawn of the cow; it approximates to *Pale Ochraceous Salmon* R or perhaps a little browner than this, tending to *Light Vinaceous Cinnamon* R. The younger animals tend to be greyer than the adult cows, but juvenile bulls become steadily lighter about the mane as the white type B guard hairs develop (see p. 9).

4. *Colour variation*

In general there is little colour variation, particularly amongst the females, two of which are very seldom distinguishable by coloration alone. Individual adult bulls are occasionally considerably darker than the majority, but one would hesitate to refer to these animals as even partly melanistic. There is,

however, one striking and extreme colour variation which occurs in both sexes and all age groups, that is the complete, or nearly complete, absence of pigment from the guard hairs. These white specimens, erroneously referred to as albinos in a previous paper (Bonner, 1958), are conspicuous wherever they occur. In the newly born, the guard hair, underfur and vibrissae are all white or very pale cream, and the naked exposed skin of the flippers, rhinarium and ear-tips is a pinkish-brown. As the animals mature, more pigment is produced in the naked skin areas and the stiff hairs covering the flippers, so that there is a general darkening of those areas which are coloured black in the normal animal. The underfur also develops pigment, becoming almost indistinguishable from that of the normal animal. The few white bulls that have been observed have all been darker than the darkest white cow. This may be due in part to staining or to the underfur showing through the bristly guard hairs (Plate IVb).

The frequency of the white condition in pups was noted in the 1956–57, 1957–58 and 1961–62 breeding seasons. In the first of these seasons two white pups were seen in a counted population of 2,809, giving an incidence of about 1 : 1,400; in the second there were six white pups in a total of 4,968 or an incidence of about 1 : 800; and in the latest season there were, by 8 December, nine white pups in 5,400, or 1 : 600. It is not certain that this represents a trend.

The following combinations were observed:

| Combination | Incidence | |
|--------------------------|-------------|-------------|
| | 4 Dec. 1957 | 8 Dec. 1961 |
| White cow and white pup | 2 | 1 |
| Normal cow and white pup | 4 | 8 |
| White cow and normal pup | 1 | 6 |

In 1956–57 and 1957–58 there were no white breeding bulls, and it was not until the 1960–61 season that a white bull was first seen holding harem territory. In the following season, three white bulls were holding territories out of a total harem bull population of 727. Subsequently one of these animals deserted its territory, but the others remained ashore till the end of the period of observation. Observations did not reveal any special behaviour either in or towards white bulls or cows, in comparison with normal-coloured animals, and there is no evidence that the condition of white coloration affects either the viability or the breeding success of the animals concerned.

It is interesting that Rayner and Etheridge in 1933 reported a “pale golden” animal in an estimated total of 60 at Bird Island. One of the fur seals photographed by Øritsland on Michelsen Island, South Orkney Islands, in 1960 shows this white coloration (Øritsland, 1960).

Scheffer (1962), reporting on true albino animals in the northern fur seal, states that albinos older than pups are rarely seen, though light brown individuals with pink eyes appear once or twice each year in the commercial sealing drives. Observed incidence of albinism (in pups) is between 1 : 30,000 and 1 : 100,000. Piebald seals are commoner than albinos in *Callorhinus* but no frequencies are given. Scheffer comments on a pup about a month old with eyes and flippers pink, underhair white and guard hairs greyish brown; he suggests that the characteristic fur pigments in guard hairs and underfur are perhaps distinct, a supposition which is reinforced by the condition in the South Georgia seals.

C. STRUCTURE OF THE PELAGE

1. General description

The pelage of all pinnipeds (as well as many other mammals) is dual in structure, a layer of longer, coarser guard hairs overlying a layer of much finer underfur. This underfur reaches its greatest luxuriance in the fur seals and is much reduced in many of the phocids.

The hairs are not randomly distributed over the surface of the body but occur in groups of one guard hair and a cluster of about 20–40 underfur elements, all sharing a common piliary canal. The guard hairs, at least in their proximal portions, are directed caudad and the underfur cluster is developed posterior to the guard hair follicle. The follicles of the underfur elements are more superficial than those of the guard hairs, a fact of considerable importance in dehairing the pelts during dressing for the fur trade. Individual underfur elements are slightly waved, having about 4–8 waves along their length. When the guard hairs are removed during dressing, the underfur presents a closely curled appearance similar to the fleece of a lamb and is known commercially as “wool”.

Sweat and sebaceous glands are associated with each hair group and open into the piliary canal. The sebaceous glands are neither so large nor so numerous as those described in *Phoca vitulina* by Montagna and Harrison (1957). As the skin and underfur do not become wetted when the fur seal is in the water, it is likely that any waterproofing role the sebum may have will differ from that in the phocids. The sweat appears as solid matter in the ducts of the glands in prepared sections, and this is probably so in life also. Montagna and Harrison found solid sweat casts in frozen sections of the skin of *P. vitulina*. The significance of solid sweat in the Pinnipedia is not understood, but it is probably associated with the problem of water conservation. In fur seals, at any rate, liquid sweat could be of only limited value in thermo-regulation owing to the dense mat of underfur that effectively insulates the skin.

The fullest development of the various hair types is seen in the adult bull. A section of the pelt in the region of the shoulder (Fig. 3) shows three distinct layers of hair. The deepest layer represents the underfur

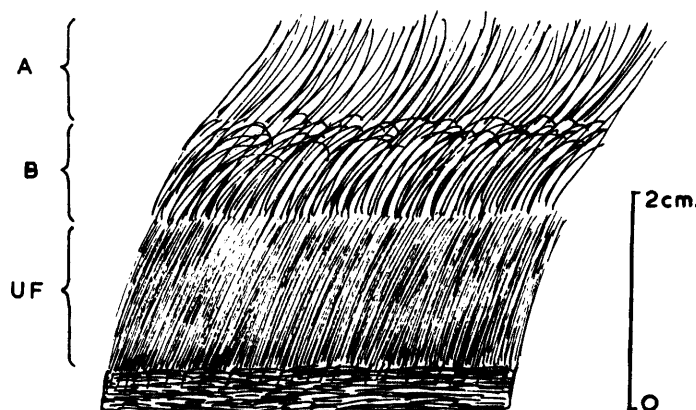


FIGURE 3

Section of pelt from the back of an adult bull, showing arrangement of hair elements.

- A. Type A guard hairs.
- B. Type B guard hairs.
- UF. Underfur.

and is some 15 mm. in depth. Protruding through this are two types of guard hair. The most superficial, type A (Fig. 4), is black with white tips and relatively straight, while below this lies more strongly curved and slightly finer hair, type B, which is completely white apart from a slightly fuscous pigment in the basal third (the part covered by the underfur). Type A is common to both sexes and all age groups, while type B is most highly developed in the bull, particularly in the mane area, and is extremely scanty in the cow. On the belly and flippers hairs of type A only are found and they lack the white tips.

The parts of the guard hairs lying clear of the underfur layer give the seals their characteristic coloration, and this depends very largely on the length of the white tipping. Thus, the pale cream breast and neck of the cow is formed by the relatively longer white tips of the hairs in those regions, while the shorter tips to the hairs on the shoulders of the adult bull give it its dark yoke. The mane of the bull, where the type A guard hairs may be as long as 62 mm., largely owes its grizzled appearance to the type B guard hairs which are visible through the superficial layer. As mentioned above, some of the underfur may also be visible in the mane.

Both guard hairs and underfur elements are elliptical in cross-section. Samples of type A guard hair from the mane of a sub-adult bull had mean diameters of $124\mu \times 248\mu$; the slenderer type B hairs from the



FIGURE 4

An individual type A guard hair from the flank of an adult female.
(Total length of original—22.0 mm.)

same region averaged $55\mu \times 138\mu$. The underfur was approximately $15\mu \times 20\mu$ in diameters, i.e. much more nearly circular in section. Guard hairs from the back, posterior to the mane, were shorter but did not differ significantly in cross-section.

The frequency of distribution of hair groups was studied in the skin of an adult cow (FS 46). Samples of formalin-fixed skin about one inch square were shaved with a razor and cleared in terpineol after dehydration. Sections parallel to the surface of the skin were then cut free-hand with a microtome knife. These were mounted on slides ruled with a millimetre grid and the number of piliary canals counted in a given area. The short stubs of hairs were plucked out of ten piliary canals from each sample and the individual underfur elements counted under the microscope. It was found that the number of hair groups per square millimetre was greater and the hairs longer in the neck region (mid-dorsal line, half-way between the crown and the level of the flippers) than the shoulder region (mid-dorsal line level of the flippers). The dorsal hair was both longer and more abundant than that of the belly (sample from mid-ventral line 5 cm. anterior to umbilicus). The results are set out in Table I. In round numbers this gives approximately 40,000 underfur elements together with their associated 1,340 guard hairs per square centimetre.

TABLE I
LENGTH OF GUARD HAIRS AND DENSITY OF HAIR GROUPS
FROM VARIOUS REGIONS OF AN ADULT FEMALE (FS 46)

| <i>Region</i> | <i>Average guard hair length (mm.)</i> | <i>Average number of hair groups/mm.²</i> | <i>Number of fur elements (average of 10 groups)</i> |
|---------------|--|--|--|
| Neck | 21.8 | 14.7 | 30 |
| Shoulder | 18.5 | 12.6 | 32 |
| Belly | 12.7 | 13.0 | 27 |
| AVERAGE | — | 13.4 | 30 |

Although quantitative data are not available it is believed that a similar situation exists in the bull, and that the hairs of the mane besides being larger are also more dense than those elsewhere. The average length of type A guard hairs in the mane of an adult bull was 60.0 mm. while in the middle of the back they averaged only 41.7 mm. Guard hairs taken from the crown of the head between the ears averaged 40.2 mm. in length (Table II).

In general, the composition of the pelage of the South Georgia fur seal is very similar to that of the northern fur seal, described in detail by Scheffer (1962), but Scheffer's estimates of the density of hair

TABLE II
GUARD HAIR LENGTHS (MM.) FROM VARIOUS REGIONS
OF MALE FUR SEALS

| <i>Region</i> | <i>Adult</i> | | <i>3-year old</i> | |
|---------------|---------------|---------------|-------------------|---------------|
| | <i>Type A</i> | <i>Type B</i> | <i>Type A</i> | <i>Type B</i> |
| Crest | 40.2 | 18.3 | not measured | |
| Mane | 60.0 | 36.4 | 56.4 | 36.6 |
| Back | 41.7 | 18.2 | 38.9 | 17.4 |

The measurements represent the average of ten hairs. Hairs from the mane were plucked from the mid-dorsal line half-way between the crown and the shoulders; those from the back were plucked from the mid-dorsal line, half-way between the shoulders and the tail.

groups and the number of fur hairs per group in *Callorhinus* are greater than those given here for *Arctocephalus tropicalis gazella*. He states that the number of follicular bundles per square millimetre on three samples of skin have been estimated at 11, 17 and 15, and that the number of fur hair elements per bundle varies from 35–40. His final figure of 570 fibres per sq. mm. is based on a value of 38 fibres per bundle and 15 bundles per sq. mm. The difference is probably not significant.

Scheffer finds that the underfur fibres of the yearling are about as long as those of subsequent crops, and that the only significant changes in the lengths of the guard hairs are in those of the mane and back of the adult bull. He attributes the sexual discrepancy in hair length to the difference in body size between the sexes.

2. "Mange"

Occasionally cows are seen with an affliction of the coat resembling mange. The condition consists of patches of skin from which the guard hairs are absent so that the curled fleece of the underfur is exposed. In extreme cases the underfur itself may be absent. Such patches may be only a few centimetres in diameter or cover nearly the whole dorsal surface of the seal. They are most frequent over the rump or on the crown of the head (Plate IVc). Superficial examination of the "mangy" patches has not revealed the presence of mites or similar ectoparasites, nor is there evidence of inflammation of the underlying skin. The aetiology of the condition is unknown.

Scheffer (1962) records similar conditions in the northern fur seal; again no causative agent has been discovered, but an investigation by the U.S. Public Health Service found no evidence of ringworm or mite infestation. I am informed by Mr. Nessling of C. W. Martin and Sons Ltd., that many of the *Arctocephalus pusillus* skins received by his firm for dressing suffer from a similar if not identical condition. It is referred to in the trade as "rub" or "insect bite".

3. Vibrissae

The vibrissae are well developed in pinnipedia and are probably sensory receptors of considerable importance. In phocids both the superciliary and mystacial vibrissae are numerous and conspicuous; in otariids the superciliaries are reduced in number and size though the mystacials are luxuriant, the adult males in particular having fine moustaches. Vibrissae, unlike unmodified pelage hairs, are not moulted and presumably continue to grow throughout life. Although some of the whiskers examined showed blunt apices, indicating breakage, the majority terminated in a fine point and were probably intact, apart from general abrasive wear.

The largest whiskers measured from a South Georgia fur seal were from a harem bull and spanned 106.5 cm. between their tips, the longest individual vibrissa measuring 48.0 cm. from base to tip. Such long whiskers are, however, relatively uncommon, a length of about 35 cm. being more usual. The longest mystacial vibrissa of an adult cow is about 13–22 cm. in length, while that of a pup about three weeks old is about 8 cm. For *Callorhinus*, Scheffer (1962) gives 334 mm. as the greatest length in the male and 220 mm. in the female (an "extremely large" specimen of unknown age).

The general arrangement of the vibrissae is shown in Fig. 5, but this is not very constant and deviations from the normal number (28 on each side) and position occur frequently. Rand (1956b) gives the arrangement of the whiskers in the Cape fur seal as six rows (counted from in front downwards from the ridge of the nose) of 3, 5, 6, 6, 6, 4 = 30 bristles. In adult males of that species they attain a length of 13–22 cm. Scheffer for *Callorhinus* gives the formula for horizontal rows counted from above downwards as 0 or 1; 3, 4 or 5; 5 or 6; 5 or 6 = 20–23. The South Georgia fur seal counted in the same way has 1, 4, 5, 7, 7, 4 = 28. The longest bristles are the posterior ventral ones, i.e. those nearest the angle of the mouth.

The superciliary vibrissae in the South Georgia fur seal number two (or occasionally three) on each side. They rarely exceed 5 cm. in length in adult bulls and may be lacking. When present, the upper one is the longer. Rand stated that the superciliary vibrissae of the Cape fur seal seldom exceed 4 cm. in length. Scheffer found two superciliary vibrissae in the northern fur seal, and notes that they gradually become worn down to, or break off at, the level of the guard hairs and are seldom seen in a seal older than six years.

In all three species the vibrissae of the pups are black (with paler tips), but later become white at the base.

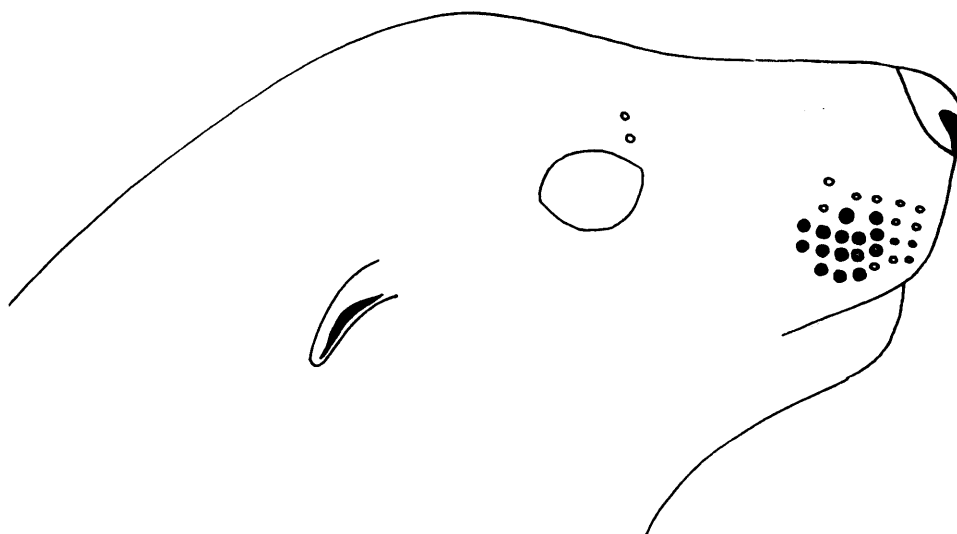


FIGURE 5

Head of a male fur seal, showing distribution of vibrissae.

- Longer vibrissae.
- Shorter vibrissae.

D. BARNACLE INFESTATION

From time to time fur seals are seen with varying infestations of the pedunculate barnacle *Lepas australis* Darwin. The barnacles are attached to the guard hairs or, less frequently, direct to the skin of the naked ear pinna. When attached to guard hairs the barnacles may occur anywhere on the dorsal surface of the seal, though perhaps infestations are commoner on the rump or directly between the shoulders than at other sites. They have not been seen attached to the ventral surface of a seal. They vary in size from the smallest, less than 3 mm. in total length, to well-grown specimens over 30 mm. long. The largest measured was 44 mm. in total length with a capitulum 21 mm. long and 14 mm. wide. Where large barnacles are found they are almost invariably accompanied by smaller specimens (Fig. 6; Plate IVd).

So far only breeding cows have been observed to be infested with barnacles. It is, of course, this class which is accessible in the largest numbers for observation, but the number of sightings of barnacle-infested cows indicates that if the harem bulls had been equally liable to infestation several sightings of males with barnacles would also have been made. There is some evidence that barnacle infestations are more common in some years than in others.

According to Nilsson-Cantell (1930), *Lepas australis* is a pelagic form with a wide distribution in the Southern Hemisphere. Nothing seems to be known of its growth rates, but seals with barnacles over 25 mm. in total length form only a very small proportion of the total number. Unfortunately, quantitative data are lacking, as until the larger specimens had been observed the smaller ones were not looked for.

The same cirripede is found occasionally on elephant seals (Laws, 1953c, and personal observations). In three instances of infestation of the latter species, the carriers were two four-year-old males and an adult cow.

The barnacles do not seem to have any deleterious effect on the seals of either species. In one instance a very heavy infestation of a fur seal was associated with a patch of the "mange" already referred to, but there was no indication of a causal relationship. The cirripedes are very firmly attached to the guard hairs and it is unlikely that they could be dislodged by scratching; in order to collect specimens it is necessary to tug violently, pulling out a tuft of hair with the barnacles. The barnacles die when the seals haul out for breeding, and the empty shells are shed with the guard hairs at the subsequent moult.

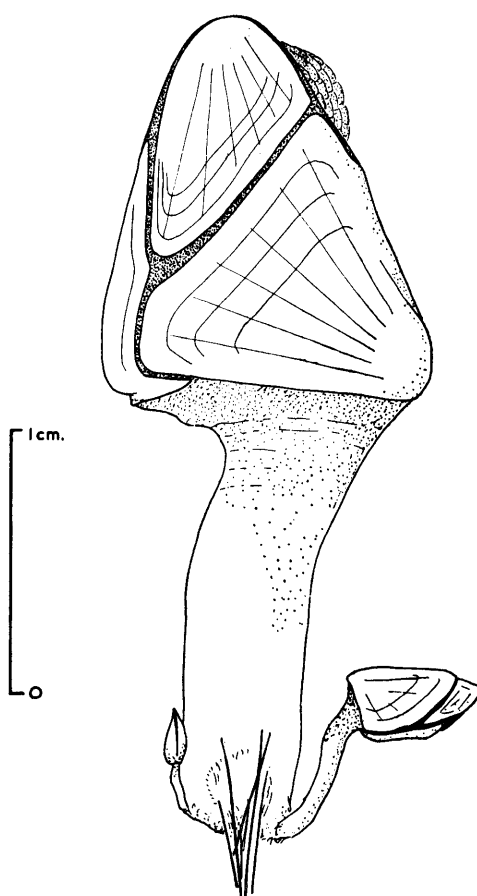


FIGURE 6

Lepas australis attached to guard hairs of a female fur seal.

III. BIOGEOGRAPHY, TAXONOMY AND HISTORY OF EXPLOITATION

A. THE IDENTITY OF THE FUR SEAL OF SOUTH GEORGIA

Largely owing to the lack of specimens, the taxonomic status of the various populations of the southern fur seals is still far from being resolved. Despite the huge numbers of seals slaughtered in the nineteenth century very few skulls or skins found their way back to museums, and the sealers' records generally refer to the various populations simply as "seal" and do not differentiate between the species. In the absence of concrete evidence, the seals of South Georgia were generally referred to the species *Arctocephalus australis* (Zimmermann) which is the fur seal of the neighbouring Falkland Islands and South America (e.g. Matthews, 1929). Clark (1887), in his account of the Antarctic fur sealing industry, followed this practice to the extent of referring only to *A. australis* when considering the fur seals of the South Atlantic area and the Scotia Ridge. Peters (1875) described the fur seal of Iles de Kerguelen as *Arctophoca gazella*. Poland (1892) published an account of the pelts of seals in which he recognized the affinity between the seals of South Georgia and the South Shetland Islands. Although he did not name the species he goes on to say (p. 172) that "this seal closely resembles that of Kerguelen and Crozet Islands (*Otaria gazella*)". He left the matter rather confused, however, as he did not distinguish between the seals of Iles de Kerguelen and Iles Crozet, yet said that the South Georgia seal is rather yellower than that of the South Shetland Islands and appears to be intermediate between the South Shetland and Crozet seals.

Brass (1911) refers the seals of the South Shetlands and South Georgia to *Arctocephalus shetlandii*, but gives no description to allow separation of these populations from others. Rather surprisingly he regarded

the seals of Ile Amsterdam* and Ile Saint Paul as providing a superior pelt to those of the South Shetlands, while Poland specifically stated that the South Shetland seal was at the head of the family and that as much as 212s. had been paid in London for the skin of a "large pup" (a three-year-old male). This would certainly have been an impressive amount for a seal skin in the last decade of the nineteenth century.

Thereafter, references made to the seals of South Georgia usually placed them with *A. australis*. Sivertsen (1954) questioned what kinds of fur seals inhabited Tristan da Cunha and South Georgia, and correctly concluded that the seals of the former would be either *A. gazella* (= *A. tropicalis*) or *A. pusillus*; less happily and rather strangely he thought that the South Georgia seals would be *A. australis*. Scheffer (1958) included the seals of South Georgia and the other islands of the Scotia Ridge under *A. australis australis* for convenience, but recognized that they were not certainly of that race. In 1958, the present author in the first account of the South Georgia seals named them as *A. australis*. This identification was made from two beach-worn skulls lacking the teeth. The following year complete skulls were obtained and were identified by King (1959a) as *Arctocephalus gazella gazella*, but in a later paper in the same year (King, 1959b) the priority of the specific name "*tropicalis*" was established and the South Georgia seals became correctly known as *Arctocephalus tropicalis gazella* (Peters, 1875).

B. DISTRIBUTION OF THE GENUS *Arctocephalus* AND SPECIFIC IDENTITY OF THE FUR SEALS OF SOUTH GEORGIA

It is appropriate at this stage to say something about the distribution of the genus *Arctocephalus* as a whole. Owing to the great similarity of the various species and the lack of a good series of skulls from most of them, it is a matter of great difficulty to decide at what levels the specific and sub-specific limits should be drawn. The latest review of the genus is by Scheffer (1958) who compromises by recognizing six species. With two aberrant exceptions the populations of the genus are found in the Southern Hemisphere, having a circum-polar distribution with a break in the Southern Pacific region where there are no suitable breeding places (Fig. 7). Only one sub-species penetrates into the cold waters south of the Antarctic convergence, yet most breeding animals are found to the south of a summer isotherm of 20° C.

A. pusillus (Schreber), the Cape fur seal, which has been the subject of a series of papers by Rand, is the largest, best known and probably the best defined species. It occurs off the southern tip of Africa from Cape Cross in South West Africa to Algoa Bay in the east, and the cooling influence of the Benguela current is felt over most of its range.

On the opposite side of the Atlantic, off the coasts of South America, is found *A. australis* (Zimmermann). The sub-species from the Falkland Islands, *A. a. australis* (Zimmermann) has been shown by King (1954) to be slightly larger than the mainland form, *A. a. gracilis* Nehring. The former seal is not uncommon on some of the more remote islets off the Falkland Islands (Volunteer Rocks, Elephant Jason Island, New Island) but does not occur as a breeding species on either of the two main islands of the group. The mainland sub-species is now much reduced in numbers. Vaz Ferreira (quoted in Scheffer, 1958) thought that Recife dos Torres in Southern Brazil marked the northern breeding limit. At present the main breeding colony is that at Islas de Lobos, Uruguay, in the mouth of La Plata estuary. Some fur seals probably breed in the tortuous channels of Magellanes and on the islands off the outer west coast of Tierra del Fuego. Lobell (in Scheffer, 1958) stated that fur seals were to be found in Archipelago de los Chonos and to the southward. A third sub-species, *A. a. galapagoensis* Heller, is found today on several of the Galapagos islands but was formerly more widespread in this group (Lévêque, 1963).

At the Juan Fernandez group (the islands of Más a Tierra, Más Afuera and Santa Clara) and the San Felix group (San Felix and San Ambrosio) another species of seal once occurred in vast numbers. Although now very imperfectly known, the species from Juan Fernandez has been described as *A. philippii philippii* (Peters). A closely related form is found today in small numbers on the island of Guadalupe off Lower California and was once extremely common on the Farallones and other islands off the coast of California. King (1954) regarded these animals as conspecific with the "*philippii*" seals of Juan Fernandez while Sivertsen (1954) recognized them as a separate species. Scheffer took the middle course and assigned the Guadalupe seals to the sub-species *A. philippii townsendi* Merriam.

* Formerly known as "Ile Nouvelle Amsterdam".

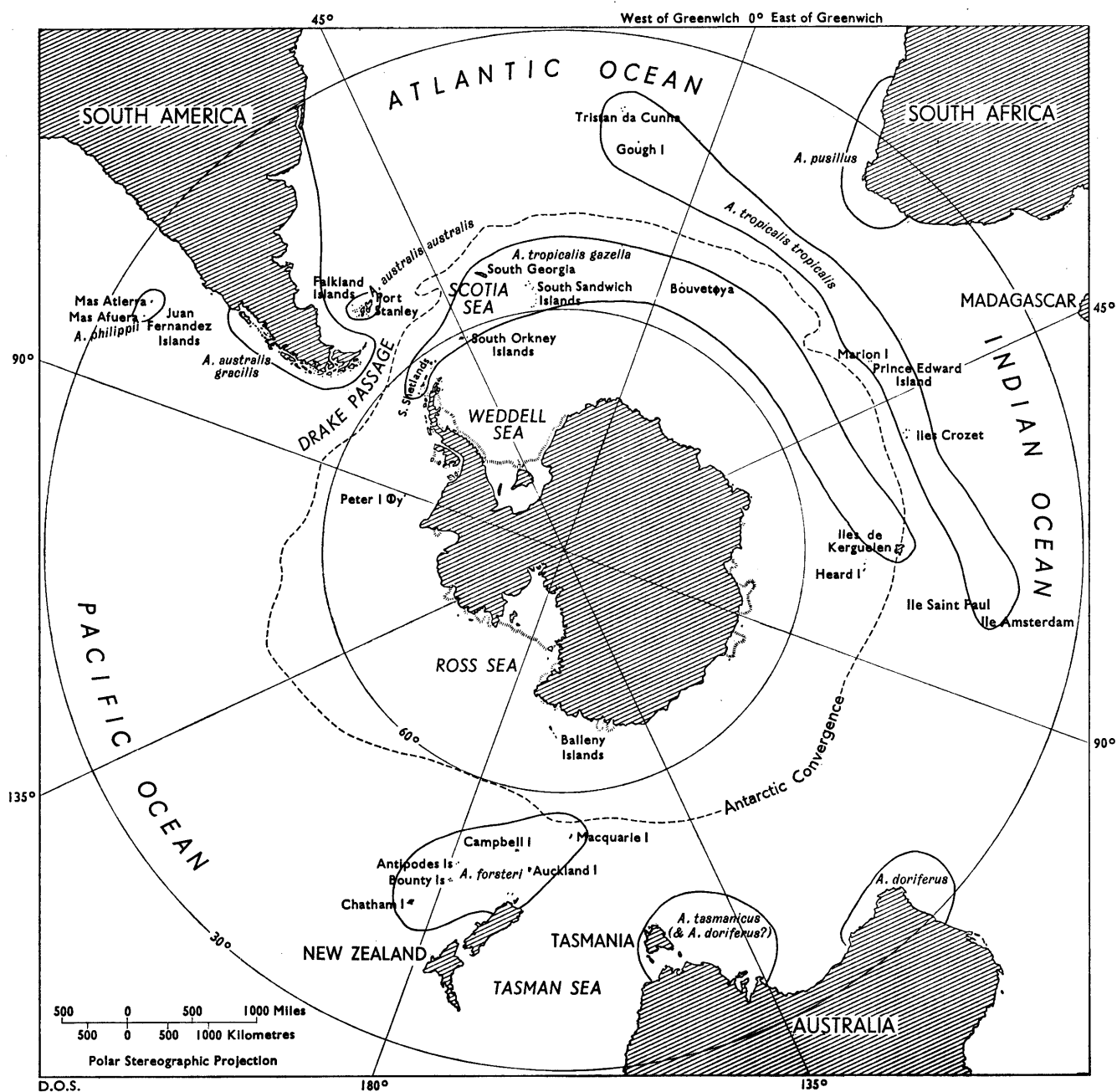


FIGURE 7

Distribution of the southern species of *Arctocephalus*.

The status of the fur seals of the Pacific coast of South America is doubtful. King thought that the common species on Juan Fernandez was *A. australis*, with *A. philippii* occurring sympatrically. Scheffer rejected this view and excluded Juan Fernandez from the range of *A. australis*. Poland stated that the Lima fur seals caught at Juan Fernando (Más a Tierra) and Más Afuera were of the lowest quality, and that the Cape Horn and Lobos Island seals were better, implying at least a difference in the skins discernible to the furrier. One might suppose that there was a distinction here between an oceanic stock (*philippii*) and a continental one (*australis*), but Philippi reported in Peters (1871) that his assistant had taken a skin of *philippii* type from Archipelago de los Chonos while King regards *australis* as being reliably recorded from Juan Fernandez. The presence of an *australis* type seal in the Galapagos, neatly dividing the range of the *philippii* seals into two, requires some explanation. Davies (1958) suggested that an *Arctocephalus*

population spread northward from South America to California during a Pleistocene glacial period, and was cut off in the succeeding inter-glacial and speciated into *philippii* type seals. In the next glacial period, this population spread southward to occupy Juan Fernandez while the main *australis* population moved north to the Galapagos. Davies produced this hypothesis to explain the sympatric *australis* and *philippii* seals at Juan Fernandez postulated by King. The same argument can be used to explain the present distribution of fur seals in the eastern Pacific, supposing that the two species do not occur sympatrically, but the difficulties are many. Further light would be thrown on this problem if good series of skulls were obtained from Guadalupe, the Galapagos and Archipelago de los Chonos. It is perhaps too much to hope that living material could still be obtained from Juan Fernandez, though Nybelin collected a parasite there in 1931 from a seal said to be *A. australis* (Nybelin, 1931), but some sub-fossil material might be obtained.

From Australasia, three species of fur seals are known. Scheffer recognized only one species from Australian waters, *A. doriferus* Wood Jones, but quoted a letter from E. le G. Troughton of the Australian Museum confirming the validity of *A. tasmanicus* Scott and Lord; King also regards this species as distinct. *A. doriferus* is found from Eclipse Island off Western Australia, around the Great Australian Bight to Kangaroo Island off South Australia. *A. tasmanicus* occurs in the neighbourhood of Tasmania, the coasts of Victoria and the southern part of New South Wales. Lewis (1942) recorded fourteen colonies of fur seals in the Bass Strait, the four principal ones on the Victoria coast and the remainder in Tasmanian waters.

The fur seal of New Zealand, *A. forsteri* (Lesson) is comparatively well known. It is found today, according to Turbott (1952), on parts of the coast of South Island and on many of the islands to the south and east of New Zealand, including the Chatham Islands, Bounty Island and Campbell Island. In the last century enormous herds inhabited the Antipodes Islands, Auckland Island and Macquarie Island. On the last of these the species has re-established itself; the first record for many years of fur seals pupping at Macquarie Island was made in 1955 (Csordas, 1958), and two or three pups have been located every year since then (Ingham, 1960).

The remaining fur seals of the Southern Hemisphere are ascribed to the species *A. tropicalis* (Gray). This is entirely an island form, having no connection with any of the continental land masses except the tip of the Antarctic Peninsula. In recent times all the oceanic island groups below the 20° C warm-month isotherm in the Atlantic and Indian Oceans have supported breeding populations, though many of these are now much reduced if not altogether extinct. North of the Antarctic convergence the species is known to breed at Gough Island, where Swales (1956) estimated 13,000 animals including pups, and at Nightingale and Inaccessible Islands in the Tristan group where there are thought to be about 600. At Marion Island (Prince Edward group), Rand (1956a) in 1951–52 estimated not more than about 500 animals, including 160–170 territorial harem bulls; the status of the species at the smaller neighbouring Prince Edward Island is not known. Fur seals once swarmed at Iles Crozet, but whether any remain alive today is uncertain though it seems probable in view of the situation at other groups. Paulian (1964) estimated that about 2,600–2,700 seals inhabited Ile Amsterdam in the 1955–56 season; probably some survive on the neighbouring Ile Saint Paul. Iles de Kerguelen are only some 1,000 miles from Ile Amsterdam and lie on the Antarctic convergence. In the nineteenth century huge numbers of fur seals bred at Kerguelen; Paulian (1953 and 1956) encountered a single individual (a male) there in 1951 and a few were seen in subsequent years. To the south of the Antarctic convergence Bouvetøya supported a population of 1,000–2,000 animals in 1928–29 (Sivertsen, 1954) after some exploitation the previous season.

All the island groups of the Scotia Ridge, from the South Shetland Islands to South Georgia, support some breeding fur seals. The distribution of the fur seals of South Georgia is discussed on p. 32–38, and the colonies of the Scotia Ridge on p. 75. The range of the species is considerable, and great distances separate some of the colonies. From the Tristan da Cunha group (12°W.) to Ile Amsterdam (78°E.) is some 5,200 miles, and south of the Antarctic convergence from Livingston Island (61°W.) to Iles de Kerguelen (70°E.) is almost 5,000 miles. Fur seals have been reported from Heard Island (73°E.) but there appear to be no records of their ever breeding there. There is also a solitary record of a specimen of *A. tropicalis tropicalis* occurring at Macquarie Island (Csordas, 1962), and there is a slight possibility that this was the original species there rather than *A. forsteri* which currently breeds in that locality.

Paulian (1957), commenting on the marked differences between the fur seals of Iles de Kerguelen and Ile Amsterdam, suggested that the species *Arctocephalus gazella* (as *A. tropicalis* was then known) might be split into northern and southern groups. King (1959a), in a careful study of the material then available,

comprising skulls from Gough Island, Marion Island and Ile Amsterdam on the one hand and Iles de Kerguelen and Bouvetøya on the other, concluded that the animals belonged to two separate sub-species. The northern group, *A. gazella elegans* (= *A. tropicalis tropicalis*), is characterized by a tuft of hair on the forehead and a bright yellow chest in the adult males, the lack of any great reduction of the last two upper molars and a generally narrower skull, while the southern group, *A. g. gazella* (= *A. t. gazella*), has a browner chest, no tuft on the forehead, very reduced upper molars 5 and 6 and a wider skull.

King presents ten characters in which statistically significant differences can be shown to exist between the northern and southern races when the measurements are expressed as percentages of the condylo-basal length. These are (in order of decreasing significance): width at supraorbital process, palate width at m 6, width of lower zygomatic root, length squamosal-jugal suture, width at pre-orbital process, palate width at m 3, palate width at m 1, anterior width of nasals, snout width at canines, length gnathion to pre-orbital process. The means of all the characters are greater in the southern group than in the northern, except for the length of the squamosal-jugal suture in which the reverse applies. The second character, the palate width at m 6, is the only one in which the extremes of the northern and southern forms do not overlap. In addition to these entirely bony characters, there is a striking difference in the form of the postcanine teeth of the two races which is well displayed in plate IV of King's paper. The postcanine teeth of the northern race, while certainly slender and of relatively simple construction, are nevertheless typical *Arctocephalus* teeth. The cusps are reduced and do not extend much beyond the level of the cingulum; the ultimate and penultimate upper postcanines (m 5 and 6) show no greater reduction than is normal for the final teeth of a row in this genus. The teeth of the southern form, on the other hand, completely lack cusps in both upper and lower jaws and the crown of the last two upper postcanines are reduced to mere buttons of dentine. Upper postcanine 6 is occasionally entirely wanting and one skull (British Museum registered number 1960.8.10.8) was found to be without teeth in the position of upper postcanines 4 and 6, there being a wide diastema between the third and supposedly fifth teeth of the maxilla. Although the crowns of the last two upper teeth show this strong reduction, the diameters of the necks of the teeth remain much the same as in the northern form; the ultimate tooth often shows reduction of the posterior limb of its bifid root which may lack an alveolus.

Besides this genetically determined reduction of the dentition, the teeth of the southern form are subject to a peculiar sort of wear. In almost all skulls above the age of three years, and in many younger ones, the inner (lingual) surfaces of the teeth are worn smooth, being flattened or even concave (Fig. 8). Of the lower five postcanines, generally only the last three show this wear and it is never as marked as in the upper jaw where it may be so severe as to remove enough dentine to expose the pulp cavity. The cause of this wear is not understood. In normal occlusion the postcanine teeth of the upper and lower jaws do not meet, or occasionally the upper pc 1 and 2 occlude in the gaps between lower pcs 1-2 and 2-3, but these are the teeth least affected by wear. Although the wear is confined to the lingual surfaces it is unlikely to be caused by the tongue, as the tongue is a perfectly normal pinnipede organ and does not seem to have any special developments that would cause abrasion. However, the diet of the South Georgia seals (p. 46), and possibly of all southern populations, consists very largely of the crustacean *Euphausia superba*, and as the seal licks the inside of its mouth in the process of feeding, it could cause their hard exoskeletons to wear away its teeth. This would account for the wear being confined to their lingual surfaces, and also explain the greater wear on the more posterior teeth especially in the upper jaw. The general reduction of the chewing dentition and the widening of the palate may also be adaptations to planktonic feeding.

Another feature of the teeth of the southern form, which may be mentioned here, is the blackish discoloration of the crowns of the postcanines. This colour is unaffected by the usual methods employed in preparing skulls for collection, but is slowly converted to a yellowish tinge by the action of caustic alkalis. Its nature is not known. Rand (1959) mentions that the teeth of the Cape fur seal, *A. pusillus*, become black- or brown-stained around the base as a result of eating cephalopods, the ink of which forms a deposit round the bases of the teeth. Although the South Georgia seals are known to take squid it is not thought that the tooth colour in this species is derived in this manner, as the abraded surfaces of the teeth, which are presumably being freshly exposed, are as darkly coloured as the labial surfaces.

Besides the cranial and dental characters discussed above, the northern and southern populations also differ markedly in coat coloration. Good descriptions of the coloration of species of *Arctocephalus* are for the most part lacking, though *A. pusillus*, described by Rand (1956b), is an exception. Many of the skins available in collections are stained, faded or filthy, or a combination of all three, but a series of fur seal

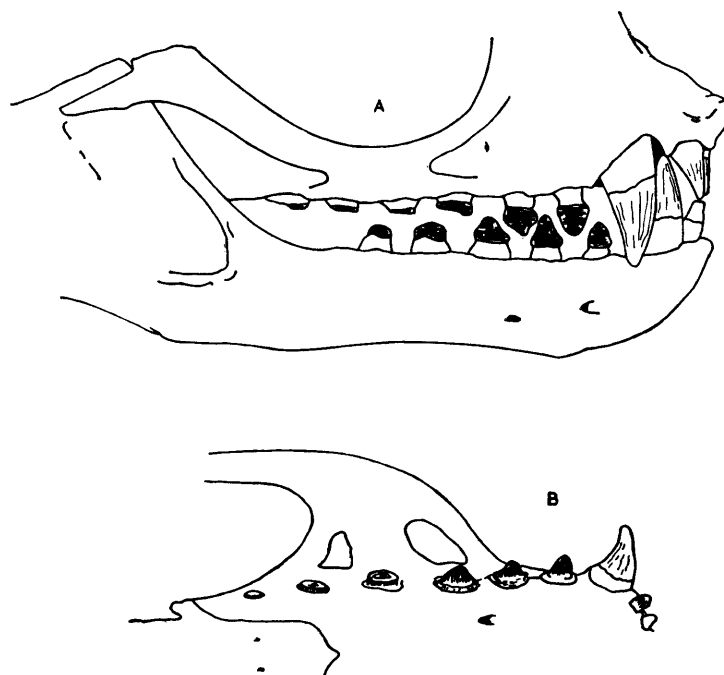


FIGURE 8

Tooth row of an aged female fur seal from South Georgia (AA BI 1960), showing wear. Although none of the postcanine teeth occlude when the jaws are closed, all the upper row show signs of wear on the lingual surface and the last three are so worn down that they are mere stumps with the pulp cavities exposed. There is slight lingual wear on the last three lower postcanines.

A. Lateral view.

B. Linguo-palatal view.

skins collected on Gough Island in 1955 and 1956 was fortunately available for comparison with the South Georgia specimens. All the Gough Island skins are slightly oily, but this has probably not affected the hair coloration to any great extent, though the pelts have oxidized to a darker yellow than the South Georgia skins. It is in the adult bull that the most striking differences are apparent. The adult bull of Gough Island was said by Swales (1956) to be recognizable by the prominent tuft of hair on its forehead, the nicotine-yellow breast and face, black back and dark brown belly. Rand (1956*a*) described the adult bull of Marion Island as dark grey, strongly grizzled on its neck and shoulders, with the throat and chest yellowish and the abdominal region almost fuscous with darker axillae. Paulian (1964) said of the Ile Amsterdam animal that the general colour of the dorsal surface is dark brown with many white or white-tipped hairs in the region of the shoulders; the lower jaw, throat and chest are yellow. Three skins of adult bulls from Gough Island in the collection of the British Museum were also examined. The ground colour of the dorsal surface is dark brown trending to black immediately above the hind extremities. White or pale-tipped hairs are commonest over the shoulders and decrease in frequency towards the lumbar and sacral regions; they are never nearly as frequent as in the South Georgia animals. The tips are rarely more than 3 mm. in length and are pale ochraceous, not white, though entirely white hairs do occur. The belly is fuscous, as Rand states, but is noticeably lighter than the back, in contrast to the South Georgia animals of which the reverse is true. The distribution of the yellow coloration (identified as varying from Ridgway's *Ochraceous-orange* and *Ochraceous-tawny*) over the lower jaw, throat and chest, which extends as a browner hue over the upper jaw, is quite characteristic and would probably serve to distinguish the northern race from all other members of the genus.

The Gough Island skins can be distinguished from those of South Georgia also by the prominent crest of hair on the crown of the head and the lesser development of the mane in the former. Rand states that

the crest is 75 mm. or more in length; Paulian more conservatively suggests up to 70 mm. The largest crest on the three Gough Island skins measured is 50 mm. in length but is perfectly distinguishable from the much shorter (about 15–20 mm.) hair surrounding it. South Georgia seals do not have a crest of longer hair on the head but the hairs on the top of the skull are set vertically in the skin, or recurved slightly forward, and thus stand out as an apparent crest when viewed against the flattened and sleeker pelage of the sides of the skull. Paulian states that the Ile Amsterdam bull can erect its crest when angry; the “crest” of the South Georgia bull is permanently upright. The mane described for the northern animals is much less luxuriant than the shaggy mass of hair that invests the shoulders and neck of the South Georgia bull. As described earlier (p. 9), hair lengths of up to 62 mm. have been found in the mane of a southern bull, while average mane lengths (measured mid-way between nape and shoulders) for three bulls from Gough Island were 35, 32 and 43 mm. The mane of the northern form is interrupted by the yellow coloration ventrally, while that of the South Georgia animal (and, judging from the photograph in Sivertsen (1954), the Bouvetøya animal also) is continuous. Table III sets out the results of hair-length measurements for the two populations, together with data from two specimens of *A. pusillus*.

TABLE III
LENGTHS (MM.) OF GUARD HAIRS FROM CREST, MANE AND BACK OF BULLS
OF TWO BREEDING POPULATIONS OF *ARCTOCEPHALUS TROPICALIS*

| Region | South Georgia | | | Gough Island | | | <i>A. pusillus</i> * | |
|--------|---------------|-------|------------|------------------|-----------------|-----------------|----------------------|----------------------|
| | Adult | Adult | 3-year old | Adult 56.487† | Adult 56.486 | Adult 56.490 | Adult 6.8.1915 | Adult 1868.3.17.3 |
| Crest | 40.2 | 37.5 | — | 50 | 40 | 50 | 17.5 | 26 |
| Mane | 60.0 | 60.0 | 56.4 | 35 | 32 | 43 | 30 | 46 |
| Back | 41.7 | 43.2 | 38.9 | 21 | 20 | 23 | 15–20 | 27 |

* Two specimens of *A. pusillus* are included for comparison.

† Numbered specimens are in the British Museum collection.

Although the colour differences are most clearly discernible in the adult males, the skins of all classes except the black pup are distinguishable in the two forms. The Gough Island animals are always browner and darker while those from South Georgia are greyer and more silvery. In particular, the underfur of the northern form is, even in the juvenile, darker than that of the adult South Georgia cow.

The northern and southern forms are thus distinguishable on the basis of the skull characters analysed by King, on their dentitions and on their colorations. Although their ranges run parallel to each other across the South Atlantic and Indian Oceans, it is probable that the Antarctic convergence forms an effective barrier and there is no reason to doubt that they are geographically isolated. Too little is known of the northern form to determine whether there are also differences in behaviour. Their foods must differ as *Euphausia superba*, which is the staple diet of the southern form in South Georgia and presumably elsewhere, does not occur in the waters inhabited by the northern populations. Considering these matters, it would seem reasonable to assign the northern and southern races to two different species, *A. tropicalis* (Gray) in the north and *A. gazella* (Peters) in the south.

However, amongst the skulls from Marion Island examined by King, one (Rand's No. 3791) possessed a dentition resembling a typical southern skull:

The width and concavity of the palate and the lateral extension of the posterior ends of the maxillae are characters which are far more like those of a Kerguelen skull. The palate width at m 6 does fall within the range of variation of the Northern group, but in the other aspects it is unlike more typical Marion skulls. The squamosal-jugal suture is short . . . and forms the lower limit of the range of this measurement in the Northern group. . . . The upper molars are very like those of Kerguelen and Bouvet Island skulls, both in the reduction of the 5th tooth (the 6th is missing) and the state of wear. This deviation from what is otherwise called normal occurs only once in the 63 skulls of the Northern group available for comparison. (King, 1959a, p. 31–32.)

King considered that *Arctocephalus tropicalis* was on the point of evolving into two species but, on the basis of this intermediate form skull, regarded the process as incomplete. The present author is inclined to

regard this single variant skull as less significant than the considerable body of other data indicating a specific difference between the two populations, but little would be gained at this stage by further revision of the nomenclature and King's conclusions should stand.

The specific identity of the fur seals of South Georgia is thus *Arctocephalus tropicalis gazella* (Peters, 1875).

C. PREVIOUS HISTORY OF THE SPECIES IN SOUTH GEORGIA: THE EARLY SEAL HUNTERS

The first authentic record of a landing in South Georgia (Fig. 9) is that of Captain James Cook who went ashore from the sloop *Resolution* on 17 January 1775 in Possession Bay on the north coast. Cook (1777) wrote:

Seals, or sea-bears, were pretty numerous. They were smaller than those at Staten Land; perhaps the most of those we saw were females, for the shores swarmed with young cubs. We saw none of that sort which we call lions; but there were some of those which the writer of Lord Anson's Voyage describes under that name; at least they appeared to us to be of the same sort; and are, in my opinion, very improperly called lions, for I could not see any grounds for the comparison.

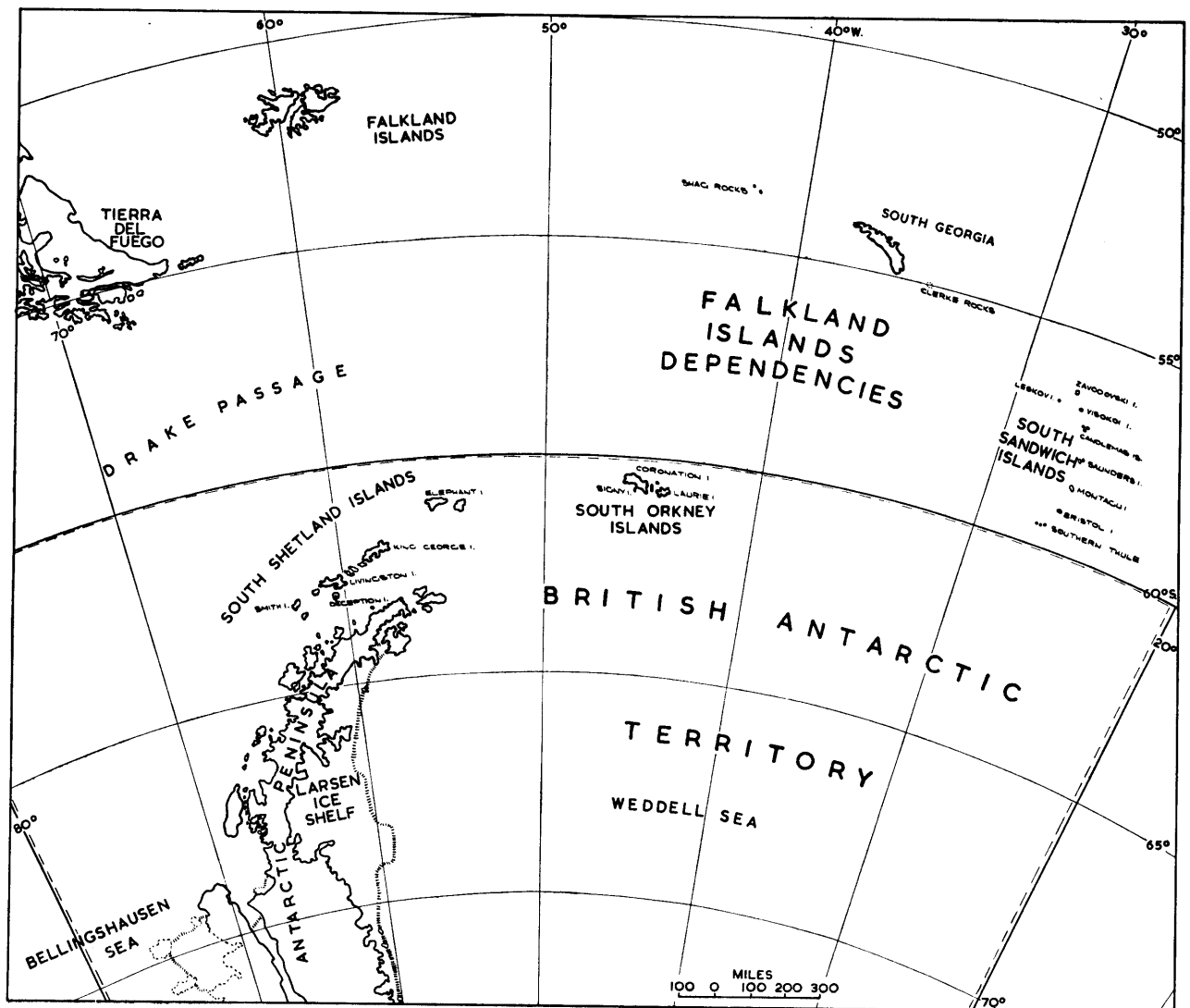


FIGURE 9
The islands of the Scotia Ridge.

Lord Anson's "Lions" were elephant seals; the others were fur seals. Forster, the naturalist who accompanied Cook on board the *Resolution*, remarked that the seals of South Georgia were more fierce than those that they had seen before.

The youngest cubs barked at us and ran after our heels when we passed by, trying to bite our legs. (Forster, 1777.)

Forster commented also on the absence of the southern sea lion (*Otaria byronia*) from South Georgia.

Cook's expedition was concerned with discovery and not with exploitation. The first commercial sealers known to have visited South Georgia were Roswell Woodward and Daniel F. Greene, who fitted out at Connecticut for a sealing voyage to the Falkland Islands. Some time during their voyage between 1790 and 1792 at least one of their vessels visited South Georgia and there obtained part cargoes of fur seal skins. Captain Greene was an innovator not merely in opening new sealing grounds but also in pioneering the route to the Canton market, being the first recorded sealer to carry skins direct from the sealing grounds to China. In 1791 an English sealer, the *Ann* (Captain Pitman), visited South Georgia (Roberts, 1958) but it is not certain if there were other vessels in that year.

Thereafter, the sealing expeditions to South Georgia increased enormously, the trade being almost exclusively in the hands of the Americans (particularly from Massachusetts and Connecticut) and the English, with an occasional French, German or Russian vessel. The peak of the sealing was around 1800-01; in that season Edmund Fanning recorded that seventeen sail of American and British vessels were working the island, the total catch being 112,000 skins of which Fanning's ship, the *Aspasia*, secured no less than 57,000. Weddell (1825) calculated that by 1822 at least 1,200,000 furs had been taken from South Georgia alone, and that the species was virtually extinct there.

In the meantime, other sealing grounds were being exploited. The Falkland Islands and the Cape Horn region had been the locale of the initial fur sealing ventures in the Southern Hemisphere from about 1784, when the ship *States* secured a cargo of 13,000 furs from the Falklands. (The reference to sealing on Ile Amsterdam in 1773 by Allen (1899) is an error for 1793; see Staunton (1797).)

The vast colonies of seals at the Juan Fernandez Islands (Más Afuera and Más a Tierra) were first hunted in 1792 or 1793, and by 1806 had been almost completely exterminated. Kerguelen was visited between 1791 and 1794 by three American vessels, *Alliance*, *Asia* and *Hunter*, commanded respectively by Bartlett Coffin, Elijah Coffin and Simeon Starbuck, all of Nantucket (as might well be gathered from their names). The Crozets were first sealed in 1805 by the *Favourite* of Nantucket (Captain J. Paddock), for though Henry Fanning in the *Catherine* had landed there previously the same year, he had passed on to the Prince Edward Islands without stopping to seal. Further east in Australasian waters sealing seems to have begun in New Zealand in 1792 when the *Britannia*, sent to Dusky Sound by the whaling firm of Enderby Brothers, obtained 4,500 seals. In 1798 the *Nautilus* took 9,000 skins from the Bass Strait, and the sealing trade in New South Wales (probably the coast of what is now known as Victoria) was said to be at its height between 1810 and 1820. The Antipodes Islands (originally known as the "Penantipodes") were discovered in 1800 and first exploited in 1804 when the American vessel the *Union* left a sealing gang there. It was stated by Scott (in Allen, 1899) that in two years, 1814 and 1815, no fewer than 400,000 skins were taken from the Antipodes. In 1810 Frederick Hasselberg discovered Macquarie Island in the *Perseverance* and, as at the other islands, the stock of seals was speedily exterminated, more than 180,000 being taken by 1813 (Csordas, 1958).

The South Shetlands, the last great sealing grounds of the nineteenth century, were discovered on 18 February 1819 by the brig *Williams* (Captain William Smith), which had been blown southwards off its course while on a trading voyage from Buenos Aires to Valparaiso. The first vessel actually to hunt seals in the South Shetlands was the Argentine *San Juan Nepomuceno* which secured a cargo of 14,600 skins there and brought them to Buenos Aires on 22 February 1820 (Bruce, 1920, p. 38). In the same season a British vessel from Buenos Aires, the *Espirito Santo*, and the brig *Hersilia* (Captain James P. Sheffield) of Stonington, Connecticut, both had good hauls. In the following season sealers flocked to the South Shetlands, at least 47 American and British vessels working the beaches of the group in 1820-21. The next season there were no fewer than 44 vessels sealing there, though by that time the stock had so declined that many went back practically empty-handed. The peak catch was in 1820-21 when about a quarter of a million seals were taken and many thousands killed and lost. Weddell (1825) wrote:

The quantity of seals taken off these islands, by vessels from different parts, during the years 1821 and 1822, may be computed at 320,000, and the quantity of sea-elephant oil at 940 tons. This valuable animal, the fur seal, might, by a

law similar to that which restrains the fishermen in the size of the mesh of their net, have been spared to render annually 100,000 furs for many years to come. This would have followed from not killing the mothers till the young were able to take the water; and even then, only those which appeared to be old, together with a proportion of the males, thereby diminishing their total number, but in slow progression. This system is practised at the river of Plata. The island of Lobos, in the mouth of that river, contains a quantity of seals, and is farmed by the Governor of Monte Video, under certain restrictions, that the hunters shall not take them but at stated periods, in order to prevent the animals from being exterminated. The system of extermination was practised, however, at Shetland; for whenever a seal reached the beach, of whatever denomination, he was immediately killed, and his skin taken; and by this means, at the end of the second year, the animals became nearly extinct; the young, having lost their mothers when only three or four days old, of course all died, which at the lowest calculation exceeded 100,000.

Webster, who visited the group on board H.M. Sloop *Chanticleer* in 1829 was greatly impressed with the wanton destruction of the seal stocks:

The harvest of the seas has been so effectually reaped, that not a single fur seal was seen by us, during our visit to the South Shetland group; and, although it is but a few years back since countless multitudes covered the shores, the ruthless spirit of barbarism slaughtered young and old alike, so as to destroy the race. Formerly 2000 skins a week could be procured by a vessel; now not a seal is to be seen. (Webster, 1834.)

The more enterprising of the sealers, unable to obtain a cargo at the South Shetland Islands pushed farther afield and rapidly depleted the smaller stocks at the South Orkney Islands, South Sandwich Islands and Bouvetøya.

In South Georgia the fur seals had so declined by the 1820's that the sealers were compelled to turn their attention to taking cargoes of elephant seal oil, a much less valuable product but still worth fetching. In 1822 the schooner *Wasp* visited the island, and by the account of her mate, Benjamin Morrell, searched the entire coast without finding any fur seals; little reliance can, however, be placed on this report as Morrell claimed that the whale boats circumnavigated the entire island in four days, a distance of some 250 miles, which would have left no time at all for entering the small coves and harbours where seals might have been lurking. In 1829 the schooner *Pacific* (Captain James Brown) of Rhode Island took a cargo of elephant oil but only 250 furs. Another schooner, the *Mary Jane* of New York, secured 600 seal skins in the season 1838–39. (Murphy (1948) gives the name of this vessel as *Elizabeth Jane*, but a headstone at a grave at Prince Olaf Harbour refers to the mate, John Anderson, of the schooner *Mary Jane* of New York (Captain Joseph Parsons), and this is presumably the same vessel. The brig *Medina* was also in South Georgia that season; Anderson was aboard this vessel when he died.) In 1846 the *Esther* of London buried some of her crew at Grytviken, but there are no records of her catch, if any, nor is it known whether she was in fact a sealer. No further voyages are recorded till 1870, when the schooner *Flying Fish* took 500 furs at South Georgia. In 1874 Captain W. Buddington of the schooner *Franklin* of New London took 1,450 skins, and the following season five vessels secured 600; in 1876 the entire catch for four vessels was only 110. Buddington worked the island again in 1892 when he took 135 furs “none, however, coming from the old rookeries” (Buddington in Allen, 1899). George Comer visited South Georgia in 1885 and 1886, having heard reports of seals formerly taken there, but “we did not get a seal and saw only one” (Comer in Allen, 1899). Roberts (1958) gives Comer's ship as the *Express* of Stonington, though Murphy (1948) states that Comer first visited South Georgia in 1885 in the topsail schooner *Era*. It is possible that he travelled in both vessels. Comer had better luck the following season, when as mate of the *Francis Allyn* of New London (Captain Joseph J. Fuller) he secured three seals. The last of the old fur sealers to visit South Georgia was Benjamin D. Cleveland in the brig *Daisy* in 1907 (Murphy, 1948). Larsen (1920, p. 92) reported that an American schooner had taken 170 fur seals from South Georgia in 1907; presumably this refers to the *Daisy*.

The virtual extermination of the fur seals of South Georgia in the third decade of the nineteenth century, was thus followed by a partial recovery in the seventies, though these seals were speedily dispatched by the wandering sealers who by that time found it necessary to cruise over the whole southern ocean in search of cargoes. The South Shetlands also showed a brief recrudescence. In 1871–72 three schooners visited this group and obtained 8,000 furs; the following season eight vessels took 10,000. Williams (1888) summed up the situation as follows:

In 1872, fifty years after the slaughter at the South Shetland Islands, the localities before mentioned were all revisited by another generation of hunters, and in the sixteen years that had elapsed they have gleaned every beach and searched every rock known to their predecessors and found a few secluded and inhospitable places before unknown, and the result of all the toil and daring for the years scarcely amounted to 45,000 skins and not even a remnant now remains save on the rocks off the pitch of Cape Horn. . . . So in wretched and wanton destruction has gone for ever from the southern seas a race of animals useful to man and a possible industry connected with them.

A reference to seal hunters from Nova Scotia operating in the South Shetlands in recent times may have originated in pelagic sealing around the Falkland Islands. Allen (1899) recorded that the schooner *Director* of Halifax (Captain Frederick W. Gilbert) spent 36 days fishing fur seals in the waters to the south of the Falklands, and secured 620 skins in that time which were taken to Victoria. (See also Brown, 1927.)

Although records of the visits of the early sealers to South Georgia are fairly plentiful, very little is known of their activities at the island. Fur sealing, unlike elephant-oiling, left few enduring traces on the beaches. The important elephant sealing grounds of Cumberland Bay, the south-eastern tip of the island and the south coast up to King Haakon Bay, where relics of former activities in the form of try pots, casks, hoops and even boats, are still to be found, are not mentioned by the fur sealers. According to Matthews (1931), the largest fur seal rookeries in the days when the seals were still plentiful were at Antarctic Bay (known then as "Woodward's Harbour"*, after the pioneer of 1790), the Bay of Isles, north along the coast to the Willis Islands, and on the south coast eastwards to Wilson Harbour ("Flying Fish Bay"?*) and Annenkov Island.

Clark (1887) gives a fairly full account of early sealing methods. At the time that he was writing, or just before it, sailing vessels were mostly schooners, well coppered and caulked, of 60–150 tons, though previously they had been far larger and included ships of up to 300 tons. (The vessel that pioneered the sealing industry in the Falklands, the ship *States*, was of the enormous size for a sealer, then as now, of 1,000 tons.) The sealing vessels were equipped with three to five boats similar to the standard 28-ft. whale boat, but built rather stouter to endure the buffetings of coastal waters and the stresses of landing. It had formerly been the custom for large vessels to carry down boats in frame and build them on the sealing grounds. Fanning, who had the best catch in South Georgia with *Aspasia* in 1800–01, built a shallop of about 30 tons displacement and used it together with two others to visit the rookeries while *Aspasia* lay at a permanent anchorage throughout the season. Salt was brought down in bins either from the home port, or frequently from the Cape Verde Islands where the vessels often called to recruit crew. About 300 bushels of salt was reckoned sufficient for 5,000 skins.

The sealers endeavoured to reach the grounds before the main body of seals had hauled out, and parties of men would be sent ashore to erect tents or build huts where they lived throughout the season, killing the seals as they hauled out. Recent exploration of Livingston Island in the South Shetland Islands (Simpson, 1959) has revealed the remains of several sealers' huts. They were generally built against a rock outcrop and the three walls were made of boulders from the beach, roofed in with sail cloth, probably supported by an oar; occasionally the floor was covered with matting. Caves were also inhabited. The seals were stunned with an oak or hickory club about 5 ft. long, and afterwards stabbed if necessary; the larger bulls were lanced. Firearms were avoided where possible to prevent damage to the pelt, and also probably to save the expense of ammunition. The seals were flayed as soon after killing as possible; to flay fifty in a day was reckoned good work for one man. After flaying, the skins were washed in salt water and piled in a "book", one on top of the other with heavy stones on top to press out as much of the water as possible. After a day or two, depending on the climate, the skins were salted by rebuilding the book with alternate layers of salt. After the salt had penetrated thoroughly or "struck", the skins were packed away in casks or in pounds in the hold. There seems to have been no general rule as to how much blubber, if any, was left adhering to the skins. Clark states that between 1820 and 1840 the skins were flayed with a quarter of an inch of blubber, but in later years were flayed with all their blubber and afterwards beamed to remove the fat. Fanning (1924) gives the following account:

If the seals are to be skinned for the China market, the fat, and portion of the meat should be taken off with the skin, the whole then washed and spread on the rocks to drain, afterwards taken to the beamer, where the fat and blubber are cleanly beamed off, the flipper holes sewed up with twine, and the skins stretched out by means of ten wooden pins . . . on the turf to dry, and when plentifully dried are in order for that market. But for the European, London, or American markets the skin should be flinched off, taking half to one inch thickness of the fat with it, then washed perfectly clean from the blood and dirt, and while wet plentifully salted, and booked or kentched away.

According to Clark, the skins were invariably dried prior to 1815 but afterwards were always salted. The difference in treatment probably reflects the final use to which the skins were to be put. The dried skins were, as Fanning relates, destined for the China market and it has generally been held that the skins were there mostly used for leather, the fur being shaved off and thrown away. It seems likely that, in fact, the fur

* Unofficial place-names are given in inverted commas throughout this report.

would have been used in the preparation of felt (extensively used for garments in China) and that the pelt, which after no better means of preservation than drying followed by a long voyage through the tropics would hardly have been in good condition, would have been discarded. The salted skins, usually consigned to the London market, would, of course, have been entirely suitable for dressing and the preparation of the furriers' furs. However, a sad tale is told of the *Pegasus* which secured a fine cargo of 100,000 skins from the Antipodes Islands, but had insufficient salt for them; the skins heated on the homeward run and on arriving in London had to be dug out of the hold and sold as manure.

A very vivid light is thrown on the methods and attitudes of the nineteenth century sealers by a letter written by an old sealing captain, George F. Althearn, to a friend about to set off on his first sealing voyage to the "Bounty Rocks" (Bounty Islands?). The letter (which is quoted in Clark, 1887) is undated but was probably written some time in the late seventies, and seems worth reproducing here fairly fully. Althearn writes:

I will now write what I should do if I was going on a sealing voyage such as you are now about to start on. First, I should use every reasonable means of making the best of my way to the seal islands. I have always found it best to be on hand and in season, so as to have some leeway for bad weather. The great trouble in working fur seal islands and rocks is in landing the salt and provisions. There is not much trouble in taking off skins, for they can be taken off with ease when you could not land a thing.

Now I will state the habits of the fur seals of Cape Horn: About the first of November the old wigs (which are the old male seals) come on shore to form the rookeries for the pupping season which is soon to follow. When the old wigs come ashore all the clapmatches (or female seals) that reared pups in the year past are still on the rookeries with their young, which are now yearling, and prime skins. The old wigs when they arrive make it their business to drive all the yearling off the rocks, and as soon as they accomplish this the clapmatches leave and take to the water, leaving the rocks in charge of the old and young wigs.

About the 25th of November the young clapmatches of four or five years, that are to have their first pups, come on shore, and I have seen a pup as early as the 20th of November, but the main herd of old clapmatches do not begin to haul out in any great numbers before the 5th of December, and from that to the 25th of December they come in fast. I don't think it is a good plan to commence killing until they get well into pupping. Don't kill any of the old wigs until you have worked off most of the clapmatches, or near the end of the pupping season, as they hold the other seals and will not let them go off the rocks if they can prevent it. If you should want all the seals that are on the rocks to make up your cargo, you can all through the pupping season be working off the young wigs, which are always hauled in small rookeries near the pupping seal, driven there by the old wigs.

Great care should be taken, if the men are landed when the wigs begin to haul, to make as little show as possible for a few days, until they get well settled, and when the wind blows from the house direct to the rookeries to make as little smoke as possible, for the seals have a scent equal to any dog.

You will bear in mind that the full grown clapmatches or young wigs that are larger, are the most valuable. The next in value are the two and three year old seals, that haul at different times on the rocks. The yearlings that are driven off in November are prime skins, and taking into account how much less work it is to skin them, and how much less salt, and room they take, they are worth striving for. The large old wigs are of the least value, taking more work, salt and room. Still they are better than nothing. You must try to get to the island in time to get all of last year's pups with the clapmatches. If you can get there thus early it will give you a great start and make everything smooth for you; but if you cannot get there in time to take the young seal season, get there as soon as possible, and be sure that you examine the islands and rocks thoroughly.

What I have written about the habits of the fur seal applies to the region of Cape Horn. It may be possible that where you are going their habits may be different, for at the South Shetlands there are no seal ashore from March to the middle of November. Also at South Georgia, with a lower latitude than Cape Horn the seal after shedding the last of February, take to the water and do not return till the following November. If they should work the same where you are going you see that if you arrive there in September, or up to the middle of October, there may be very few if any seal hauled, so of course you will have to land and examine the rocks, and it will be easy for you to tell if there has been any number of seal in the habit of hauling there, although the frequent rains of that latitude will wash away much of the evidence of the past season, so you will have to use your own judgement. Don't condemn in haste. Make sure you are right.

There follows an account of how Warren should manage his business, if he had the good fortune to discover an undisturbed colony of seals in the Bounties:

If you got out there early and saw a great show of seals, I should get as many on board as I could without running any risk of not getting back in time. I would leave on the rocks all the men that I thought would blab; go to the most convenient port, ship my skins, get what I needed [more salt] and go back to the rocks, and finish up the season and go to Valparaiso without touching at New Zealand, and I should expect to have another season without company. . . . You will remember that you cannot get all the seal from a rookery in one season. If you get 3000 the first season you may expect to get 1000 or more the next, and in the same proportion for a larger or smaller number.

Althearn went on to recommend various stores and gear. The men were to be warned to pitch their tents and store their salt and provisions in as high and sheltered a place as possible. He advised Warren to have his crew eat plenty of seal meat to keep the scurvy at bay and cited an instance of his successful use of this specific. (No doubt it also helped out the ship's stores.) He continues:

The way to skin a seal is to cut around the flippers; then rip the belly open from tail to throat; then cut around the head forward of the ears, leaving the ears on the skin. Be sure and soak the blood well out, for on this depends in great measure the curing of the skin. After being well soaked pile them in small heaps to drain. Then flinch them by cutting the blubber smoothly off, leaving from one eighth to one fourth of blubber on the skin, be sure to caution the men to hold their knives flat in flinching if they will [not] cut down to and into the skin in steps the whole length. A skin so flinched, although there may be no holes clean through it, will go "damaged in dressing", and of course they will make a damaged skin of it. Every defect will be seen in London.

A flinching board should be about 6 feet long and $1\frac{1}{2}$ to 2 feet wide, with legs long enough for a man to work without bending too much. The legs can be made to unship so as to save room. Brace up the board the right slant, take the skin by the neck, swing it over the board with the flipper holes on the board, draw the knife across the blubber where it hangs straight on the board, and cut it off smoothly to the tail, leaving the tail on the skin. Then turn the skin around and flinch the neck. In salting care should be taken to rub the salt well into the edges and the neck of the skin, for in kenching or booking them up the edges are very apt to roll up and if not well rubbed with salt will get pink and damaged.

I think the best way to salt skins on the rocks is to build up a place with rocks high enough to let the rain water run under them. Take the largest skins and form a circle with the tails in the center, each skin laid down blubber side up. After rubbing well with salt and leaving enough on to cure it, which will depend, of course, on the size and thickness of the skin, take and fold in the sides far enough to take in the flipper holes. Then fold over the neck far enough so that it will not turn back. By so doing the outer edge of the circle will be kept the highest and will keep in all the pickle. If the edges get too high the small skins can be salted spread out flat in the center.

When taken on board the vessel the skins should be examined, and if there are any places that are clear of salt and feel soft and look pinky, and a little thicker than the rest of the skin, care should be taken to rub salt well into those parts. On board the vessel they can be salted anywhere there is room for a kench clear of water underneath, or they can be booked up and stowed away.

To book a skin, fold the sides just as in kenching, then fold the neck and tail in until they meet equal then fold again. A large skin would have to be folded more times than a small one.

There are a few things that are handy for the men to have on the rocks, such as a small hook like a cotton hook, for each man; also a hook or two for each rock, like a chain hook, only shorter, shanked with an eye large enough to bend a rope in. These are always useful to haul seals out of caves, gulches and cracks in rocks. Almost always in killing a large number of seals at one time a good many will tumble down in gulches in heaps. These should be hauled out as soon as possible and laid separate on the rocks so as not to heat. If there are a great many and the day is warm it would be well to rip them open to let the heat out.

In resalting skins for shipment I just cover the lower head of the cask with salt, book up the skins, stow in a course as tight as possible, stamp them down, sprinkle salt on them, and so on with successive layers until the cask is full.

D. STATUS OF THE SPECIES IN THE PRESENT CENTURY

In the twentieth century, the establishment of the steam whaling industry in South Georgia and the resumption of commercial elephant sealing by the *Compañía Argentina de Pesca* in 1910 resulted in a fairly thorough and continuous inspection of the accessible coasts of the island. It is fairly certain that the lingering remnant of fur seals that had survived the depredations of the previous century and the haul of 1907 remained at the north-western extremity of South Georgia, on the off-lying islands of Bird and the Willis group (Fig. 10). In 1909, a party of men left ashore at Bird Island from 24 to 27 December (probably to collect the eggs of the wandering albatross), reported that they saw no fur seals. At the same time, Wilson Harbour, Schlieper Bay and Right Whale Bay were also searched with a negative result. The first definite record of a fur seal in South Georgia in the present century was in 1915, when a juvenile male was taken (allegedly by mistake) by the elephant sealers at "Green Harbour". There is no harbour at present known by this name in South Georgia. A small cove on the mainland near Green Island is generally known as "Green Bay", and other bays of the same name exist in Cumberland West Bay and to the east of the Lucas Glacier in the Bay of Isles. There is an oral tradition in South Georgia that the seal was taken at Smaaland Cove, at the south-eastern end of South Georgia, but as the animal was a juvenile male, the class most given to wandering, the precise location is not of great importance. The skin, but not the skull, of this specimen was preserved and deposited in the British Museum. Four years later, on the 5 or 6 October 1919, the master of one of the local whale catchers had occasion to go ashore at a small harbour on the south-east side of Bird Island (this can only be Jordan Cove) and there saw five fur seals. About three weeks earlier he had seen one at the Bay of Isles. The following year it was reported to the Magistrate that several fur seals had been seen on a number of occasions on a few small islands, "where landing is almost impossible", at the entrance to King Haakon Bay. These are either the Samuel Islands, or more probably Anvil Stacks, though the latter are a good way from the entrance of King Haakon Bay. In the winter of 1921 a search for fur seals was made at the Bay of Isles, Undine Harbour, King Haakon Bay, Holmestrand, Drygalski Fjord, Larsen Harbour and Gold Harbour. No seals were seen, though this is not surprising at that season. There were occasional reports of fur seals being seen at sea at about that time.

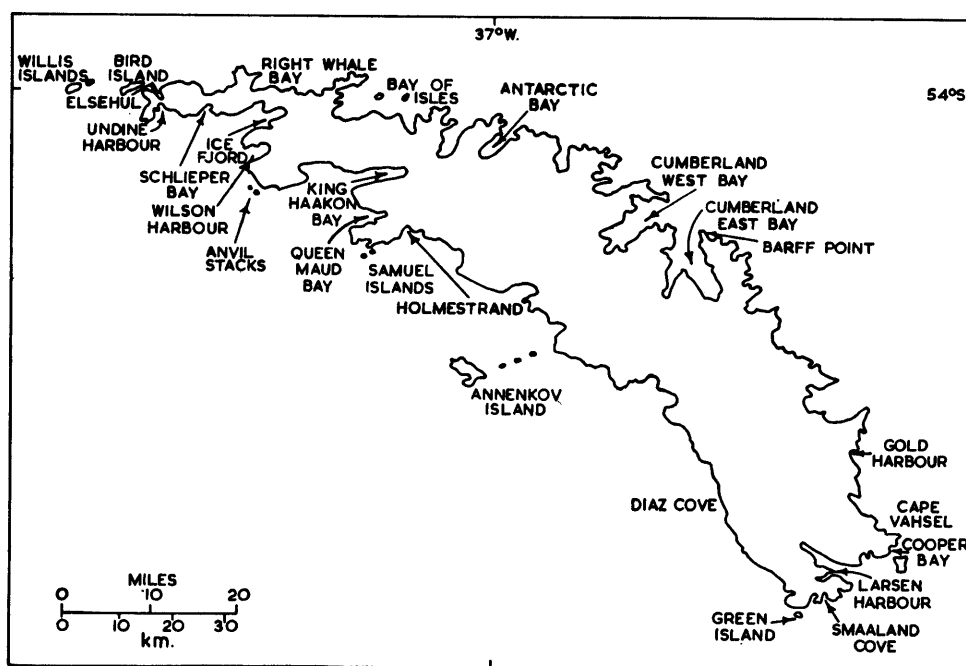


FIGURE 10
South Georgia.

In May 1921, one of the whalers reported seeing a fur seal 25 miles out to sea north-east from Cape Saunders. The Magistrate thought that little reliance could be placed on this report, but it is hard to see why as fur seals at sea are easily recognizable from their characteristic way of swimming and surfacing. On 7 December 1922 the whale catcher *Don Ernesto* was hunting a whale near to the shore of "Braff Point" (almost certainly Barff Point) "and while the catcher had stopped the engines awaiting the whale to blow, a Fur Seal was seen to come up close to the catcher. It stayed on the surface observing the boat for a fraction of a minute and then swam off". Four months later, on 10 April 1923, a shoal of fur seals, estimated to number between 15 and 20 animals, was seen near to Antarctic Bay close in to the shore. The Magistrate considered that it was hardly likely that the seals could be indigenous to South Georgia, in view of the searches that had been made of the coastline, and suggested that it was not impossible that they had migrated from the Falkland Islands or South America.

Between 1933 and 1936 three visits were made to the north-western extremity of South Georgia by members of the "Discovery Investigations" team. The unpublished reports of these visits (and other sightings of seals) are summarized in a paper by Mackintosh (1967). In February 1933 Rayner and Etheridge, the Assistant Customs Officer who had previously been a Guardian of Fur Seals at the Falkland Islands, set off on one of the sealing boats, *Lille Carl*, to search the north-western end of the island for fur seals. On the 15th of the month they steamed round the Willis Islands, searching the shores thoroughly from the ship, with the exception of parts of the south and west shore of Main Island, without seeing any fur seals. From a consideration of the courses on which it is possible to sail round Main Island, it is unlikely that Rayner would have inspected the small peninsula on which fur seals breed today. The following day they entered a small bay north of Pearson Point on Bird Island (this is Johnson Cove). Here otariids were seen playing in the water and on the outlying rocks.

... about 20 in all were present in the cove. They were to be found not only on the rocks and the beach, but in the tussock and as far as 70 to 80 yards from the water's edge. They were very tame, showing no alarm at the closest approach, whilst some evinced great curiosity, coming to within two or three feet of the intruder and giving no sign of fear. They varied in size from a large old bull to small immature individuals, probably in their second year. (Rayner 1933.)

Rayner and Etheridge searched the shores to the north and east of their landing and found a total of 38 fur seals, but no rookery was seen and the only indication of breeding was a "family group" consisting of a bull and a cow and what Rayner took to be a yearling pup. It seems likely, however, that the majority

of seals regarded by Rayner as probably in their second year were, in fact, moulted pups of the same season. The chief engineer of the vessel later told Rayner that he had seen a very small pup about 2 ft. long and without teeth which was presumed to be a few months old, but he could not have examined his seal very closely to suppose it to be without teeth. There is no doubt from Rayner's report that no black pups were seen.

Rayner assumed that there were at least 60 individuals in the colony. Etheridge was able to say that in appearance the seals differed in no respect from those at the Falkland Islands (*Arctocephalus australis*) but "their utter fearlessness together with their marked preference for shingle beaches and a liking for lying in the tussock being in great contrast to the shy, petrophilous nature of the Falkland Island Fur Seals, but this may only be indicative of an unmolested existence for very many years." Rayner was, however, prudent enough to refer the seals of Bird Island to *Arctocephalus sp.* rather than to *A. australis*, as had been done by all previous, and many subsequent, authors of this century.

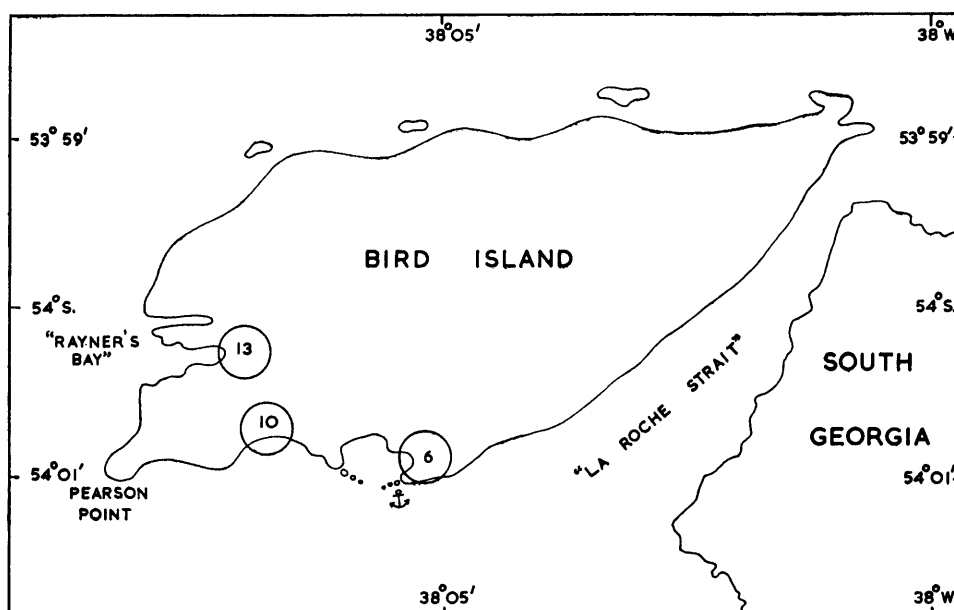


FIGURE 11

Marr's map of Bird Island, showing the numbers of fur seals found (Marr, 1936). Superseded place-names are given in inverted commas. "La Roche Strait" is now known as Bird Sound, and "Rayner's Bay" as Johnson Cove. Other features and place-names are shown on Figs. 13 and 14.

Two and a half years later, on 23 October 1936, Marr, also of "Discovery" Investigations, made a landing on Bird Island from R.R.S. *Discovery II* (Marr, 1936a). The main party went ashore at Freshwater Inlet in Jordan Cove. This is explicit from the map (Fig. 11), though the description of a "shingle and sandy beach several hundred yards in length with gently inclined tussock slopes behind" does not fit particularly well, there being no beaches of anything like that length on Bird Island. Six fur seals were found in Jordan Cove and another ten either in Evermann Cove or on the coast between Evermann Cove and Pearson Point. At "Rayner's Bay" (Johnson Cove) another thirteen fur seals were found.

Marr was unable to determine the sex of the seals he found, but he correctly argues that the majority were probably males. Those found in the tussock were exceedingly hostile and aggressive but those on the beach were more timid. Evidently the harem bulls had not yet taken up their territories on the beach.

Another visit by R.R.S. *Discovery II* was made on 19 December of the same year. Marr (1936b) again reported on the seals ashore. Johnson, Jordan and Evermann Coves were investigated and a total of 59 fur seals was sighted; 12 were pups. Marr commented that the seals seemed less hostile than they were in October.

In the post-war years Rankin (1951) reported seeing about 20 fur seals ashore in the summer of 1946-47, though he gives neither the place nor the month. From photographs published by him there is reason to

believe that the locality was Cooper Bay, at the south-eastern end of South Georgia. A member of the South Georgia Expedition reported fur seals ashore in this bay in 1954 (personal communication and Sutton, 1957).

In December 1956, by the courtesy of K. S. Pierce Butler, manager of the whaling station at Grytviken, the author was lent a seal-catcher in which to search for fur seals. Flourishing colonies were found at two localities on Bird Island and on the most easterly point of Main Island in the Willis group (Bonner, 1958). The total population at that time was estimated to be 8,000–12,000 animals, excluding pups.

IV. THE FUR SEAL IN RELATION TO ITS ENVIRONMENT

A. THE HABITAT

The north-western tip of South Georgia, where the main stock of fur seals is at present to be found, lies in lat. 54°S., long. 38°W. The only weather recording station on South Georgia is at Grytviken, some 100 km. to the south-east. The climatic data collected at Grytviken are not very characteristic of the island as a whole, the recording station generally enjoying warmer and clearer weather than the rest of the island. A summary of the data is given in Table IV. Limited observations made during the summer of 1958–59 by Tickell and Cordall (1959) show the main points of difference between the climate of Bird Island and that of Grytviken; these and further observations are summarized by Richards and Tickell (1968). Precipitation is higher at Bird Island than at Grytviken, but there is far less snow cover in winter and probably the winter temperatures are higher. Prevailing cloudy conditions, due to the passage of moisture-laden westerly winds, restrict sunshine, so that a clear day at Bird Island is a rare event. The absence of a high inland massif prevents the formation of the föhn conditions that account for most of the higher maxima during the summer months at Grytviken.

Of the other islands of the Scotia Ridge (Fig. 9) inhabited by fur seals, climatic data are available from the South Shetland Islands and the South Orkney Islands (though not from actual fur seal breeding stations). These indicate a climatic pattern similar to that of Bird Island, at least in the summer months when the fur seals are present on the beaches. The summers are cool without extremes of temperature; the sky is generally overcast, it is moderately windy and the relative humidity is high. The equinoctial seasons produce no sudden changes of temperature and though the winter minima vary considerably the fur seals are absent at this season. An attempt has been made in Table V and Fig. 12 to indicate surface-water temperatures at some of the breeding stations shown in Fig. 7. Although not shown in the original data (taken from Mackintosh, 1946) pack ice is not infrequently encountered off the southern coast of South Georgia. It has encircled Bird Island on at least one occasion in the last five years, though by mid-October, at the latest, it has retreated to at least 50 miles off the coast.

Discussing the effect of sea ice on the distribution of fur seals in the South Orkneys, Marr (1935, p. 373) pointed out that this group was generally subject to very heavy pack from June to December and wrote:

Had they [the fur seals] tried, then, to reach the South Orkneys in November and December, it is clear that unless they were capable of travelling long distances over sea-ice the seal must generally have been seriously handicapped or held up altogether by the pack which blocked the coasts. This would appear to be the only possible explanation of the scarcity of the species on these islands. It is interesting to note in this connection that even at the height of the slaughter at the South Shetlands, the southern side of the Bransfield Strait, which like the South Orkneys is usually blocked by ice in November and December, appears to have been equally unproductive of fur seal. Indeed, as far as I am aware, there is no record that any were ever captured there.

It is, of course, quite possible that fur seals are capable of travelling long distances over sea ice (which would probably offer no greater locomotory resistance than a land surface), but their absence from regions further south, as well as their distribution in the South Orkneys and the South Shetlands as pointed out by Marr, indicate that as a species they have failed to adapt themselves to sea ice. Fur seal pups are fed by their mothers for about five months and this would preclude breeding on sea ice, since its break-up in the summer months would lead to the death of the pups; moreover, travelling over fast ice to reach the land would burden the cows with very long journeys to and from the feeding grounds during the lactation period.

On one occasion, in early September 1960, when Bird Island was visited during moderately heavy pack ice conditions, bulls of breeding age, two-year-olds and yearling males were present on the shore and,

TABLE IV
CLIMATIC DATA FROM VARIOUS LOCALITIES ON THE SCOTIA RIDGE

| Locality | | Temperature (°C) | | | | | Relative humidity (per cent) | Mean wind speed (kt.) | Mean cloud amount (oktas) |
|------------------------|--|---|--|---|--|---|--|--|--|
| | | Mean daily | Mean maximum | Mean minimum | Extreme maximum | Extreme minimum | | | |
| SOUTH GEORGIA | † Elsehul (54°01'S., 37°59'W.) 20–31 October 1–16 November | +0.5 +1.5 | +2.1 +3.3 | −0.6 +0.3 | +5.0 +7.2 | −5.0 −2.8 | 89 89 | 14.7 9.3 | 7.9 7.0 |
| | † Bird Island (54°00'S., 38°05'W.) 26–30 November 1–31 December *1–31 January *1–28 February *1–4 March | +2.9 +1.8 +2.9 +2.5 +4.4 | +4.0 +3.0 +4.2 +5.6 +5.4 | +1.6 +0.9 +1.9 +1.4 +3.1 | +5.0 +5.0 +8.9 +7.2 +6.1 | +0.6 −1.7 −1.7 −1.7 +2.2 | 94 89 91 88 93 | 8.6 8.0 9.6 6.7 10.1 | 8.0 7.4 7.5 7.3 7.4 |
| | AVERAGE | +2.2 | +4.4 | +1.1 | — | — | 90 | 9.0 | 7.4 |
| | ‡ Grytviken (54°17'S., 36°31'W.) January February March April May June July August September October November December | +5.4 +3.2 +3.6 +2.7 −0.8 −1.2 −2.4 +0.5 +1.6 +2.4 +4.2 +3.4 | +9.7 +6.4 +7.4 +6.2 +2.9 +1.8 +1.4 +4.2 +5.4 +5.7 +7.8 +7.2 | +1.7 +0.5 +0.6 −0.3 −3.8 −4.0 −5.2 −3.0 −1.9 −1.1 +0.8 +0.7 | +19.5 +10.6 +16.1 +15.6 +10.0 +10.0 +12.2 +10.0 +12.2 +12.8 +18.8 +15.0 | −1.7 −1.7 −2.8 −3.3 −9.4 −10.6 −10.0 −8.3 −6.7 −5.6 −2.2 −1.7 | 74 84 72 79 78 82 79 73 69 74 76 71 | 10.3 7.1 9.1 8.3 10.1 7.5 8.6 11.0 11.4 10.8 8.6 9.5 | 6.7 6.6 5.7 6.0 5.9 5.5 5.6 5.5 4.8 6.1 6.4 6.6 |
| | AVERAGE | +1.9 | +5.5 | −1.2 | — | — | 76 | 9.4 | 5.9 |
| SOUTH ORKNEY ISLANDS | ‡ Signy Island (60°43'S., 45°38'W.) January February March April May June July August September October November December | +0.3 −0.9 −1.4 −2.2 −13.3 −11.0 −13.3 −8.8 −4.1 −0.9 −0.2 −0.6 | +2.4 +1.3 +0.7 +0.4 −7.8 −5.7 −9.4 −4.3 −0.6 +1.3 +2.0 +0.9 | −1.1 −2.6 −3.9 −5.6 −20.5 −16.1 −18.7 −14.7 −7.4 −2.4 −1.7 −1.7 | +6.7 +6.1 +5.6 +7.2 +4.4 +3.3 +1.7 +5.0 +6.1 +8.3 +8.9 +5.6 | −3.3 −7.8 −8.3 −12.8 −28.9 −27.8 −32.8 −27.2 −18.9 −9.4 −4.4 −3.9 | 87 86 85 86 82 84 81 84 86 87 90 84 | 11.2 10.7 13.6 14.6 10.6 16.1 14.6 19.7 24.8 18.3 15.7 15.2 | 7.5 7.2 7.5 6.9 5.9 6.4 5.0 6.1 7.3 7.4 7.7 7.6 |
| | AVERAGE | −4.8 | −1.0 | −8.0 | — | — | 85 | 15.2 | 7.6 |
| SOUTH SHETLAND ISLANDS | ‡ Deception Island (62°57'S., 60°38'W.) January February March April May June July August September October November December | +1.8 +0.4 −0.1 −2.0 −7.2 −12.8 −13.1 −11.1 −8.7 −2.6 −0.1 −0.4 | +4.4 +2.1 +2.0 +0.1 −4.3 −8.5 −8.8 −5.8 −4.1 −0.3 +2.2 +2.1 | −0.1 −1.3 −2.2 −3.7 −10.5 −15.9 −17.7 −14.6 −13.8 −4.9 −1.6 −1.9 | +8.9 +6.1 +5.6 +5.0 +2.2 +3.3 +1.1 +1.1 +1.7 +2.8 +5.0 +5.0 | −1.7 −7.8 −8.3 −12.8 −17.2 −25.0 −27.8 −27.8 −25.6 −12.8 −5.0 −5.0 | 85 86 90 90 87 89 87 89 90 92 91 84 | 9.1 9.5 13.5 15.1 17.2 14.7 14.3 16.6 16.0 14.0 12.8 12.6 | 7.1 7.1 7.0 6.9 6.5 5.8 4.5 6.1 5.8 6.8 7.1 6.8 |
| | AVERAGE | −5.6 | −1.6 | −7.3 | — | — | 88 | 13.8 | 6.5 |

* 1959 data. All other data in table is for 1958.

† Data from Tickell and Cordall (1959).

‡ Data from *Falkland Islands and Dependencies Meteorological Service, Annual Meteorological Tables* (1958).

TABLE V
APPROXIMATE TEMPERATURES (°C) OF SURFACE-WATER AT
VARIOUS FUR SEAL BREEDING STATIONS

| Month | South Shetland Islands | South Orkney Islands | South Georgia | South Sandwich Islands | Iles de Kerguelen |
|-----------|------------------------|----------------------|---------------|------------------------|-------------------|
| September | pack ice | pack ice | −1 to 0 | pack ice | 2 |
| October | pack ice | pack ice | −1 to 0 | pack ice | 2 |
| November | pack ice | pack ice | 0 to 1 | pack ice | 3 |
| December | −1 | pack ice | 1 | pack, −1 | 4 |
| January | 1 | 0 to 1 | 1 to 2 | 0 | 6 |
| February | 1 to 2 | 0 to 1 | 2 to 3 | 1 | 5 |
| March | 1 | 0 to 1 | 2 to 3 | 0 to 1 | 5 |
| April | 0 | −1 to 0 | 1 to 2 | 0 | 4 |
| May | pack ice | pack, −1 | 1 | −1 | 4 |
| June | pack ice | pack ice | 0 to 1 | −1 | 4 |
| July | pack ice | pack ice | 0 | pack ice | 3 |
| August | pack ice | pack ice | −1 to 0 | pack ice | 3 |

Data from Mackintosh (1946).

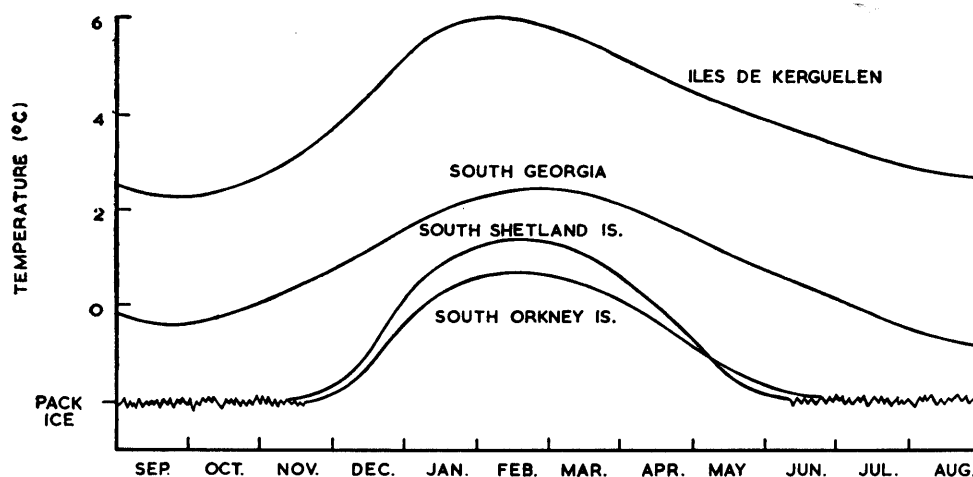


FIGURE 12

Sea-water temperatures at the Iles de Kerguelen, South Georgia, the South Shetland Islands, and South Orkney Islands. (Data from Mackintosh, 1946.)

judging from faecal remains, had evidently been in the water recently. The total number ashore was very small, probably less than 40 for the entire rookery area (ice conditions, however, prevented investigation of the heads of the coves), and these were quite probably aberrant individuals analogous to the occasional elephant seals seen ashore during the winter months.

The southern fur seals as a group show a marked preference for rocky habitats, in contrast to the other gregarious pinnipeds with which they occur sympatrically. Thus, in the Falkland Islands the southern sea

lion, *Otaria byronia*, is found breeding on the open beaches around the coasts while the fur seals, *Arctocephalus australis*, are confined to rocky islets; in Australia the hair seal, *Neophoca cinerea*, is found on sandy coasts while the fur seals, *A. doriferus* and *A. tasmanicus*, are again to be found on the rocks. This division is not, of course, absolute; elephant seals (the only social pinnipeds occurring in the range of *A. tropicalis*), though predominantly seals of broad open beaches, are not infrequently found in rocky coves. If fur seals were as common as elephant seals, it is probable that their habitat would show similar latitude.

Paulian (1964) has commented on the preference shown by *A. tropicalis tropicalis* on Ile Amsterdam for rocky shores exposed to the full force of the prevailing west and north-west winds. He sees this as a general tendency in the genus, quoting the distribution of fur seals on Gough Island, Inaccessible Island, Marion Island, Bouvetøya and the Auckland Islands, though he acknowledges that the situation is different at Bird Island. He has put forward two hypotheses to account for this distribution: the first is that it might be due to the need for the seals to regulate their body temperature, though, as he points out, this could hardly be the case in the colder localities such as Bouvetøya; and the second is that it might be the result of "un réflexe de défense contre les chasseurs", though the present distribution on Ile Amsterdam (where one of the three rookeries is easily accessible from the land) does not entirely bear this out. Neither of these hypotheses seems satisfactory; the present distribution of fur seals (which is rather imperfectly known) represents only a fraction of the territory occupied before the onset of human exploitation, and the total potential distribution of the genus may not conform so closely to the pattern quoted by Paulian.

The common features shared by most of the fur seal breeding beaches in South Georgia are:

- i. The presence of some feature, such as the lie of the coast, off-lying rocks or kelp beds, which provides sufficient shelter to protect the beach from all but the most severe storms.
- ii. A rock platform continuous with the beach and projecting out into deeper water, or a seaward fringe of rocks.
- iii. The presence on the beach of boulders or other irregularities of contour to break up its general surface.
- iv. Access from the beach, or some place near it, to the interior.

How much these features indicate a habitat preference on the part of the seals, and how much they are dictated by the general topography of the region, is not easily decided. Currently all the beaches on Bird Island and Willis Island support some breeding seals, and the small colonies that exist on the mainland are insufficiently established to be taken into consideration. As shown later (p. 53–54), however, there is some evidence that seals within the breeding colonies show a preference for the rockier stretches of beach. The relatively level expanses of rock platform, which jut out from the cliffs a few feet above sea-level and are deeply fissured and often strewn with boulders, are a typical feature of these beaches. On their landward side they frequently collect small shingle patches which merge into the talus of the cliffs, and on their seaward side occasionally terminate in a barrier of rock, as much as 7–10 m. high, which acts as a breakwater. Rock platforms are absent from the heads of coves, and are found most frequently where there are cliffs or headlands (Plate IIa).

In the coves the shore presents a very different appearance. The beach slopes fairly steeply between tide marks and then more gently to the storm mark, which is generally the seaward limit of the tussock grass. It then flattens off to form a level plain which is covered with lush vegetation, except where it has been worn bare by the comings and goings of the seals. These beaches are narrower than those of the rocky shores, as the storm beach of the sheltered coves is rarely more than 7–10 m. wide (measured down the slope). The beach itself is also generally more open and less broken up, though washed-up driftwood or whale bones may help to break the surface. The open beaches and rocky beaches are, of course, connected by intermediate types (Plates IIb and IIIa).

In South Georgia, though not elsewhere in the range of the species, a lush terrestrial vegetation is developed (Greene, 1964). The dominant plant of the coastal region is the tussock grass, *Poa flabellata*, which is a coarse grass growing, as its name suggests, in clumps or tufts. In the areas immediately behind the beaches the tussocks are generally 50–60 cm. in diameter and about 40 cm. high, but may exceed one metre in both diameter and height. The leaves, when undisturbed, grow out from the centre and overhang the edges of the peaty stool or pedestal formed by the dead bases of the previous year's growth, leaving deep gutters between neighbouring plants. The presence of numerous fur seals, which show a marked

predilection for lying on the tops of the tussocks, results in the blades being worn away in the centre leaving a rosette of downwardly directed leaves surrounding the pedestal. Ultimately, the process of erosion leads to the total destruction of the grass so that only the pedestal remains standing.

Besides the tussock growth, considerable areas near the beaches are covered with a mat of the smaller grass *Deschampsia antarctica*. This, too, is subject to erosion by the puddling action of the seals' flippers and, with the large increase in fur seal numbers at Bird Island in recent years, extensive areas once green and lush with a carpet of *Deschampsia* are now reduced to bare expanses of muddy peat. There are several other plants of small size, but these do not appear to be of great importance to the seals nor are they much affected by them.

B. THE SOUTH GEORGIA ROOKERIES

1. Bird Island

a. *The main rookeries.* The coast line in the neighbourhood of Jordan Cove and Evermann Cove has been divided into a series of areas, identified originally in field notes by the use of arbitrary local names and referred to here by numbers. Figs. 13 and 14 show the limits of the various areas.

Area 1. This is a fairly extensive beach about 200 m. long which forms the eastern extremity of the main rookery at Jordan Cove. The beach is of the rock platform type backed by cliffs but the platform is, at least in the southern half, very irregular and dissected. Four shingle beaches formed at the foot of cliffs have been used in the past as census units but, with the exception of the third from the southern limit, their boundaries are not well defined. The cliffs are steep but well invested with tussock, and it is possible for both men and seals to scale them.

Area 2. This important beach is immediately to the north of the preceding one and commences at the point where the cliffs turn sharply inland. It is approximately 70 m. broad and is bordered on the seaward side by a lower extension of the rock platform system of Area 1, most of which lies below high-water mark. At the northern corner of the beach a channel cuts through the platform and gives access to the shingle storm beach. The latter contains one of the largest continuous aggregations of breeding seals in the whole rookery complex. It is divided by a corridor free from breeding seals where a small trickle, in line with the channel, keeps the shingle permanently wet. Behind the storm beach there is a small level plain with some rather sparse tussock, flanked by low tussock-covered hills rising to the main valley system of Bird Island. Small water courses open into this plain and are used as routes inland by the seals.

Area 3. This is a rocky stretch of coast about 60 m. long which divides Area 2 from Freshwater Inlet. It is not of great importance as a breeding beach owing to the rather small area available to the seals, but it is regularly resorted to by moulting elephant seals. A ridge extending inland from Area 3, separates Areas 2 and 4.

Freshwater Inlet. This beach, into which discharges the only considerable stream of this part of the coast (hence the name), has been divided for census purposes into two parts, Areas 4 and 5. *Area 4* in the south-eastern part of the inlet contains by far the greater number of the breeding seals. Where it adjoins Area 3 there is a very small shingle beach, but for the rest of its southern half the beach is very narrow and the territories form a single rank along it. At the head of the inlet, the beach broadens to a clear expanse of shingle backed by a plain covered with tussock and *Deschampsia*. This plain is intersected by small streams which are fed from the valley system that opens into Area 2 and discharge through a common mouth. The tussock on the southern side of the plain was used as a breeding territory even as early as the 1957–58 season; since then, the extent of the area occupied by "tussock harems" has greatly increased, and territories with mature bulls are now to be found as much as 100 m. from the sea. The area around the mouth of the stream is unoccupied, and the only sizable aggregation of breeding seals in *Area 5* is at its northern end where a small beach of roughly broken rock and boulders from a gully in the cliff behind provides territories for about 10 bulls. On 10 December 1961, the entire inlet had 62 harem bulls holding territories with cows; of these 42 were in Area 4. The floor of Freshwater Inlet slopes very gradually so that there is an expanse of shallow water little disturbed by even the severest storms. Here, dozens of juvenile seals are to be seen at play the whole season through. The shingle spit by the river is occasionally used by leopard seals as a hauling-out ground. In the years 1958–60 a male leopard seal, recognizable by its scarring, regularly hauled out here, but it has not been seen since and is believed to have been shot by a visiting expedition.

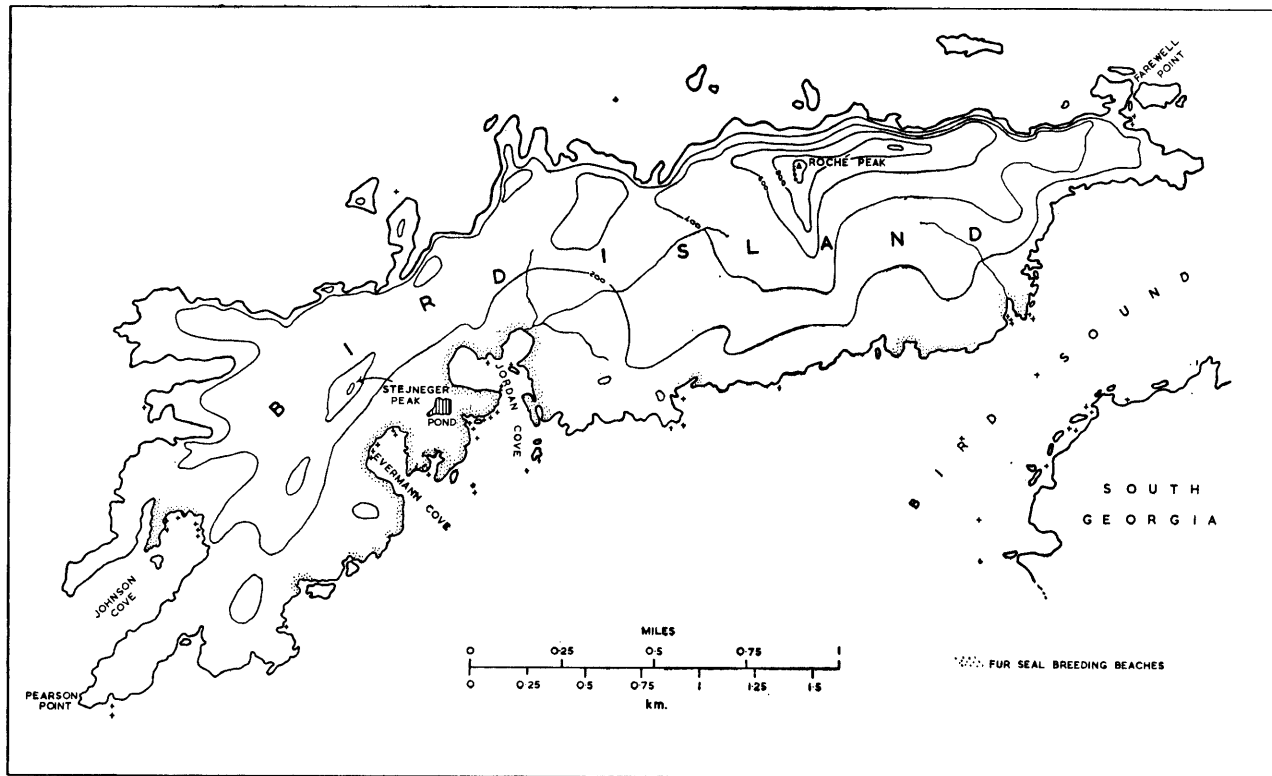


FIGURE 13
The fur seal breeding beaches, Bird Island.

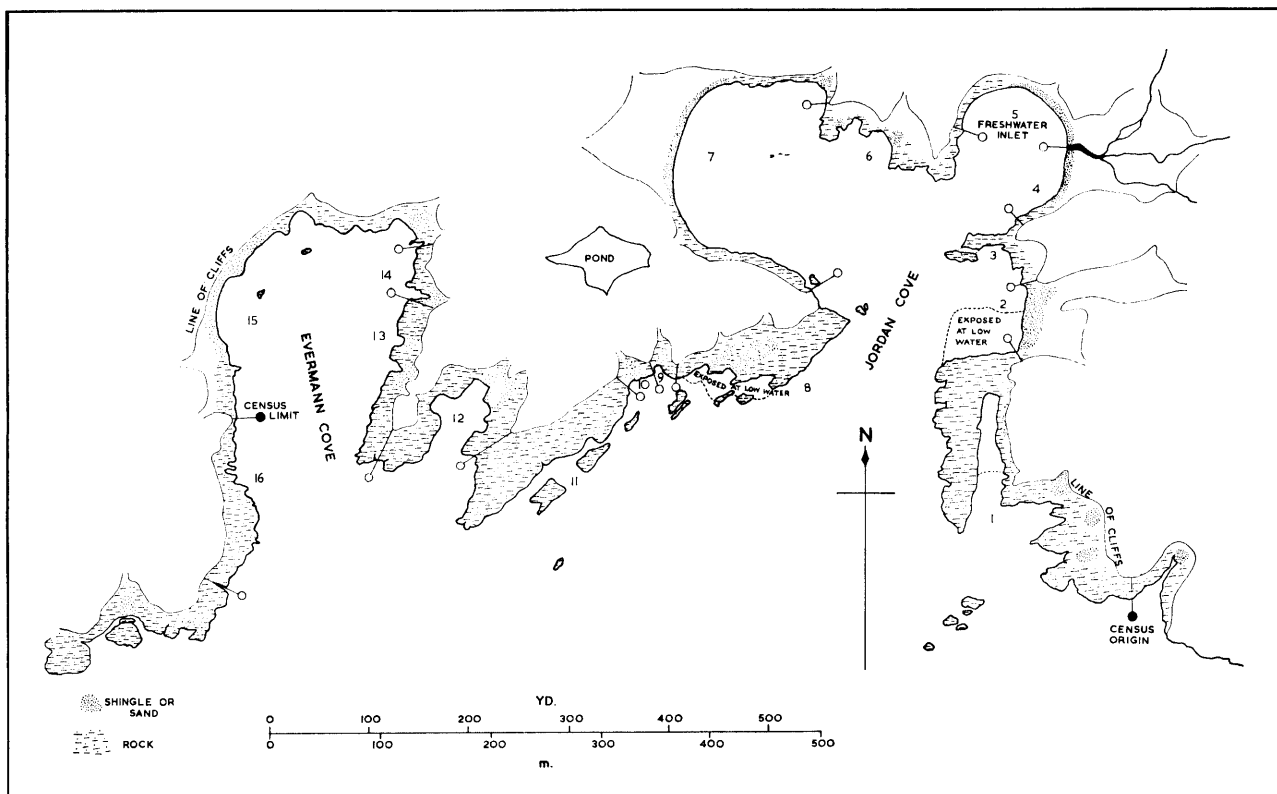


FIGURE 14
The main fur seal breeding beaches, Bird Island.

Area 6. This very irregular run of coast, about 130 m. long, separates Freshwater Inlet from Area 7, the western division of Jordan Cove. Area 6 is much divided by rocky reefs and has three main breeding aggregations, though the seals can move freely overland between them. Behind the beaches there are two tussock-covered terraces, the higher being some 10 m. (33 ft.) above sea-level, and then the land rises sharply to about 50 m. (160 ft.). Area 6 forms a useful unit for census purposes, as a low rock wall clearly marks its boundary with Area 7, and it is also reasonably distinct from Freshwater Inlet.

Area 7. This area is one of the most extensive in the complex; its features resemble those of Freshwater Inlet but it is on a larger scale. There are promontories where territories are established several ranks deep in the tussock above the storm line, as well as on the beach itself, and two small coves backed by tussock-covered cliffs where the territories form a single rank along the water's edge. The plain at the head of Area 7 does not open into a valley system and is restricted by low hills and cliffs. It supports only about 40 territories out of a total of about 130 in this area.

Area 8. The peninsula between Jordan Cove and Evermann Cove to the west shows the rocky beach and associated platforms at their best. The first sector, Area 8, extends from the mouth of Jordan Cove to the first small cove to the west. The eastern half of this section is a rock platform, dry at all but the highest tides and protected by the trend of the coast and outlying reefs from all but the most severe storms. There are numerous intersecting gutters in the rock and a raised seaward reef. About midway along this stretch of coast is a fairly extensive shingle beach which is much cluttered with boulders and effectively divided up. Area 8 supports about 60 harem bulls of which fewer than half are on the shingle beach and its immediate environs. The cliffs behind are low and easily scaled, and at the back of the shingle beach there is a gully giving easy access to the interior. A gentoo penguin rookery situated on the point between Jordan Cove and Area 8 has been occupied every season since observations started in 1956.

Area 9. This is a very small cove, or recess in the cliffs, between Areas 8 and 10. It is similar to the latter except for its smaller size. In 1961 it supported 11 harem bulls.

Area 10. This beach is formed by a small embayment in the cliffs where a watercourse, now dry, once reached the sea. There is a small triangular shingle beach, flanked on the east by a low rock cliff and on the west by low outcrops of rock. At the back of the beach are a few boulders and some scattered tussocks, and then the gully and cliffs densely covered by tussock. Seaward, the rock platform skirting the peninsula has been broken into isolated reefs in front of Areas 9 and 10. Both these beaches are liable to flooding in times of storm but receive a limited amount of protection from the rocks and kelp beds. Area 10 forms a useful unit for census purposes, being separated from Area 9 by a sharp rock wall and from the next main breeding site, Area 12, by a virtually uninhabited rock platform.

Area 11. This consists of a relatively smooth table of rock, scattered with boulders and talus where it backs on to a near-vertical cliff. Its surface is 1–1.5 m. above high-water mark, and on the seaward side it drops vertically to the water. It is very exposed and the sea frequently breaks over the platform, which doubtless accounts for the small numbers of seals to be found there. Only six harem bulls were present in 1961.

Area 12. This is an important breeding beach of typical rocky facies, around a roughly cruciform cove at the south-western angle of the peninsula. Although its approach channel lies wide open to south-western seas it affords good protection from most storms, though wreckage piled at the head of the cove shows that this is not always so. It is densely populated (it supported about 50 territories in 1961) and, being well isolated, is potentially useful for census purposes, but unfortunately there is no vantage point which affords an unobstructed view of the entire area. Several massive angular rocky outcrops (paralleled on the beaches some 200 m. away on the other side of Evermann Cove) divide the beach into long strips. At the head of the beach the cliffs dip sharply to give easy access to the interior.

Area 13. The remaining beaches of the census area form the shores of Evermann Cove. The first of these, Area 13, runs from the western limit of Area 12 to a steep rock wall by a watercourse which drains the pond in the centre of the peninsula between Evermann Cove and Jordan Cove. There are only two breeding aggregations in the area, numbering about 30 harems in all. The beach is composed of a rocky indented shore at the foot of fairly steep cliffs. The southern part is very exposed.

Area 14. A very small stretch of coast between Area 13 and the main part of Evermann Cove was treated as a census unit because of its fair isolation. It is of the same character as the preceding area—a rocky coast with a tiny shingle beach.

Area 15. This very large division is difficult to classify and would be treated as several units if spatial

barriers existed to divide up the seals. Though predominantly of the rocky type with much-dissected off-shore reefs along most of its length, its middle third consists of a relatively broad sandy beach where there is a close aggregation of breeding seals, similar to that on Area 2. At its northern and western extremities Area 15 has inland extensions; these are not, however, very densely populated, and the northern one provides a corridor inland analogous to that extending in from the approach channel at Area 2. The southern limit of Area 15, where the cliffs come right down to the sea even at low water, provides the limit to that part of the main rookery which is counted in normal censuses.

Area 16 (the "extra beaches"). The southerly continuation of the coast of Evermann Cove beyond the census limit marks the beginning of the next census unit, Area 16. At the northern end are a number of small gullies, similar to those of the northern part of Evermann Cove, while to the south are massive rock walls which provide a sheltered hollow between the sea and the cliff. There were 26 harem bulls on this beach on 29 November 1961; there are indications that the beach has only recently been colonized by the seals.

The extra beaches, when counted under this name, are considered to terminate at a high rock wall, some 10 m. (33 ft.) above sea-level, just before a dark and cavernous shingle beach scoured by frequent storms. There are two further minor breeding beaches in the next kilometre. The first of these is a small triangular beach flanked by high cliffs and scattered with huge blocks of rock from a recent fall. Further along, by a small rocky islet separated from the shore by a turbulent channel 5–10 m. wide, is a large beach of rocky facies where a small waterfall tumbles over an overhanging rock. These beaches supported ten harem bulls in late November 1961.

b. *Johnson Cove*.* This is an extensive embayment at the south-western tip of Bird Island (Fig. 13). The head of the cove is divided by a spit of rock with a few stacks on it, the eastern arm being larger than the western. Just to the east of the spit a stream enters the sea. The fur seals breeding here are clustered around the base of the spit on a relatively exposed storm beach. Territories are established on the rocks bordering the western arm, and a single-rank structure exists on the shore on the eastern side of the base of the spit which provides a measure of protection from south-westerly storms. Johnson Cove had 63 harem bulls on 14 December 1961, and an estimated final pup production of 493. A large gentoo penguin rookery is established on the plain at the head of Johnson Cove, and the eastern arm of the cove is a favourite hauling-out place for leopard seals. A bull Weddell seal was seen here in January 1961—the only record of this species on Bird Island.

c. *Bird Sound beaches*. The main valley system of Bird Island extends west-south-west from the highest point of the island, Roché Peak (c. 370 m. (1,200 ft.)), towards Jordon Cove. Beneath a corrie on the southern flank of Roché Peak facing Bird Sound is another extensive beach system used by fur seals for breeding. These are referred to as "the Bird Sound beaches". The most westerly beach consists of large shingle and is very exposed; it never supports many seals. To the east of this is a rocky tongue extending into the sound, and beyond that is the main beach of the system of shingle scattered with large boulders. On the east, this is flanked by an extensive rock platform which juts out 60–80 m. from the foot of a high and very steep cliff; the seaward border of the platform is higher than its general level and protects the beach from the violent seas of Bird Sound. Kelp beds off-shore afford further protection. Inland, the beach rises in two main steps to a relatively level area where there is a large gentoo penguin colony. The fur seals form a dense aggregation on the shingle beach and on the flanking rock platforms, the two habitats being similar as pockets of shingle have accumulated in depressions on the rocks. This part of the Bird Sound beaches is terminated by a salt-water pool on the rocks, which is fed by wave splash and lies partly in a shallow cave in the cliff. Continuing eastwards is a further extension of the rock platform on which are a few scattered harem groups, and this ends in a steep shingle beach with a fine natural arch on it. There are also a few harems here, though it is not an important breeding area. In the 1961–62 season the entire beach complex had 87 harem bulls and an estimated final production of 700 pups.

d. *Shoemaker Point*. This very minor breeding station lies in a narrow cleft midway between Jordan Cove and the Bird Sound beaches, north-north-east from Shoemaker Point. This bay is the only part of the very steep coast in this region which has any beach at all. An arm of rock running parallel with the coast provides a little shelter, and a few seals breed on a boulder-strewn shingle beach, much set about with massive rock outcrops. There were 19 harem bulls there in mid-December 1961, though the estimated final

* Referred to by Marr (1936a) as "Rayner's Bay".

production of pups was only 84. It is not a fully developed breeding beach and has only recently been colonized by fur seals.

These four localities (the main rookery with its extension—the extra beaches, the Bird Sound beaches, Johnson Cove and the minor Shoemaker Point beach) include all the breeding colonies of fur seals on Bird Island. They are the only areas where beaches have been developed. The entire northern coast of the island consists of high steep cliffs which enter the water either sheer or in a jumble of wave-swept talus. On the southern side, eastwards beyond the Bird Sound beaches, is a narrow fringing beach but this is very exposed and it is doubtful if fur seals will ever breed there successfully. At Farewell Point and Pearson Point, the north-eastern and south-western extremities of the island respectively, there are inlets whose rocky heads might provide secure enough ground for breeding colonies to be established, but it seems unlikely. As all the available beaches of Bird Island are occupied by breeding colonies of fur seals, further increase in the numbers of the species there can take place only by increasing the breeding density on the beaches or, where the terrain is suitable, by an extension of the breeding area inland.

2. The Willis Islands

The Willis group was searched for breeding colonies of fur seals in December 1956 and January 1961. The group is composed of two larger islands, Main and Trinity, three smaller ones and a large number of rocks and stacks (Fig. 15). The coasts are very steep-to and the only place where a beach was found was on an easterly extension of Main Island pointing towards Trinity, and at the foot of a stack some 20 m. seaward of this. The area inhabited by the seals consists of a rocky table, about 5 m. above sea-level, from which several stacks rise abruptly. The surface is very broken, and in the centre is a shingle-filled depression scattered with many large boulders where the majority of the breeding seals are located.* Similar terrain was found at the base of the seaward stack, and the colony in both these places was estimated to have

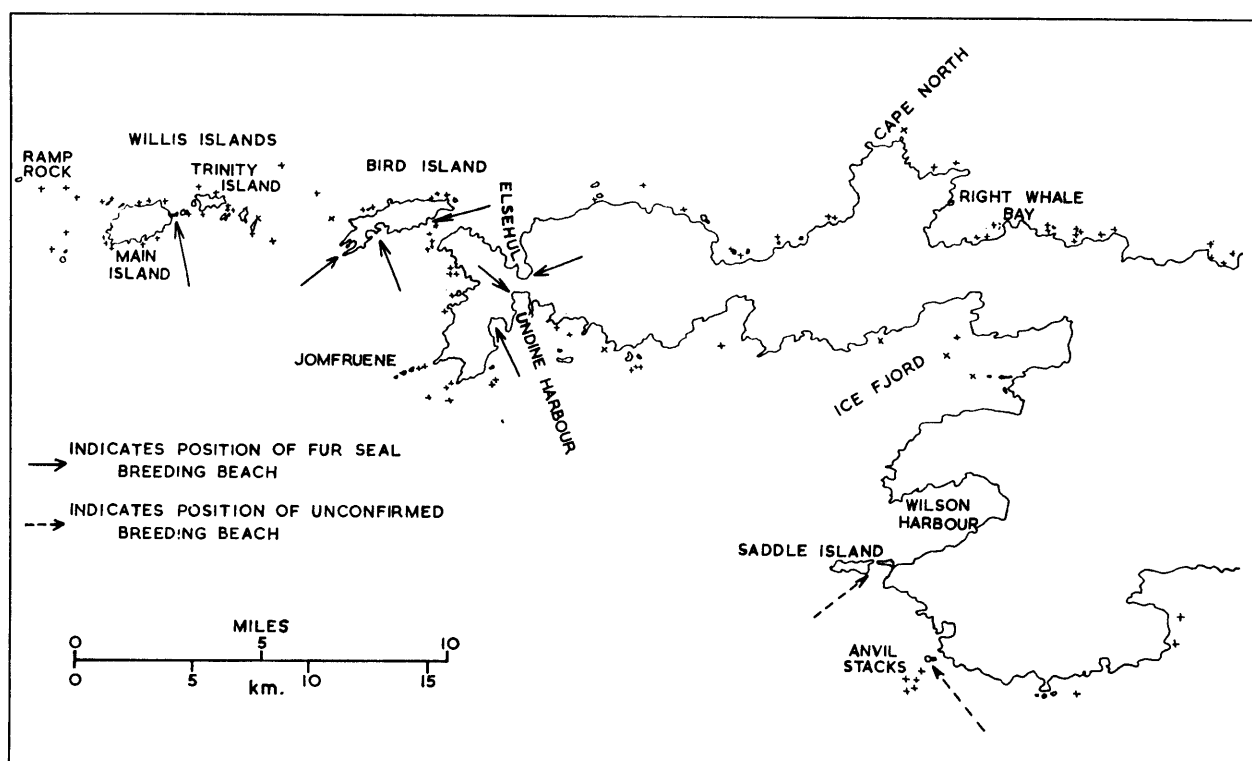


FIGURE 15

Fur seal breeding beaches on the north-western tip of South Georgia, Bird Island and the Willis Islands.

* See Plate IIa.

produced about 800 pups in the 1960–61 season. When the area was visited on 23 January 1961 a rather high proportion of cows were observed with their pups in the harem area, and it was at first thought that breeding at the Willis Islands was probably a little later than at Bird Island. Subsequently, however, it was realized that, owing to the high density of the breeding seals and the lack of other available sites, the lactating cows were compelled to feed their pups in the harem areas. There is no vegetation, other than small rock plants and mosses, on the rocks where the seals are found and the seas probably break over the entire area in the winter storms. Landing is extremely difficult owing to the big surge of the sea, even on the calmest days, and the rugged nature of the rocks which form the only available landing place. It seems probable that the Willis Island rookery was the residing place of the remnant of the seals that survived the depredations of the commercial sealers and that the species has spread from there.

3. *The Mainland of South Georgia*

Owing to the elephant sealing activities, which in recent years have extended well into the month of November, the coastline of the mainland is comparatively well known and it is unlikely that there are any breeding colonies of fur seals other than those described below.

a. *Johan and Undine Harbours*. These two small coves, together with the one immediately to the east, were once known under the convenient comprehensive term of "Discovery Bay" but this name has fallen into disuse. Johan Harbour, in particular, seems to offer good breeding sites for fur seals, as there are sheltered rocky beaches in the north-western corner of the cove and on the promontory separating it from Undine Harbour. It is much frequented by juveniles, and breeding was first confirmed there in the 1961–62 season when three harem bulls and twelve pups were found. In the following season the number of harem bulls had increased to eight, and 29 pups were present. There were thirteen pups on the rocky beaches of the western side of Undine Harbour in December 1960, but the cove has not been visited since.

b. *Elsehul*. A near-minimal breeding group of one bull and three cows and their pups was found here on 21 December 1960. The harem was established at the head of the inner cove of this exceedingly well-protected harbour, on a narrow fringing beach composed of talus from the low cliff behind it. There are two fairly extensive shingle beaches, but the entire coastline of this cove seems to offer suitable breeding spaces mostly of the rocky type for fur seals.

A detailed search of the coast and off-lying islets between Chaplin Head and the eastern extremity of Elsehul was made in December 1960. No other colonies of breeding seals were found, though juvenile males and resting bulls were common enough on most stretches where beaches had been formed.

c. *Anvil Stacks*. This is one of the traditional localities for fur seals in South Georgia, seals having been reported from here as early as 1918. Anvil Stacks ("Elephant Rocks", as they are invariably known in South Georgia) consist of two main rocks, the larger of which has its summit in the south-west and a lower rocky heel extending out about 7 m. above the water; on this heel is a shingle-filled bowl-shaped depression about 10 m. in diameter, surrounded by boulders and rocky walls. The whole structure is reminiscent of the breeding site at Willis Island, but is on a smaller scale. In January 1961 five adult fur seals were seen here together with what were believed to be two pups, though as landing was impossible this could not be confirmed. It is almost certain that some seals do pup on Anvil Stacks but their numbers are inconsiderable. In January 1960 an isolated fur seal pup was seen on some rocks on the mainland side of the very narrow channel separating Saddle Island from the mainland, about 4.5 km. (2.8 mi.) north-west of Anvil Stacks at the mouth of Wilson Harbour. No breeding colony could be seen in the neighbourhood from the sea, and conditions at the time of observation prevented landing; it is unlikely that there is any other colony in that region. The pup could have been a wanderer from Anvil Stacks.

d. *Cooper Bay*. Fur seals, including adults, have been sighted several times, since 1946 at least, in this well-protected system of rocky coves at the south-eastern extremity of South Georgia. Rankin's (1951) plate 80 shows an adult male fur seal in Cooper Bay, although the caption does not give the locality and refers to the animal as a female. Adult fur seals frequently play in the waters around the rocks off Cape Vahsel. It has never been confirmed that they breed at Cooper Bay but, apart from an expedition which went there in 1954–55 (Sutton, 1957), the area has not been visited later than November, so a breeding colony may have been overlooked. Although wandering juveniles may be encountered anywhere along the coasts of South Georgia during the summer and autumn months, the very frequent reports of fur seals and in particular the presence of adults in this region are highly suggestive of a colony in the vicinity, especially as it is as far away as possible from the known breeding areas. The east and south coasts of

Cooper Island, only 2 km. (1·2 mi.) away from Cooper Bay, are even today quite unknown. The general aspect of the island renders it unlikely that any large beach system could be developed and the elephant sealers report that there are no beaches there, but so far as the author is aware none of the present sealing skippers has ever inspected that part of the coast closely. O'Gorman (1961) reported that fur seals had been seen on Clerke Rocks (about 64 km. (40 mi.) east-south-east of Cooper Island), but it is not known whether they breed there.

C. INTERSPECIFIC RELATIONS

Apart from the predator-food and host-parasite relationships, the fur seals do not form any close associations with other animal species. Four species of birds, the sheathbill *Chionis alba*, the brown skua *Catharacta skua lönnbergi*, the giant petrel *Macronectes giganteus*, and the Dominican gull *Larus dominicanus*, frequent the rookeries and find at least part of their sustenance there. Of these, the sheathbill is the most closely associated with the seals, many of them obtaining the major part of their food from the rubbish of shed placentae, dead pups and faeces that are scattered over the beaches. The other three species are invariably present at a fur seal rookery but their pickings there are sporadic and form only a part of a wider diet, the skuas feeding mainly on prions, the giant petrels on plankton and the gulls on limpets and other shellfish. The general reaction of the seals towards the birds is one of indifference, though cows with pups will snap aggressively at any bird that comes close.

Nowhere in its range does *Arctocephalus tropicalis gazella* come in contact with any indigenous land mammals; this is generally true of all fur seals, as their breeding grounds are usually on isolated islands or off-shore rocks. In South Georgia, the fur seals regularly come in contact with two other species of seals—the elephant seal and the leopard seal. Occasionally, but more frequently in the more southern parts of the range of the species, they also encounter the Weddell seal. The most frequent contact on shore is with the elephant seal. The present locations of the breeding rookeries of fur seals and elephant seals in South Georgia do not coincide, though two of the beaches on Bird Island (Freshwater Inlet and Evermann Cove) are the site of minor elephant seal colonies in the breeding season. In the nineteenth century, however, the distribution of the fur seals must have very largely overlapped that of the elephant seals. Although sealers' records are vague it is known that "Woodward's Harbour" (Antarctic Bay) was an important anchorage for the sealers, and the fur-sealing grounds extended westwards from there around the north-western peninsula and southwards to at least Queen Maud Bay, where the remains of a shallop are still to be seen. That this run of coast was frequented by the elephant sealers is shown by the finds of try-pots and other gear associated with the boiling down of blubber, as well as by observations on the present distribution of the elephant seals. It is interesting to speculate whether under these circumstances there would have been any competition between the two species for breeding sites. Although both animals are to be found in varying habitats, the elephant seals show a preference for broad open beaches of sand or shingle while the fur seals more typically frequent the smaller rocky coves. This results in spatial separation of the two species, though some overlapping no doubt occurs.

At the present time there is no clear temporal separation. The peak of the breeding season of the two species is separated by approximately two months, that of the elephant seals occurring in about the third week of October and that of the fur seals following in mid-December. Sporadic breeding in the elephant seal goes on well into mid-November, although by this time the harem structure has largely decayed, while the first fur seal pups are produced not much later than this and the majority of the harem bulls have taken up their positions. However, Matthews (1929) showed that the elephant seal haul-out 25 years ago was considerably earlier than it is today, the peak of the season then occurring in September. It has been assumed (Laws, 1953*b*) that this retardation of the breeding season has been brought about by the intensive commercial exploitation of the species in the last 50 years, though the mechanism underlying it is not fully understood. There is no evidence of a similar change in the habits of the fur seals, accounts of the breeding season by Weddell (1825) and Althearn (in Clark, 1887) fitting today's observations very well. In the undisturbed state of two centuries ago, the two species would have had clearly distinct breeding seasons with their peaks separated by about three months, and the last of the elephants would have departed before the arrival of the first of the fur seals so that there would have been no competition for breeding areas. Now, in addition to the retardation of the breeding season, the elephant seals are also showing a tendency to desert the open beaches for the rocky coves and headlands, and this might well

result in an increasing fur seal stock being hampered by competition with elephant seals for breeding sites.

Although, at present, breeding elephant seals do not come in contact with breeding fur seals, wandering juvenile elephant seals and moulting adults frequently stray on to beaches occupied by breeding aggregations of fur seals. Pods of moulting elephant seals in the tussock behind the breeding beaches are ignored by the fur seals, but those which wander into harem groups are continually pestered by their smaller relations. The pestering usually takes the form of threat behaviour from the harem bulls consisting of vocal challenges followed by short charges, actual contact and the infliction of bites being rare. On one occasion an adult bull elephant seal, estimated as 4·5 m. (14·75 ft.) long with a probable weight of about 1,500 kg. (1·48 tons), was seen to haul out on a breeding beach; he slowly hitched his way up the beach until he came within the territorial boundaries of an aggressive harem bull. The fur seal challenged the elephant seal twice and then charged him and seized him by the proboscis. The elephant seal reared up in a typical fighting position, with the anterior half of its body clear of the ground, leaving the fur seal bull hanging by its teeth from the larger seal's nose. As the fur seal must have weighed 180–200 kg. (c. 3·5–4·0 cwt.) this testifies both to the tensile strength of the elephant seal's proboscis and the tenacity of the bite of the fur seal. After hanging suspended in the air for a second or two the fur seal released its hold, dropped to the ground and shuffled back to the centre of its territory. The elephant seal at the same time backed away, and re-entered the sea, to haul out again on another beach some 100 m. (c. 110 yd.) distant. Cow fur seals will also threaten elephant seals and much more frequently deliver bites, though these are rarely serious and as elephant seals are extremely irresponsible to trivial injuries they have little effect in hindering their progress through a rookery.

Adult elephant seals which fall asleep on a fur seal rookery are soon ignored by the fur seals unless they occupy a position on the beach, such as a dividing line between two territories, where they attract the bulls' attention. Juveniles of the same order of size as the fur seals, on the other hand, are constantly harried and bitten and, with the exception of weaned pups, rarely stay long in the vicinity of the fur seals.

As leopard seals spend only a small proportion of their existence on land and are a relatively uncommon species, their chances of encountering fur seals ashore are slight. At two localities on Bird Island (Freshwater Inlet and Johnson Cove), however, solitary leopard seals are fairly regularly seen hauled out at low water between tide marks. Inspection of faeces has shown that these leopards feed mainly on a diet of penguins and fish.

Fur seals show no special reaction to leopard seals. Adult fur seals rarely come in contact with them owing to the preference shown by the leopards for hauling out below high-tide mark. On one occasion only a territory-holding bull was seen to challenge a leopard seal about 8 m. away; the leopard ignored the challenge and the fur seal did not repeat it. Troupes of wandering fur seal juveniles spend much time playing at the water's edge and sometimes encounter leopards. The fur seals inspect the larger animal, as they will inspect any unusual object on the beach, but if the leopard seal raises its head and vocalizes the fur seals promptly depart. This does not indicate any specific negative reaction to leopard seals, as any sudden movement or sound will send these groups of wandering juveniles into abrupt retreat.

On the single occasion when a Weddell seal was seen hauled out on a beach occupied by fur seals, the juveniles treated it in exactly the same manner as they would a leopard; there were no adults in the vicinity at the time.

As mentioned earlier, the fur seals do not anywhere in their range come in contact with any indigenous land mammals, but all known colonies have at one time or another had a disastrous association with man. The reactions of the fur seals to man vary with age classes and season, but none can be interpreted as a specific fear and it is not necessary for an observer to conceal himself, to approach the seals down-wind or to take the other precautions that usually have to be observed when watching wild mammals.

Juvenile fur seals will not permit very close approach, and retreat hastily if one comes within 5–10 m. of them. If a juvenile is disturbed while sleeping it will on waking hold its ground, growl aggressively and occasionally snap until the intruder has passed on. If the situation is further exacerbated—for example, by teasing the seal with a stick—it will move away at full speed. A juvenile rarely flees more than a few metres and if the observer remains still, particularly if he sits or lies down, it will soon come hopping up to examine him. It will approach to within the maximum range of the extension of its neck and thrust its muzzle into the face of the observer, occasionally making contact with its forwardly-directed vibrissae. When this reaction was first observed it was thought to represent an olfactory inspection, and this may

indeed be its primary purpose, but its similarity to the "whisker-snapping" reaction of the cows (see p. 50) is unmistakable and it may partly be a warning gesture.

The adult seals during the breeding season appear to be more fearless than the juveniles as, owing to the bonds they form with their territories, they are less likely to show the flight reaction. It is virtually impossible to drive harem bulls from their territories, and the only occasion on which this was seen (other than as a conclusion to intraspecific territorial fighting) was when a helicopter flew low overhead.

The cows when newly hauled-out prior to producing their pups are restless and may make off to the sea when approached, but their leisurely departure is clearly distinct from the rapid retreat of the juveniles. Once the pups have been born, the cows exhibit either indifference to a human observer or an aggressive reaction which is indistinguishable from that shown towards the bull—rapid darting of the head and snapping of the jaws just short of the target. Cows rarely move far to menace an intruder nor is it usual for them actually to bite, but on one occasion when the author was passing through a loose aggregation of breeding cows in an area of low tussock, he was attacked by a cow which charged from a distance of at least 10 m. and inflicted two severe bites. This high-intensity attack by a cow from a distance was a unique piece of observed behaviour; its motivation is unknown.

Breeding bulls either ignore or threaten an intruder. Their aggressive behaviour towards man is in all respects similar to that shown towards other bulls (see p. 52–53) and does not require further description. The bulls are individually highly variable in their reaction to man, some allowing extremely close approach, even to the point of being touched without responding other than by turning their heads to examine the cause of the disturbance, while others will threaten before the observer has entered their territories. Harem bulls rapidly learn to tolerate an observer, and bulls whose territories are frequently passed by can be treated with far greater familiarity than those more rarely visited, as the following example shows. A territory near the base hut was visited daily for the purpose of weighing two of the pups. Catching the pups frequently involved a considerable measure of disturbance to the cows, and the bull (which was handicapped by being blind in one eye) became very agitated in his efforts to herd the cows. Not infrequently it would happen that the bull, in his rushes to and fro after the cows, would collide with one or another of the observers who were equally liable to stumble over the bull, but at no time was any attempt made by this animal to bite or to show more than token threat behaviour. Such extreme tolerance by a bull is unusual, but harem bulls generally show less aggressive behaviour towards man than do the cows.

Bulls not occupying territories (either defeated harem bulls or sub-adult animals) vary in their reaction to man. As mentioned in the section on body temperature (p. 43–44), defeated harem bulls are often in a rather torpid state in which they show a lesser response to all situations and may permit very close approach. The sub-adults are generally aggressive and will challenge and snap, but are easily put to flight with a stick as they have not formed territorial attachments.

It was found that at all times groups of seals could be safely approached by crawling up to them. By this means it was possible for an observer to enter the limits of a harem bull's territory and lie within a few inches of the bull or his cows, provided that the approach was made cautiously and unnecessary movement avoided. After a few preliminary examinations of the sort described above for the juveniles, the seals paid no further attention to the observer. This difference in response to upright and prone postures is shown also by elephant seals. In both species, animals showing aggressive or threat behaviour elevate the fore quarters off the ground (this is highly exaggerated in the bull elephant seal which can raise as much as the anterior two-thirds of its body vertically), whereas a prone position is characteristic of neutral or submissive behaviour. This difference in attitude of the seals may act as a "sign stimulus" and account for the difference in response to the two kinds of approach.

Towards the end of the breeding season, when territorial bonds are less firmly established, the adult seals exhibit a greater timidity, the cows in particular deserting the beach in droves when disturbed. The bulls remain at all times less easily scared than the cows, but the general behaviour of both sexes approaches more nearly to that of the juveniles.

Throughout the early sealers' accounts of their depredations of the fur seal colonies, the phrase "the seal have deserted their rookeries" constantly occurs. This probably means nothing more than that the seals had been exterminated in their old haunts, and there is no definite evidence that any surviving population has shifted its breeding grounds on account of human interference. Nevertheless, it should not be assumed that interference could not cause seals to desert their breeding grounds, but it is likely that any such movements would be either on a small scale or of a temporary nature.

The sealers were generally most careful to dispose of the flensed carcasses of their victims by tumbling them into the sea, believing that if this were not done the seals would fail to haul out at the same rookery in subsequent years. Some governments even made regulations requiring the proper disposal of carcasses when granting concessions to take fur seals. Observations have shown that the seals are completely indifferent to the presence of corpses of their own kind. The smell of blood and dissolution must, after all, be commonplace on a fur seal rookery where territorial fighting is constantly shedding blood and the rotting bodies of dead seals are scattered over the beaches. On one occasion when a cow was shot for examination of the reproductive tract (it proved to be pregnant with a full-term foetus), the only response of its attendant harem bull was to attempt to copulate with the dead animal. This reaction was probably evoked by the prone position of the dead cow and the absence of any resistance when the bull attempted to mount.

The South Georgia fur seals appear to be particularly indifferent to the activities of man. Rayner (1933) commented on the distinction between the fearless South Georgia seals and the timid animals inhabiting the Falklands, and other authors (e.g. Holdgate, 1958, on *A. tropicalis tropicalis* on Gough Island) give the impression that the other species of *Arctocephalus*, though not *Callorhinus*, are more retiring and difficult to approach. The fearlessness of the South Georgia seals is probably innate and may be associated with their island habitat (island forms often show relative fearlessness when compared with mainland relatives), but it is not clear why *A. tropicalis tropicalis*, living in comparable isolation, should be more timid.

V. GENERAL BEHAVIOUR

A. LOCOMOTION

1. *Terrestrial locomotion*

One of the most important diagnostic characters separating the otariids from the phocids, is the ability of the former to rotate the hind limbs under the body and use them for propulsion on land. The agility displayed by a fur seal in travelling over all kinds of terrain is surprising and at times disconcerting, as an angry fur seal can progress over slippery rocks or through dense tussock considerably faster than a man. The main propulsive effort on land is exerted through the fore flippers. During locomotion the head and neck are held forward and the somewhat posterior insertion of the fore flippers ensures that the weight of the body is taken by them, the hind flippers serving mainly to support the pelvic region and to provide the third leg of the tripod that maintains stability. Only the "heel" of the hind limb is used for weight bearing, the fan formed by the digits and web often being held clear of the ground.

On a hard surface, and when not particularly hurried, the fur seal progresses by alternate movements of the fore flippers, bringing the hind flippers up together. There seems to be no fixed rhythm for the movement of the hind flippers, though they are generally brought up after each movement of a fore flipper when both fore flippers are in contact with the ground. The belly is at all times carried clear of the ground. When moving in a very leisurely fashion the seals will waddle, moving the hind limbs alternately with the basic sequence of contralateral limbs being moved successively, i.e. right fore, left hind, left fore, right hind, but this is difficult to determine (as are all the gaits of the seals) as the animal rarely progresses more than a few paces in any direction before pausing. At the highest speed on a smooth surface, which is probably about 12 m.p.h. in the case of an adult bull, a seal will gallop by a series of long bounds in which the fore limbs are moved simultaneously, followed by an abrupt arching of the back and swinging the hind limbs forward together. This type of locomotion is more commonly observed in the juveniles which rush about the beach in the course of their play; it is least common in adults, but is sometimes performed by bulls when passing between territories or when chasing a rival.

Over rough ground—for example, broken rocks or hillocky tussock—a seal will progress from vantage point to vantage point. The fore flippers are generally set down alternately, but when the seal has to extend itself in making a longer than usual pace they may be moved together, so that the seal seems to be making a dive towards its next position. While balancing on the fore flippers the hind flippers are brought up together and positioned behind the fore flippers, the long flap of the foot often overlying the hand. The seals are very agile in moving over broken country and rarely, if ever, slip, the serrated ridges of the callus of the palms and soles providing a sure grip on even the most slippery surface. Seals evidently learn the

character of the local terrain, newly hauled-out individuals progressing in a halting manner in contrast to the confident unhesitating movements of those which have been longer ashore.

Over ice or compacted snow, fur seals may move in a typically phocine manner, hitching themselves along with the fore flippers and dragging the hinder parts of the body after them. Normally the seals adopt the ordinary waddling gait and the hitching is probably a play action. Young seals in particular take a great delight in snow and will ascend a snow-filled gully for no other observable purpose than to slide down it again, much in the manner of tobogganning otters.

2. *Swimming*

The movements of fur seals in their principal habitat, the sea, are less accessible to observation than the terrestrial locomotion already described. The movements of swimming fur seals have been studied from time to time on calm days in the small bays around the rookery area by binocular observation from the cliffs above. Under these circumstances the seals are usually playing in the water and their movements are not necessarily associated with prime purpose of locomotion, i.e. to get from one locality to another, and therefore may not be at their full intensity; some forms of locomotion may not have been observed at all.

The body of the seal is of course highly specialized for aquatic locomotion, but the specialization has proceeded along lines other than those of the phocids whose primary propulsive force for swimming is provided by undulatory movements of the hind flippers and posterior part of the body in a horizontal plane. In the otariids the fore flippers are relatively more developed, and they are used with a rowing motion to provide the propulsive effort.

In the normal swimming movements the fore flippers are advanced, edge first, to a position slightly forward of a line at right angles to the body axis, and then swept backwards with the palmar surfaces opposed to the resistance of the water, thus driving the body of the seal forwards. The hind flippers are allowed to trail passively behind, though medially-directed thrusts of the hind limbs are occasionally made. Changes in direction are effected either by changes in amplitude of the stroke of one of the fore flippers or, when a more abrupt turn is to be made, by lateral flexing of the body combined with extension of the web of one hind flipper to act as a rudder. This form of propulsion is not very efficient, as it involves the reversal of the movement of the fore flippers with each stroke and a "feathering" period when their motion is opposed to the propulsive drive. The phocine method of locomotion, whereby lateral waves are originated in the posterior part of the body and are reinforced by alternate medially-directed thrusts of the hind flippers, does not suffer from these disabilities and to this extent the phocids are more efficient in the water. However, the phocine form of swimming is occasionally seen in fur seals, the fore flippers being held tightly adpressed to the sides and the posterior part of the body undulated from side to side; the hind flippers are extended and their palmar surfaces placed together. (In this important aspect the motion differs from that of the true seals.) The resulting motion is slow and is rarely maintained for more than a few yards, at least under the conditions observed. It is frequently accompanied by a rotation of the body about its long axis, the seal cork-screwing its way through the water. This type of swimming is often seen in association with washing movements, when seals which have been hauled out a long time re-enter the water for the first time. It represents a play-action and is seen in all classes of seals.

The maximum speed that fur seals can attain in the water has not been determined; there is a general tendency to overestimate the speeds of animals when swimming, and the absence of standards makes comparison difficult. It can be said with fair certainty that fur seals are faster than elephant seals but slower than leopard seals. For the southern species, Laws (1956) estimated the speed of adult elephant seals as 12–15 m.p.h., while for the northern species Bartholomew (1952) gave 10–12 m.p.h. Bartholomew's estimate is probably the more accurate of the two, and it is unlikely that there is any difference between the two species. South Georgia fur seals can probably exceed 12 m.p.h. and can possibly reach 15 m.p.h. over short distances. A bull fur seal swimming fast, just beneath the surface of calm water, will raise a bow-wave with an amplitude of about 15 cm.

When fur seals are encountered at sea they often first strike the observer's attention by their habit of porpoising. This movement, as suggested by the name, consists of the seal shooting above the surface in a shallow arc. At its highest intensity the whole body of the seal will leave the water and re-enter it at a point some 2–3 m. ahead. Even fully grown bulls have been observed to leave the water completely when porpoising. The origin of the propulsive thrust necessary for porpoising is not known; certainly the main drive is provided by a vigorous downwardly-directed thrust of the fore flippers, but whether the hind

flippers play any part is uncertain. In open waters after a bout of porpoising, a school of fur seals will disappear from sight and resume the usual pattern of underwater swimming. From their habit of porpoising when in the vicinity of a vessel, one is inescapably driven to the conclusion that this form of swimming is used to provide the seal with a better view than is available when swimming steadily.

The repertoire of swimming patterns available to the fur seals is undoubtedly much more extensive than that described, but conditions for observation at sea are rarely favourable. The degree of development of the hind limbs suggests that they are capable of playing a larger part in locomotion than that observed, and it is possible that when fur seals are on long journeys (to and from the feeding grounds, for example) they may adopt a mode of progression which makes much greater use of the hind limbs.

B. BODY TEMPERATURE AND TEMPERATURE REGULATION

The body temperatures of a series of specimens were recorded, after killing, by inserting a clinical thermometer into the thorax or amongst the abdominal viscera, within one minute of death or sooner if possible. Temperatures were taken only if the animals had not been disturbed before being shot and had died without struggling and, thus were not under any apparent temperature stress. Post-mortem changes are believed to be very small, and the results (Table VI) can be taken to be representative of the normal resting body temperature of the seals.

TABLE VI
BODY TEMPERATURES (°C) OF FUR SEALS

| | <i>Specimen number</i> | <i>Sex</i> | <i>Status</i> | <i>Temperature</i> | <i>Average temperature</i> |
|-----------|------------------------|------------|---------------|--------------------|----------------------------|
| Pups | FS 22 | ♀ | 2-day | 38·4 | } 38·4 |
| | FS 25 | ♀ | 4-day | 38·1 | |
| | FS 27 | ♀ | 6-day | 38·6 | |
| Juveniles | FS 5 | ♂ | yearling | 38·4 | } 37·8 |
| | FS 3 | ♂ | 2-year-old | 38·4 | |
| | FS 6 | ♂ | 2-year-old | 37·8 | |
| | FS 31 | ♂ | 2-year-old | 37·4 | |
| | FS 29 | ♀ | 2-year-old | 37·2 | |
| Adults | FS 24 | ♀ | breeding | 37·3 | } 37·5 |
| | FS 26 | ♀ | breeding | 37·7 | |
| | FS 32 | ♀ | breeding | 37·1 | |
| | FS 39 | ♀ | breeding | 38·2 | |
| | FS 1 | ♂ | breeding | 37·3 | |

It will be seen from Table VI that the fur seals conform to the usual mammalian pattern, the younger animals having a slightly higher body temperature (pups, 38·4°C; juveniles, 37·8°C) than the adults (37·5°C). These results correspond quite closely with those obtained by Bartholomew and Wilke (1956) who found that in the northern fur seal, *Callorhinus ursinus*, the average body temperatures of adults and pups under no temperature stress were 37·7°C and 38·2°C, respectively.

Several attempts were made to obtain temperature values from living animals using various methods, but with one notable exception none was successful owing to the difficulty of restraining the seals. The exception was an adult harem bull of the territory-holding class, which had probably been defeated in a

territorial battle and was noticed lying by a stream near the camp on 9 December 1958. Two days later, when the animal had become accustomed to the presence of an observer, an attempt was made to obtain a value for the body temperature by inserting a clinical thermometer into the rectum. This thermometer, and another similar one, failed to record a reading (minimum scale reading 95°F), but a Rototherm dial thermometer gave a value of 34·6°C when inserted 20 cm. into the rectum (Plate VIc). The ambient shade temperature was 4·4°C. This is by far the lowest body temperature recorded, being 2·5°C below the adult average (excluding this value). The bull concerned disappeared, it is believed to sea, two days after the temperature was taken. Numbers of similar dispossessed adult bulls are to be seen in the tussock behind the breeding beaches throughout the season. All show evidence of having been involved in territorial fighting and bear more or less serious injuries and some appear to be *in extremis* though, with few exceptions, after a lapse of 4–6 days they appear to recover and depart to sea. It is thought that the very low body temperature recorded represents a state of lowered metabolic activity during their recovery period. This is to some extent borne out by their sluggish movements, approaching torpor, and their great docility which allows them to be approached and even handled cautiously; no others, however, permitted such intimacies as the bull from which the rectal temperature was obtained.

The development of the fur seals' luxurious double-layered pelage and to a lesser extent the subcutaneous blubber are adaptations conserving warmth in their normally frigid aquatic environment, although the main function of the latter is as a food reserve. These insulating layers effectively hinder the passage of heat from the body of the animal to the water, i.e. to a colder outside environment of high thermal capacity. They also make the dissipation of excess heat, when the animal is ashore, a matter of considerable difficulty, for on land not only is heat-transfer slower owing to the low thermal capacity of air, but the ambient temperature is likely to be higher, perhaps very considerably so.

The two main mechanisms of heat loss in most mammals are sweating and panting. In the fur seal the dense underfur effectively prevents the flow of air over the mouths of the sweat glands and, as already mentioned (p. 9), the sweat of these animals is believed to be solid, hence sweating over the general body surface is not available to fur seals as a means of lowering the body temperature. Seals can lose heat by panting, but it is unlikely that any considerable quantity of body water is available during fasting periods ashore for cooling by this means. Seals are commonly seen to pant after periods of violent activity, but panting under these circumstances possibly serves mainly to ventilate the lungs. *Callorhinus*, on the other hand, is known to pant in circumstances where there has been no previous exertion and then the only function must be cooling.

The dual heat-retaining layers of blubber and pelage are lacking from the flippers, and it is these organs that are the main source of temperature regulation in the fur seal. The flippers, being developed primarily as locomotory organs, are provided with a considerable surface for reaction against the water when swimming or the ground surface when travelling on land. However, it has never been demonstrated that the hind flippers play a major role in aquatic locomotion, yet they are provided with peculiar flap-like extensions beyond the tips of the terminal phalanges. It is difficult to see how these very flexible structures, devoid of a rigid skeleton, could be used as a means of adding to the propulsive thrust of the hind flippers (though it is quite possible that they might play a part in reducing turbulence when swimming), and a principal function of the flaps may be to increase the available heat-exchange surface of the body. Bartholomew and Wilke (1956) found that both front and hind flippers of *Callorhinus* were abundantly supplied with sweat glands, and although no special microscopic examination has been made of the flippers of the South Georgia seal the same is believed to apply to them and to all species of *Arctocephalus*. If sweating does play a part in the cooling system, it follows, of course, that liquid sweat would have to be produced in the flipper glands as opposed to the solid sweat of the glands of the general body surface.

Conversely, those adaptations which enable the flippers to dissipate unwanted heat can, under certain environmental circumstances, function to the detriment of the animal's economy, and an active control has to be imposed upon them. Physiological mechanisms control heat losses through sweating, and there is probably some mechanism acting on the abundant blood supply of the flippers. Scholander (1958) has pointed out the importance of counter-current vascular heat exchangers in the extremities of aquatic mammals, and quotes an unpublished observation of H. Erikson that arterio-venous retia in peripheral structures are prevalent in seals. Barnett, Harrison and Tomlinson (1958), on the other hand, found that the amount of retial tissue in seals was small and that the large limb veins had a remarkably simple arrangement.

Besides the physiological control, the seal is able to regulate heat loss from the flipper surfaces by postural mechanisms. The reactions for conserving heat are less conspicuous than those for dissipating it, but the reason for this, at least in South Georgia, may be that adult seals are but little inconvenienced by low temperature conditions. When lying quiescent or asleep in the water, seals are sometimes observed to adopt a posture whereby the heat-losing surfaces of the flippers are removed as much as possible from the cooling effects of the water. The seal floats on its back with the snout raised above the surface, or the head is rotated so that snout and eyes are clear of the water, and the hind flippers are held out of the water with their palmar surfaces pressed together and the digits closed, furling the interdigital webs; one of the fore flippers is extended upwards and backwards to meet the hind flippers, so that of the four heat-losing flippers, three are removed from the water and held together so that their effective total area is much reduced. It seems that one fore flipper is required to remain in the water to maintain stability, though Bartholomew and Wilke (1956) state that the northern fur seal occasionally raises both fore flippers out of the water. Seals not infrequently adopt this position for a few seconds or minutes in the middle of aimless play-swimming and washing; it then represents part of a play repertoire, and bears no relationship to temperature control.

The normal posture of the fur seals ashore, when resting or otherwise lying quiescent, is lying on one side with the adposed hind flippers brought up over the belly, their tips being covered by the backwardly directed fore flippers which are held closely pressed against the sides of the chest. While this position helps to minimize heat losses by reducing the effective surface area of the flipper, it cannot be said to be adopted for this purpose as a similar orderly disposition of the limbs is generally to be observed in non-active mammals. Bartholomew and Wilke note that on cool or rainy days northern fur seals ashore normally lie on their bellies with the flippers tucked under. This position is commonly observed in South Georgia, and is the second most commonly adopted position, but it is not specially associated with adverse weather conditions. Low temperatures or high winds evoke no special response, though seals will close their eyes against driving snow, but in periods of heavy rain a majority of the adult seals adopt a posture in which the fore quarters are raised up in the air with the muzzle pointing nearly vertically upwards (a position that will later be described as the "alert position"). It is perhaps surprising that an aquatic animal like the fur seal should show a response to rain, and it may be assumed that the seals are not responding to the state of wetness; possibly it is the percussion of the rain drops or the muddy splash from the ground that evokes the response. There is no response to lighter showers, probably owing to their great prevalence.

Pups, lacking a waterproof pelage, soon become sodden in rain and are frequently seen shivering, a reaction that seems to be confined to this class. The gregarious nature of the pups whose mothers are away feeding no doubt enables them to endure much more severe weather than they could singly, and the formation of the pup "pods" may be associated with the need for heat conservation. The chick "huddles" of the emperor and king penguins (Stonehouse, 1953 and 1960) are analogous, but also provide protection against predators.

In the northern fur seal, the principal means of heat dissipation on land is by making fanning movements with the hind flippers, thus increasing the air flow over their surface. This conspicuous behaviour has been commented upon by many observers from Steller (1749) onwards. It has not, however, been observed in *Arctocephalus tropicalis* on South Georgia, though O'Gorman (private communication) has observed it in that species on Livingston Island and in *A. australis* on Isla de Lobos, Uruguay. Holdgate (private communication) states that it also commonly happens on Gough Island. At South Georgia the most commonly observed method whereby the fur seals dissipate excess heat, is the adoption of a sprawling posture with the limbs extended to their fullest extent (Plate VI*d*). The seal lies prone with the whole of the ventral surface of the body in contact with the ground, while the flippers are extended outwards from the body, palmar surfaces downwards, with the interdigital webs of the hind flippers spread to their fullest extent. This position is adopted on calm days when the sun is just obscured by light cloud in conditions that might be described as "muggy", irrespective of air temperature. (Such conditions are most frequently experienced when the wind swings to the south-west after a period of north-westerly weather.) In this characteristic posture, the animal is able to lose heat by conduction from the palmar surfaces of the flippers to the ground, and by convection and radiation from their plantar surfaces. The heat-reaction sprawl has been noted most frequently in bulls, the largest and most active of the seals ashore, less frequently in cows and never in pups or juveniles. Pups with their relatively inefficient pelage probably never suffer from excess heat, and juveniles respond to warm weather by sheltering under tussocks or entering the water.

C. FEEDING HABITS

No data are directly available on the feeding of the fur seals, but inspection of faecal remains and stomach contents has provided abundant evidence of the nature of their food. A very cursory inspection of a fur seal hauling-out ground will reveal two types of faeces: by far the most common is bright pinkish-red and contains small pieces of chitinous crustacean exoskeleton; the less common is greyish and contains fish scales and bones. Hamilton (1934) writing on the southern sea lion, *Otaria byronia*, commented on the colour of the faeces and pointed out that they varied from brick red when the seals had been feeding on the crustacean *Munida*, to grey when the diet had been fish, and were bright yellow when squids had been the main food. A similar state of affairs exists in the fur seals, the pink faeces being consequent on a diet of the Eucarid crustacean, *Euphausia superba* Dana, and the grey ones resulting from feeding on fish. *Euphausia* (krill) is the only food found in a fresh state in the stomachs of lactating females, the only class of fur seals available for examination ashore which is actively feeding. Fish-remains commonly occur in the stomachs of the juvenile and sub-adult non-breeding animals inhabiting the grassy hills behind the breeding beaches and the more remote hauling grounds. These remains rarely consist of more than a few scales and bones, though small quantities of partially digested fish meat were found on two occasions. It is likely that these classes are not actively feeding when found ashore and that the remains found are either the remnants of previous meals taken during a pelagic existence or, more probably, the results of casual feeding excursions made when the seals were playing in the shallow coastal waters. The species of fish concerned has not been conclusively identified, but all the remains found correspond to immature specimens of *Notothenia rossi* which are commonly found in the kelp beds around South Georgia.

Cephalopod remains are more rarely found and have been recovered from only two stomachs, but yellow faeces, which are said by Hamilton to be characteristic of the digestion products of cephalopod ink, are not uncommon. Cephalopods do not appear from this evidence to be a very important item of diet in the summer months, but it is quite possible that they are taken in greater quantity in other seasons. I am indebted to Dr. Malcolm Clarke, of the National Institute of Oceanography, for identifying the squid remains from the two stomachs. From one seal an upper beak of an Ommastrephid squid, probably *Stenoteuthis* or *Dosidicus*, with an estimated weight of about 250 g., was recovered together with upper and lower beaks (probably from the same squid) of an Onychoteuthid, probably *Onychoteuthis banksi*, with an approximate total weight of 380 g. The other stomach contained a single upper beak, probably from an Enoploteuthid squid. It is of interest to note that the two stomachs contained remains from three species of squid.

One record is available of the retrices of a gentoo penguin, *Pygoscelis papua*, found in the stomach of an adult bull shot ashore in September. It is not thought that penguins, or any other birds, form any significant part of the diet of the seals, and this instance may be compared with the anomalous feeding habits of a Hooker's sea lion, *Neophoca hookeri*, which made a practice of pursuing penguins on the beaches of Macquarie Island (Gwynn, 1953b).

Although precise data on feeding habits can be secured only by obtaining stomachs from seals on their feeding grounds, there is no doubt that the staple diet of the South Georgia fur seals is krill. However, non-breeding seals which spend much of their time in the waters just off-shore probably take appreciable quantities of fish, and quite possibly anything else of an edible nature that is available. There are few records of the diets of southern fur seals. Rand (1959) made a careful study of the feeding habits of the Cape fur seal, *Arctocephalus pusillus*. From the contents of 245 stomachs taken from seals at sea off the south-west Cape coast he found that the most important prey was fish, which comprised roughly 70 per cent of the total volume; the maasbanker, *Trachurus trachurus*, predominated, cephalopods comprised about 20 per cent, and crustacea only 2 per cent. The same author (1956a) records, on the evidence of stomach contents, that *A. tropicalis tropicalis* on Marion Island fed mainly on Nototheniid fish, cephalopods and Euphausiid crustacea; 50 per cent of the female stomachs examined contained cephalopods. In contrast, Paulian (1964) for the same species from Ile Amsterdam stated that the food was mainly squid and penguins (*Eudyptes cristatus*), no trace of fish remains or crustacea being found in the 12 stomachs examined. The Falklands fur seal, *A. australis*, is said to feed largely on squid and *Munida*, while *A. tasmanicus* in Victoria eats crayfish, *Jasus* sp. and squid, and *A. doriferus* is said to feed on fish. Fur seals are probably rather general feeders as a rule, but *A. tropicalis gazella* has perhaps specialized for a diet of krill, which may account for the reduction in the post-canine dentition that distinguishes the southern from the northern form and, indeed, from all other members of the genus.

Besides food remains and the commonly occurring round worms, varying quantities of sand and shingle are often found in the stomachs. The amounts vary from a few isolated pebbles with a total weight of less than 5 g. to considerable aggregations of shingle weighing about 500 g. There is no constancy in size of the component stones but no pebble exceeding 3 cm. in diameter has been recorded, and mixtures of varying size are as commonly found as evenly graded material. The purpose of this shingle-eating habit, which has been described in many pinnipede species, both phocid and otariid, is not known. The traditional view among sealers is that the seals swallow the stones as ballast. Elliott (in Allen, 1880) suggested that the stones in the stomach of the northern fur seal serve, in their grinding together, to destroy some of the nematodes found in the stomach. Laws (1956) showed that in the elephant seal the swallowing of sand and stones was connected with fasting periods, and suggested that the material ingested served to allay hunger pangs. Hamilton (1934) pointed out that the function of the stones could well be multiple, and put forward the hypothesis that the stones might help to grind up the food.

None of these explanations seems entirely satisfactory. The concept that such highly specialized swimmers as seals need to adjust their buoyancy by swallowing ballast is not easily acceptable, and it would, moreover, require that the fattest, most blubbery animals should contain the greatest weight of stones, which is not the case. That the shingle or stones serve to destroy some of the nematodes is remotely possible, though these worms are very resistant to crushing and are observed to exist in an apparently uninjured condition side by side with sharp-edged rock fragments. The suggestion that the swallowed stones allay hunger pangs deserves more serious consideration, though one might suppose that animals which have developed a way of life involving long periods of fasting, as have most of the pinnipeds, would at the same time have accommodated themselves to tolerating empty stomachs without the necessity of swallowing indigestible material to satisfy hunger pangs. Furthermore, the amounts swallowed are generally so small in relation to the size of the stomach that it is hard to suppose that their effects can be considerable, though Elliott (loc. cit.) recorded a Steller's sea lion stomach containing 10 lb. (4.5 kg.) of "bowlders". That the occurrence of stones is more commonly associated with fasting than with feeding phases renders Hamilton's hypothesis, that the stones assist in the trituration of the food, less probable.

The present author's observations on both fur seals and elephant seals have convinced him that the pups, at any rate, frequently ingest stones accidentally. Fur seal pups and juveniles are often to be seen playing at the water's edge or in the shallows, picking up with their teeth any small portable objects such as pieces of driftwood, seaweed or pebbles that they can find. It seems quite likely that objects of a suitable size (and these would chiefly be pebbles) might be swallowed, the action being non-purposive. While this might explain the presence of some of the stones in the stomachs of young seals it will not serve for the adults, which are not seen to play in the manner described. The function, if any, of the stone-swallowing habit in seals still awaits a satisfactory explanation.

Drinking. On several occasions sub-adult and non-territorial adult bulls have been seen apparently drinking. It cannot be stated with certainty that the animals observed actually swallowed water, but in a typical case a bull in its wanderings behind the breeding beaches was seen to pause at a fresh water stream, lower his head, sniff at the water and then suck noisily, raising his head from time to time to look around. This form of behaviour sometimes lasted less than 10 seconds, when the bull made only one inspection of the water, but could last up to 4 minutes, which included several periods of rest. This activity has not been noted in other classes of seals, save in a modified form in pups which dip their noses into water but do not suck.

The significance of this is obscure. Lewis (1930) reported a bull *Arctocephalus doriferus* (*A. tasmanicus* ?) lapping up salt water, and Brown (1952) noted that a captive leopard seal drank quantities of salt water when placed in the sea. Irving and others (1935) observed that young harbour seals drank fresh water in captivity. Prosser (1950) pointed out that the urine of seals can be more concentrated than sea water, hence they should be capable of absorbing water from sea water and excreting the salts, but that marine mammals living on fish should be able to obtain ample supplies of water from their food alone. It is possible that fur seals when ashore have a critical water relationship due to losses from respiration and perhaps sweating, and thus might drink when ashore. However, as in South Georgia they are rarely observed to drink, and the harem bulls (the class presumably most in need of water) lack the opportunity to do so while holding territories, it is likely that this is not an essential part of the seals' behaviour. It may be that the actions observed amount to no more than rinsing the mouth.

The seals in South Georgia, as stated, suck at the water; they have never been observed to lap with the tongue.

D. VOCALIZATION

The almost indescribable hubbub that greets the ear of an observer approaching a fur seal rookery indicates the importance of vocalizations in the social economy of these animals. Despite this, the repertoire of the various classes is limited, at least in so far as individual calls can be distinguished by the human ear. The only sound common to bulls, cows and juveniles of both sexes is a low-pitched growl. The sound is hoarse and vibratory and consists of a series of expiratory vocalizations, each lasting about half a second and separated by intervals of about one second. This is heard most commonly from young seals—for example, when a sleeping juvenile is disturbed in the tussock or when a pup on the breeding beach is awakened by one of its fellows passing. Cows rarely growl and when they do so they produce only one or a few elements, rather than the long series produced by the juveniles. The growl of the adult bull is more resonant and lower-pitched. It is produced when the bull is in situations of stress and rarely consists of more than two or three elements; it frequently concludes a series of whimpers which constitute the commonest vocalization of this class.

Besides growling, the pups produce a loud and penetrating bleating or baaing sound. This is first heard soon after birth when it is produced in response to a special call from the mother, and is subsequently used when the pup is hungry or separated from its mother. Pups whose mothers are away on feeding excursions will spend long periods bleating indiscriminately at returning cows.

The normal call of the cow is similar to the bleat of the pup but of higher pitch and more even tone. The individual elements of the call are longer in duration, lasting more than a second, and are separated by intervals of rather more than half a second. This call is uttered by the cow when she becomes separated from her pup or before nursing it. Similar to this call is the peculiar vocalization made by the cow within a few minutes of giving birth to her pup (p. 56). This post-partum vocalization is the highest-pitched of all the seals' repertoires and the elements of the call are of long duration, exceeding two seconds, and of very even tone, approximating to a howl. This call is heard only in the immediate post-partum period but the vocalization of a cow returning to land after a feeding excursion is often similar to it, though not of the same intensity nor as long.

The voice of the harem bull is a most unexpected one from so large an animal. The sound, which for want of a better onomatopoeic description will be referred to here as "whimpering", is made with the mouth closed and appears to be produced by a series of abrupt expirations via the nasal passages, the back of the throat acting as a resonating chamber. The call is high-pitched, often as high as the normal bleat of the pup, but the pitch varies over a wider range than in any of the other vocalizations. The elements of whimpering are less than a quarter of a second long and are separated by equal intervals (úh—úh—úh—úh . . .). At high intensity the series is terminated by a loud nasal expiration accompanied by a forward lunge of the head and fore quarters in the direction of the stimulus eliciting the vocalization. Occasionally, this vocalization is made with the mouth slightly open; when this is so each element is succeeded by an oral expiration, the sound very roughly approximating to úh chff, úh chff, úh chff. . . While whimpering, the vibrissae are rotated from their usual 40° astern position to 10°–30° ahead (Fig. 16).

During the breeding season whimpering is heard only from the adult bulls and is produced by them in response to almost any stimulus which excites their greater awareness—for example, a mild threat from a neighbouring harem bull, a movement away from the harem area by one of the cows, or the approach of a human observer. It is perhaps unnecessary to emphasize that the whimper of fur seal bulls, though suggestive of a state of fear in more familiar animals, bears no such connotation in this species. Whimpering is, no doubt, part of the general territorial maintenance mechanism developed in adult bulls during the breeding season. It is heard less frequently as the season proceeds, although the classes of seal heard to whimper increase. A field note made on 31 January records that

Earlier in the season the noise [whimpering] was apparently made only by adult bulls, but now it is heard from bulls of all sizes, down to . . . bulls barely distinguishable in size from breeding cows. It is most commonly heard from three-year-olds encountered in the tussac.

When the rookery was visited on 14 May it was recorded that whimpering was rarely heard. Although young bulls were present on the beach territorial behaviour was scarcely in evidence.

Electromagnetic recordings were made of various vocalizations and it is hoped that these will eventually be analysed.

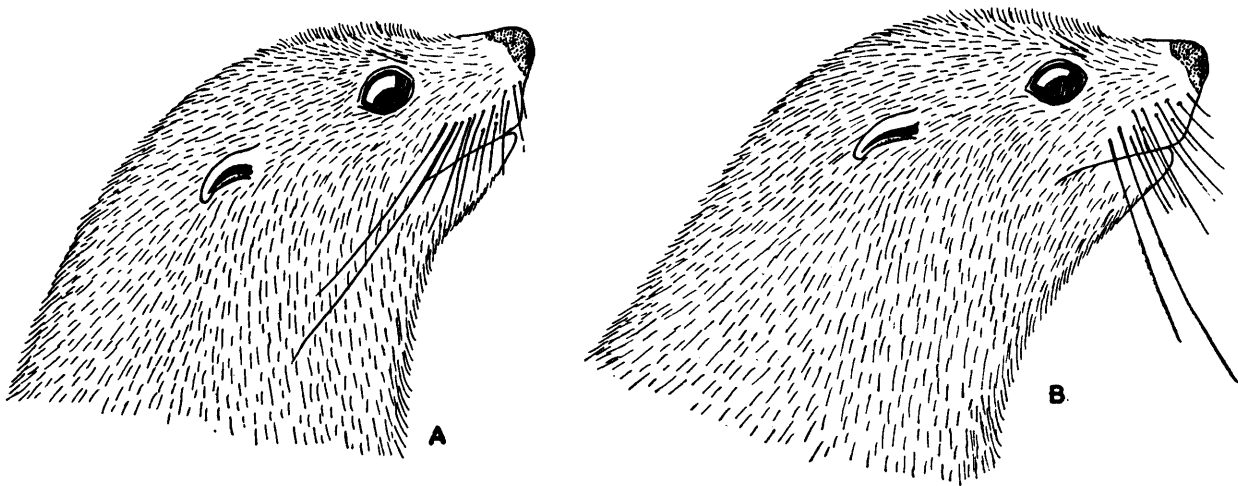


FIGURE 16
Profiles of an adult male fur seal.
A. At rest.
B. When "whimpering".

E. SENSORY EQUIPMENT

1. Hearing

In view of the wide range of sounds emitted by the fur seals, including such socially significant vocalizations as the whimper of the bulls or the duet between mother and new-born pup, it may safely be assumed that the sense of hearing plays an important part in orientating the seals to their environment.

Despite the diminutive size of the external ear the sense of hearing is acute though, in the absence of a well developed conch, it is probably not very directional. It is difficult to approach a sleeping fur seal (away from the din of the breeding beaches) without arousing it, a fact which has been recorded for other species. For *Callorhinus*, Elliott (in Allen, 1880) observed that

... such opportunity as I have had, gives me undoubted proof of the greatest keenness of hearing; for it is impossible to approach one, even when sound asleep; if you make any noise.

That a female seal can distinguish the voice of her pup from the hundreds of others which are present on a breeding beach indicates that the hearing is highly discriminatory, but there are no further data on this aspect.

It is not known what part hearing plays in the aquatic life of the fur seals. When swimming, the external auditory meatus is closed to prevent the ingress of water, but this would not necessarily mean that the animals were deaf when submerged as bone conduction would serve to convey sound waves to the inner ear. Pelagic sealers of the nineteenth century took elaborate precautions to approach seals in the water silently, and it may be assumed from this that the seals reacted strongly to noise. Fur seals, unlike some other pinnipeds, e.g. *Mirounga*, have not been heard to vocalize in the water, but it is possible that sounds produced when submerged serve to preserve the integrity of groups of seals when swimming together.

Outside the breeding season, when all classes of seals are more timid, even an adult bull can be scared into flight by clapping the hands sharply together. Fur seals in the Pribilof Islands are driven to the killing grounds by clapping a pair of scapulae together, and the rattling of pebbles in a tin can or bucket is the traditional way of driving the normally unresponsive elephant seal. An opportunity to see how seals respond to high noise levels was afforded when a helicopter flew low (about 15 m. (50 ft.)) above a breeding beach. With the exception of the youngest pups all the seals, including even the territory-holding harem bulls, deserted their positions and fled into the sea. This was the only occasion on which harem bulls were seen to desert their territories during the breeding season, other than as a result of territorial fighting. Other factors besides noise were, of course, involved in this incident; the down-draught from the rotor was sufficient to blow pieces of seaweed and small stones about the beach, and the approach of a large unfamiliar object from an unfamiliar direction may also have affected the seals, but it is likely that noise was the chief factor.

2. Vision

Vision is probably the primary receptive sense of the fur seal, at least for the part of its life associated with the land. One has only to watch a bull fur seal waiting his chance to come ashore on a crowded beach, bobbing up in the shallows and surveying the scene before making his dash up the beach, to realize the importance of sight to these creatures. Much of the social organization of the fur seals is based on visual stimuli, and the general decline of activity in the rookeries at nightfall is another indication of the importance of sight.

Eye injuries are common in fighting between males and, although one-eyed seals are often seen and appear to be at no disadvantage, seals blinded in both eyes have never been observed, which perhaps indicates that the loss of both eyes is fatal. If this is so, it is in strong contrast to many phocids of which healthy individuals lacking both eyes have often been observed (e.g. harbour seal (Scheffer and Slipp, 1944); elephant seal (personal observations and Sorensen, 1950)). Probably a fur seal deprived of both eyes could feed adequately, as do blinded phocids, but would be at great disadvantage when approaching land and when once ashore.

3. Olfaction

The olfactory mechanism in the fur seal is moderately well developed. The turbinal bones are large and complex and the olfactory lobes of the brain are well developed for a pinnipede. The only situation in which fur seals have been observed to make use of their olfactory sense is in the final stage of recognition of a pup by its mother (see p. 63).

During the breeding season the bulls give off a strong and characteristic odour. Like most smells it is virtually indescribable, but several observers have agreed that it is musky and sweetish. The source of the odour has not been detected. There are no obvious scent glands and the perineal region does not smell stronger than the rest of the body. The breath of the adult bulls is certainly pungent, but it is doubtful whether the characteristic odour is more highly concentrated about the mouth as it is here confused with the general halitosis from which all seals suffer after they have been ashore some time. Dorsal musculature from an adult bull tasted so strongly of "harem bull" that it was uneatable after cooking. Whether this odour serves any purpose, or is merely a by-product of the physiological changes associated with the male rut, is not known. It is worth noting, however, that the females are frequently brought into close contact with the bull's muzzle during the "whisker-snapping" reaction (see below), and that the threat lunges of the bulls are accompanied by violent expirations.

Hamilton (1956) suggested that the scent of male otariids could possibly serve as a direction indicator to the females at the time of the breeding haul-out. He rightly pointed out that though not particularly strong to human senses we have no means of knowing at what distance it is detectable to the seals. He compared the smell of *Arctocephalus australis* to that of a civet when pleasurably excited.

4. Tactile sense

No observations are available on this. The great development of the mystacial vibrissae, innervated from the second branch of the trigeminal, probably indicates that they have an important function in the life of the seals, though the experiments of Pearson (1962) on mice deprived of their vibrissae casts some doubt on this general supposition. The only observed use of the vibrissae has been in the "whisker-snapping" reaction between the cows and bulls, but it is likely that they play an important part in feeding.

Whisker snapping is commonly observed and is the normal response of the cow when molested by the harem bull. It consists of the cow making rapid lunges directed towards the muzzle of the bull, rarely touching his snout but generally contacting his vibrissae (Plate Vc). Each lunge is accompanied by a short expiratory pant or grunt. Whisker snapping has the effect of restraining the bull's activities; it is used, for example, to prevent a bull trampling over a suckling pup, or to deter a bull which is attempting to detain a reluctant cow. At high intensity the cow will make repeated lunges at the bull's muzzle or even bite at his chest, holding on and wrenching in the manner of fighting bulls. This last behaviour pattern is regarded as of a different origin from whisker snapping.

Whisker snapping is of very frequent occurrence in the course of territorial maintenance as the bull moves about his territory. Apart from its obvious function in keeping the bull from injuring the cow or

her pup, it may also serve to make the bull aware of oestrous cows in his harem as it brings the muzzle of the cow close to the bull's nose.

Advantage can be taken by the human observer of a bull's almost invariable response to whisker snapping. If a bull becomes too antagonistic it is a simple matter for an observer to check its advances by lightly striking or brushing the bases of its vibrissae with a pole. Violent blows delivered to the top or side of the head may have no effect whatever on an enraged bull, but in the present author's experience whisker tickling has invariably been successful.

The tactile sense of the soles of the flippers is probably well developed. The careful exploratory movements of the hind flippers, on being brought up to a rock in the course of locomotion across broken ground, indicates the possession of sensitive receptors. Fur seals react swiftly to a light touch on the flippers, less so on the fur.

F. GROOMING AND THE MOULT

Fur seals spend much of their time in grooming movements which constitute one of the major activities of the adults while ashore. The pelage is normally tended by scratching with the claws developed on the second, third and fourth digits of the pes. These claws, in the absence of other functional nails, may be regarded as specially preserved for toilet purposes and comparable to, for example, the syndactylous second and third digits of diprotodont marsupials.

When scratching, a seal supports itself on its fore flippers and one of its hind flippers and with the other hind flipper makes vigorous movements of small amplitude (rarely more than about 20 cm. even in large bulls) at a frequency of about five scratches a second. All parts of the body can be reached with one or other of the hind flippers with the exception of the rump and the posterior part of the ventral surface, but to reach some of the less easily accessible parts a seal will throw its body into remarkable contortions. Seals will also nibble at their coats with the incisors, females in particular often tending the region around the vulva in this way. Although scratching and nibbling constitute the major part of the grooming activities, seals will occasionally wipe their heads with a fore flipper, the preaxial edge of the flipper being used to stroke the head from the ears to the nose. It is believed that this motion is used to allay irritation of the eyes. No doubt in such circumstances the normal scratching action would be too vigorous.

The source of the stimulus which initiates grooming activity was not identified. Ectoparasites were not found in the pelage of specimens killed, although it is possible that some were present in the dense underfur. In connection with this lack of ectoparasites, it may be remarked that the elephant seals of South Georgia are free from infestation by the louse *Lepidophthirus macrorhini* which infests the same species at Macquarie Island (Murray, 1958). The common infestation with the barnacle *Lepas australis*, has already been commented on (p. 12).

Some, at least, of the grooming is directed at removing mud or other dirt from the coat; the cows are especially meticulous at this and the bulls least so, the bulls' coats becoming matted with filth towards the end of the breeding season. Young pups only occasionally engage in toilet activities.

Bathing by adult cows in the early part of the breeding season may also be considered with grooming. After the haul-out for breeding purposes in the spring, the cows normally stay on shore until after oestrus, some eight days after the birth of their pups. During this time, and especially if the weather is hot, they will enter the sea for brief periods and indulge in extensive and thorough washing. They dive in and out of the surf, never going more than a few yards from the water's edge, and from time to time one will float on its back stroking its belly with the fore flippers alternately. Meanwhile, the water around it soon becomes discoloured, and the operation undoubtedly serves to free the seal's ventral surface from much of the filth which it accumulates from the floor of the rookery. Harem bulls normally endeavour to prevent cows from leaving their territories, and the opportunity for these bathing parties usually occurs when two or more bulls are engaged in reproductive fighting. The primary cause of bathing activity may be a flight reaction to escape the mêlée of the bulls, the washing activity occurring when the females find themselves in the water. On the other hand, fights between bulls in inland territories do not result in concerted rushes of groups of cows further inland.

The moult of fur seals has been described by Rand (1956b) for *Arctocephalus pusillus*, and by Scheffer (1962) and Scheffer and Johnson (1963) for *Callorhinus ursinus*. In both of these species it is a protracted

process taking several weeks or even months, and is very similar to that of *A. tropicalis gazella*. Its onset is gradual and a distinct moulting line cannot be distinguished. The first moulting adult female was observed at Bird Island on 5 February and the first moulting male on 11 February. By the last week of February moulting was in full swing. Lack of observations during the winter prevented an accurate estimation of the duration of the moult. Scheffer found it lasted 4–5 months in *Callorhinus*, and this is probably true of the South Georgia seals also.

The hairs of the moulting animal are shed individually so that the pelage retains its thermal insulation and water-repellent characteristics which are, of course, essential with a moult of such long duration. Cows in full moult continue to feed their young and to return to the sea to find their own food. There appears to be no physiological crisis such as that which accompanies the moult in the elephant seal and some other phocids. The moult of the pup will be described in a later section (p. 63).

VI. SEXUAL BEHAVIOUR

A. ESTABLISHMENT OF HAREMS AND TERRITORIAL MAINTENANCE

It was not possible, during the period of observation, to arrive at Bird Island early enough to see the first haul-out of the harem bulls and the initial division of the beach into territories. It is known that in the first days of September some adult bulls are ashore, but it seems unlikely that they remain there until the start of the breeding season. By the beginning of December practically all the harem bulls have established their territories, though only about a third of the cows have arrived. The earliest cows arrive in about the middle of November and the bulls probably haul out about a week before this.

In the absence of direct observations on the haul-out of the main body of bulls, observations on less favoured beaches, where the haul-out is later, help to provide a picture of the pattern of division of the territories.

The limits of a bull's territory are determined by fighting with its neighbours. In general, a bull will try to maintain as great an area as it is able to, and when the population is sparse, as on the rock-platform type of beach, a single territory may have a radius of about 15 m.; usually, however, the greatest diameter is about 5 m. The limits of a territory are mostly marked by some sort of physical barrier, however slight. In rocky coves one or more sides may consist of rock faces or boulders, leaving only a limited perimeter to be defended. More usually, the barriers will consist of low ridges of rock or clumps of tussock; even a plank of drift-wood, offering no physical barrier to another bull, may serve as a territorial limit, emphasizing the importance of visual stimuli in territorial behaviour. On open beaches no such barriers exist, and territorial boundaries are defined by opposing bulls making continual excursions to the limits of their areas of influence and challenging each other (Plate IVe and f).

The first bulls to arrive are so widely spaced along the beaches that fighting is rare. However, as the population density increases, fighting becomes more common until the entire available beach is divided up into territories. This occurs long before the final total of bulls has hauled out, as the area which a bull endeavours to maintain is in nearly all cases far larger than that which he finally controls. Fresh arrivals, therefore, have to fight for positions on the beach. Typically, a new arrival from the sea patrols up and down in the shallows inspecting the beach for a favourable opportunity to make his dash ashore. He usually charges straight through the first rank of territories at the water's edge before having to come to grips with an established bull. Fights are not preceded by any elaborate threat display, and begin abruptly.

In fighting, the opponents face each other and make ponderous slashes at each other's necks with open mouths. If a blow strikes home, the bull will wrench and worry until his opponent's hide tears or he loses his grip. Most of the blows are aimed at, and received on, the chest and the sides of the neck, exactly the area which is protected by the bull's heavy mane. That this protection is effective is demonstrated by the number of bites which result in only a tuft of hair being pulled loose. Blows in this area rarely inflict more than superficial wounds, though serious gashes have been seen; in one case a large flap of skin was hanging loose exposing the musculature of the neck and the great vessels. From time to time, however, a bull will aim at the unprotected skin at the insertion of his opponent's flipper. Such blows, which entail reaching down and extending the neck, leave their deliverer open to bites on the back and are, therefore, made as quick lunges, without the ensuing wrenching and worrying that follow bites to the neck and shoulders.

Should neither of the opponents be prepared to give ground they will rest from time to time, their chests opposed and in contact and their heads on each other's shoulders. After resting, the contest is continued until one of the participants, usually the intruder, turns tail and makes off.

If, as usually happens, the vanquished bull is unable to find a passage clear of territories, he is compelled to fight his way to the sea or to the safety of the tussock behind the beach, and severe injuries are often received on the way. Any bull moving through a harem area attracts attention from all the neighbouring bulls and is assailed from all sides, but if the fleeing bull pauses to fight with one bull in particular the others will generally desist. The "all against one" rule applies particularly to animals moving up through a harem area from the sea, and, therefore, intruders attempting to establish a territory generally move inland as fast as possible. It may be remarked here that, because of this extra antagonism of harem bulls to arrivals from the sea, it is safer for a human observer to approach a territory from the shoreward side.

The majority of the fighting seen on breeding beaches is, however, not so intense as that directed against a fresh arrival. It consists of continual minor skirmishes between neighbouring bulls. The bulls approach the boundary between their territories whimpering (p. 48) and, on reaching it, challenge each other and make a few swift lunges which rarely connect. The engagement seldom lasts more than ten seconds and the bulls then turn inwards to their territories, facing away from each other in the "alert" position, their fore quarters raised from the ground and their muzzles lifted in the air (Plate Va). This position is maintained for a few minutes after which they retreat to the centre of their territories and either lie down or enter into engagements with other neighbours.

The result of the territorial fighting is to build up a hierarchy of dominance among the bulls. The most successful fighters will have territories on the beach near the water's edge but well above the high-water mark; next in order of success will be those which have territories higher up on the beach, a group which will be larger on the broader beaches and in the deeper coves. These two classes of harem bulls together control the majority of the breeding cows. However, on the overcrowded main breeding beaches of Bird Island a third class of bulls, those controlling territories in the tussock grass backing the beaches, is also of great importance to the cows. The tussock territories are well populated, particularly in the area of Freshwater Inlet where the beach is very narrow, and the harem bulls in this area are fully mature specimens similar to those which are seen controlling seaward territories in less densely populated areas. In general, however, the tussock bulls are younger or smaller than those on the beaches. The tussock territories dwindle inland until, far back from the sea and at considerable elevations, young six- or even five-year-old bulls are found maintaining territories perhaps each containing only a single cow.

In the other direction, towards the sea, can be found two more classes of bulls. Below the dominant seaward territories are bulls which maintain territories of only a few square feet of beach submerged except at low water, or even the top of an off-shore rock. These territories, which are often only large enough for the bull itself and without space for even a single cow, are usually occupied by six- and seven-year-old bulls, though older harem bulls which have been dislodged from territories farther up the beach are sometimes to be found in them.

In a class by themselves are the roving aquatic bulls. These are young bulls which swim up and down close in-shore near the principal breeding beaches. Although these bulls maintain no territory and hence have no cows, it sometimes happens that they are able to intercept and copulate with oestrous cows which have already copulated with their harem bulls and left the beach on a feeding excursion. It is unlikely that these copulations are successful, i.e. result in the transmission of genes from the aquatic bulls, as there is no reason to doubt the success of the earlier terrestrial copulations with the adult bulls. The aquatic copulations should perhaps be regarded as analogous to the play-fighting of the sub-adult bulls.

These various classes of sexually mature bulls form a hierarchy of dominance which may be expressed diagrammatically as shown on p. 54.

B. ARRIVAL OF THE COWS

The first cows arrive at the rookery in the second week of November, but the main body does not arrive till the end of the month. There seems to be very little variation in the time of arrival from year to year, as in the case of the northern fur seal. The cows themselves determine where they shall haul out to have their pups, and are influenced firstly by the presence of other cows, as they are highly gregarious, and secondly by the condition of the beach. They show a preference for dry shingle beaches, relatively sheltered

| Status | Territory |
|--------|-------------------------------------|
| 1st | seaward territories |
| 2nd | inland territories |
| 3rd | tussock territories |
| 4th | sea edge or inter-tidal territories |
| 5th | aquatic bulls |

from both sea and wind. Muddy stretches, or shingle with water running over it, are the last to be colonized and represent a compromise between suitability of the surface and the gregarious instinct of the cows. Cows readily settle down on bare rock, so the sparsity of population on the rock-platform type of beach must be attributed to some other factor, possibly an instinctive avoidance of beaches likely to suffer flooding in time of storm.

The bull makes no attempt to gather cows as do *Callorhinus* harem bulls, which may seize newly arrived females with their teeth and toss them into their territories (Kenyon, 1960), but he makes every endeavour to prevent a cow leaving once she has entered his territory. The bull does this by placing himself between the cow and the territory boundary whenever the cow makes an attempt to move, even if she is merely changing her position within the territory. Although a bull can deal effectively enough with a single cow, as soon as his harem increases his attentions are so often divided between one or another of his cows and threatening neighbours or intruders, that any cow which wishes to change her position on the beach can do so easily. Moreover, if the cow is determined to leave she generally manages to do so, and a bull will rarely leave his territory in pursuit. Normally, of course, the hostile reactions of neighbouring territory-holding bulls prevent pursuit, but when there are no neighbours—as, for example, at the back of a beach—the bull will follow a straying cow a short distance and then turn back. The bond of the territory was well demonstrated when a cow was captured for weighing. This cow was the sole member of a bull's harem, and when she had been crated and was being carried the bull stationed himself in the position which he would have occupied had the cow been leaving the territory in the normal manner. As the tide was out the crated cow was carried, for convenience, along the beach near the water's edge and, together with the attendant bull, passed four other territories without being molested. When she was deposited at her final destination some 25 m. from the original territory, the bull remained nearby in a state of agitation, whimpering continuously for about ten minutes. He then departed, despite the fact that no attempt was made to drive him off and that two crated cows were available (and crated cows are acceptable as harem members, as was amply demonstrated in the following days). It is noteworthy that the bull returned to his own territory by the most direct route through the tussock fringe, and not the roundabout way by which the crate had come.

Owing to the gregarious tendencies of the cows, harem groups containing only one or two cows are unstable and the cows tend to wander off. In the more favoured areas, harems of more than five cows will tend to grow rapidly, and population build-up in the colony as a whole will be patchy. The bulls concern

themselves only with acquiring territories, while the cows select pupping sites and the company of other cows. As in *Callorhinus* (Bartholomew and Hoel, 1953), mate selection does not seem to exist in the South Georgia fur seal.

C. INTERVAL BETWEEN ARRIVAL AND PARTURITION

The interval between the arrival of a cow from the sea and the date of her giving birth is difficult to determine directly, as it depends on recognizing an individual cow as a fresh arrival and being certain of identifying her subsequently when the pup is born. Some information is available from records of white-coated cows. These are conspicuous and are not likely to be overlooked, and once one has been seen it is a simple matter to check at regular intervals for the presence of a pup. Two white cows pupped one day after the first sighting, and two others after two days. The longest interval elapsing between haul-out and pupping was observed in the case of two cows confined in cages (p. 58-59). These went for 11 and 13 days from capture without giving birth. A post-mortem examination of one of them indicated that the animal was pregnant with a full-term foetus, and the external appearance of the other (which was not sacrificed) indicated the same. Without doubt the normal rhythm of haul-out and parturition had been disturbed by the stresses of capture and confinement, and these long intervals may be regarded as abnormal.

A more accurate estimate of the interval between haul-out and pupping can be obtained by comparing the rates of build-up of cow and pup populations in the rookery. In the early part of the breeding season, before the picture is complicated by post-parous cows leaving on feeding excursions, the cow and pup populations increase at about the same rate, although equivalent totals are separated by an interval of approximately two and a half days, a value which agrees well with the direct observations. Bartholomew and Hoel (1953) found that the interval in *Callorhinus* was about two days, but recorded an instance of a cow still wet from the sea giving birth.

D. BIRTH OF THE PUPS

Cows about to give birth tend to be somewhat restless and irritable, snapping at their neighbours and shuffling awkwardly with their flippers. There are no visible signs of labour, apart from this restlessness and occasional abdominal straining. The first indication of an impending birth is often the appearance of the membranes, or of the pup itself, at the cow's vulva. When giving birth, the cow lies prone with the hind flippers widely spread and from time to time turns the fore part of her body round to inspect the vulva, sniffing at it or stroking with a fore flipper. (Pregnant cows have been observed to stroke the abdomen in a similar way.) From the first appearance of the pup to its final emergence is rarely more than a few minutes and sometimes only a matter of seconds, the pup being ejected into the world by a single violent contraction. Head presentation is only slightly more common than breech presentation; the pup, as it lies in the uterus with its hind flippers folded forward under the tips of its backwardly-directed fore flippers, forms a smoothly contoured, torpedo-shaped package which will glide with equal facility in either direction. On two occasions cows were seen to assist with the birth by taking hold of the partially born pup and forcibly dragging it forth with their teeth, a habit noted also in the Cape fur seal (Rand, 1955) and the Californian sea lion (Slijper, 1956). It is normal for the cow to draw the pup towards her immediately after it has been born and nibble at the membranes still enveloping it (Plate VIb). As the membranes are sometimes intact or form a close investment over the muzzle of the pup, this is a habit of considerable survival value. Even so, dead pups are from time to time seen with their heads still enveloped in the foetal membranes and no other apparent cause of death. Apart from picking at the membranes the cow makes no attempt to clean the pup; washing with the tongue has never been observed (fur seals never groom the coat by licking it), though Paulian (1964) records that in *A. tropicalis tropicalis* on Ile Amsterdam the mother licks her pup clean after birth. As the cow draws the newly born pup towards her the umbilical cord is often broken; in about half the cases the cord remains intact and when the placenta is delivered, generally about 4-12 minutes after the birth of the pup, it remains attached to the pup until the cord is shed 2-3 days later. Details of the timing of five births are given in Table VII.

Rand (1955) recorded average durations of birth in the Cape fur seal as 11·2 minutes for head presentations and 60·6 minutes for breech presentations, but it should be noted that these figures include the first stage of labour. Although the Cape fur seal is significantly larger than the South Georgia fur seal, the ratio of pup-weight to mother-weight is about the same; Rand gives 5-10 per cent for the Cape fur seal,

TABLE VII
DURATION OF STAGES OF BIRTH
(in minutes)

| <i>From first appearance of pup to delivery</i> | <i>From delivery of pup to delivery of placenta</i> | <i>Total</i> | <i>Presentation</i> |
|---|---|--------------|---------------------|
| 5.0 | 8.0 | 13.0 | head |
| 7.0 | 4.0 | 11.0 | breech |
| 1.0 | 10.5 | 11.5 | head |
| < 0.5 | 6.0 | 6.0 | head |
| 2.5 | 7.0 | 9.5 | breech |

while in the South Georgia fur seal the percentages in three instances were 10.6 and 8.8 (female pups) and 7.8 (male pup), averaging 9.1 per cent.

The births are invariably attended by crowds of scavenging birds, sheathbills being the first on the scene, followed by skuas and sometimes even giant petrels when the placenta appears. The cows are very intolerant of the birds and snap at them continually. On one occasion a cow was seen to pick up with her teeth a placenta still joined to her pup by an intact cord and drag it under her body, thus removing it from a group of skuas which had been squabbling over its possession. Such a reaction may have important survival value; elephant seal cows are indifferent to birds molesting their young, and elephant pups have been seen with the gut completely removed via the umbilicus by skuas and giant petrels tugging at the cord (Plate VIa).

On no occasion were the South Georgia fur seal cows observed to eat the placenta or to chew the placenta or the cord. Rand states that Cape fur seal cows seldom devour the placenta, implying that they sometimes do, and van Door (in Slijper, 1956) recorded a Californian sea lion in a zoo eating part of the membrane attached to the placenta. Observations on captive animals are perhaps not very reliable in this respect, and Rand's observations may apply only to a few aberrant individuals. There appear to be no records of pinnipeds consuming the entire after-birth in the manner of the fissipede carnivora, nor are there any accounts of comparable maternal tending of the young. After giving birth to her pup the pinnipede mother generally ignores it until the first feed, the minor attention of picking at adhering membranes or drawing the pup from the vulva shown by some otariids (e.g. Cape fur seal, South Georgia fur seal, Californian sea lion) being the extent of maternal tending in this group.

The pup is active from the time of birth, and immediately begins to search for food and to call to its mother. Although the cow tolerates the nuzzling of the pup she will not as a rule feed it for at least half an hour after birth and often much longer; meanwhile, she exchanges cries with her pup. This duet between the cow and her pup, which is terminated only when the cow permits the young one to suckle, is one of the most characteristic sounds of the breeding beaches. Although the pup's cry is similar to that which it uses subsequently when seeking food until weaning, the answering notes of the cow at this stage are distinctive, being higher and more even than the call given later when she returns from the sea to feed her pup. It is at this stage that the vocal bond is established between mother and offspring, and thereafter the initial recognition between them is by voice, though smell is the final deciding factor. The period immediately after birth thus represents a critical stage in the mother-pup relationship, and if disturbed at this time the cow may fail to recognize her pup subsequently. It is probable that the majority of the occasional starvelings that are seen wandering about the rookeries plaintively calling for food are pups which owing to some disturbance, such as involvement in a territorial battle, became separated from their mothers soon after birth and thus failed to establish the vocal bond. Similarly, the rare sight of two pups being suckled by one mother (two such occasions are on record for Bird Island; Plate Ve) may possibly be the result of confusion on the breeding beach whereby two pups established bonds simultaneously with a single cow. The possibility of genuine twinning exists but it is thought to be unlikely.

E. OESTRUS AND COPULATION

There are no direct observations on marked females of the interval between parturition and copulation. It is known from many instances, however, that cows leave the beaches for the sea on the day of copulation or the day succeeding it. On this basis, i.e. the departure of the cow, the interval determined from two white cows is eight days. Bartholomew and Hoel (1953), using a statistical model of considerable precision, came to the conclusion that the interval between the first arrival and first departure of the *Callorhinus* cow was 10 days and that, as in the case of *Arctocephalus tropicalis*, the interval between arrival and birth is 2 days. Rand (1955) found an interval of 5·6 days in *A. pusillus*.

There are no overt signs of oestrus in the female. The vulva and perineal region are swollen and suffused with blood from the time of parturition and no changes at the approach of oestrus have been noticed. No special behaviour is apparent prior to actual copulatory behaviour. Bulls identify oestrus cows by their odour and, as already suggested (p. 51), the whisker-snapping reaction serves to make a bull aware of oestrous cows in his harem. Sniffs to the nose are often followed by a similar investigation of the vulva. The cow, if receptive, responds by lying prone with the perineal region exposed and the hind flippers widely spread. The bull mounts the cow and straddles her with his fore flippers, the cow's head appearing below the bull's chest. The bull makes vigorous pelvic thrusts but the cow, so far as can be seen, remains passive (Plate Vb).

The attitude of the bull during copulation is nearly identical with the normal "alert" position. A bull whilst copulating can issue a vocal challenge and successfully repel an intruder. The close similarity between the copulatory and normal threat attitudes of the bull ensures that the bull remains unmolested while copulating. No bull was ever observed to be attacked while copulating.

The animals remain *in coitu* for from 2·5–6 minutes; towards the end of this period the cow frequently turns her head and nibbles at the chest of the bull with her teeth. Rand (1955) ascribes this movement in the Cape fur seal to the cow trying to free herself after copulation; in the South Georgia fur seal it does not seem to be specially connected with escape movements by the cow. After the bull has dismounted the cow usually remains lying where she is, but may shuffle off to another part of the territory; the bull usually engages in some form of territorial maintenance.

This is the usual form of copulation. Bonner (1958a) has described a single incidence of ventro-ventral copulation. Rand (1955) says that in *A. pusillus* dorso-ventral copulation is the rule, but that ventro-ventral copulation may occur if the cow is lying in a difficult position. In the incident referred to by Bonner there appeared to be no particular reason why ventro-dorsal copulation should not have taken place, as the pair were on a smooth shingle beach. Unsuccessful attempts at copulation are seen fairly frequently. One male was watched for 20 minutes endeavouring to copulate with a female which, while perfectly passive, did not make her vulva accessible to the male so that its efforts at intromission were futile. On another occasion a bull attempted to copulate with a cow that was lying on her side. The bull in this case was not supporting himself on his fore flippers but lying on the cow with his full weight. After 5 minutes the bull mouthed the female and growled at her. The cow remained lying on her side and, after a few more minutes, the bull desisted.

These two instances (and many similar which have been observed at Bird Island) are remarkable in that the cows, while presumably not oestrous as they are not receptive to the male, are not overtly antagonistic, and lie passive without attempting to drive the male away. Such behaviour seems to be rare in mammals outside the primates. The copulations of the aquatic bulls referred to above (p. 53) should be mentioned here. A field note from 1 December is typical:

One of the females that escaped to sea during the fighting [between a harem bull and an intruder from the sea] has been seized by a male in the sea. He holds her beneath him and it is possible to see a flipper over her side. Pelvic thrusts not visible but strong pelvic flexion by the male. Cow and bull part, bull makes a roll. Cow returns to him and they swim together, rolling in the water. Male now straddles female in the shallows.

On such occasions it is not, of course, possible to determine if intromission has taken place as observation is handicapped by the water but, bearing in mind the ability of phocids to copulate in the water, it seems likely. Certainly, the embracing of the female by the bull's fore flipper is a very characteristic copulatory attitude in phocids. However, even if intromission takes place it is unlikely that these aquatic copulations result in fertilization of the cow. It would be rare for an oestrus female to escape fertilization by a harem bull, owing to the ceaseless sexual activity of the harem bulls.

F. FEEDING AND GROWTH OF THE PUP

The new-born pup usually begins to feed about half an hour after birth. At first, it is not very successful at finding the nipple, and the cow does not direct it as described in some other seals. Vague backward-sweeping movements of the fore flipper may be made by the cow, but these as often as not push the searching pup away from its objective. When feeding the pup, the cow lies on her side so as to expose the nipples which are strongly erected and stand clear of the general contour of the body. The pup grips the nipple firmly with the transversely-notched incisors which are already erupted at birth, and judging from the cow's reactions this occasionally causes some discomfort. While sucking, the pup may from time to time change the position of its body without releasing its grip on the nipple (Plate Vd).

A sample of milk was obtained from the distended stomach of a pup which was shot while sucking. Analysis revealed a fat content of 26.4 per cent, which although much higher than that of terrestrial mammals (e.g. man 3.3 per cent, cow 3.7 per cent), is considerably lower than that of phocid seals. Sivertsen (1941) found 43 per cent fat in *Phoca groenlandica* (= *Pagophilus groenlandicus*), and Amoroso and Matthews (1951) 52 per cent in *Halichoerus grypus*. The difference is correlated with the much longer suckling period of the otariid seals. The milk of *Arctocephalus pusillus*, which suckles its young for an even longer period than *A. tropicalis gazella*, contains less fat, i.e. only 18.6 per cent (Rand, 1956b). The protein value for the milk of the South Georgia fur seal was determined to be 22.4 per cent, a very high value—nearly twice as great as that recorded for other seals (Table VIII). This determination could with advantage be checked on other samples.

TABLE VIII
COMPOSITION OF MILKS OF VARIOUS PINNIPEDES
(in g. per 1,000 g. of milk)

| Constituent | <i>A. tropicalis gazella</i> | <i>A. pusillus</i> | <i>Pagophilus groenlandica</i> I II | | <i>Halichoerus grypus</i> | <i>Cystophora cristata</i> |
|-------------|------------------------------|--------------------|--|-------|---------------------------|----------------------------|
| Water | 511.0 | — | 453.3 | 437.9 | — | 498.5 |
| Fat | 264.0 | 186.0 | 426.5 | 428.2 | 522.0 | 404.3 |
| Protein | 224.0 | 100.0 | 104.5 | 119.8 | 112.0 | 66.5 |
| Sugar | — | — | 0.0 | 0.0 | 26.0 | 0.0 |
| Ash | 6.0 | 8.6 | 8.00 | 9.14 | 7.0 | 8.64 |

Sources—*A. tropicalis gazella*: original
A. pusillus: Rand, 1956.
P. groenlandica: Sivertsen, 1941.
C. cristata: Sivertsen, 1941.
H. grypus: Amoroso and Matthews, 1951.

During the interval between birth and the first departure of the mother, suckling periods alternate with periods of rest or minor activity. In this time the birth weight, which is highly variable, increases by 15–44 per cent and the mother loses weight correspondingly. Fig. 17 compares the weights of mother and pup. Not all the loss of weight by the mother is accounted for by the production of milk to feed the pup; some at least is required for her own metabolic processes.

In an attempt to determine the magnitude of the weight changes, a series of newly hauled-out female fur seals was captured and confined in wooden crates (Bonner and Vaughan, 1962). The crates and cows were weighed daily and their weight changes recorded. The weighings were not of high accuracy as the tare of the cage was about half the weight of the contained animal, and strong breezes often made it impossible to obtain a steady reading from the spring balance used. Nevertheless, the general trend indicated by the weighings is consistent and reasonably reliable. Pups were weighed by putting them in a sack and using a smaller spring balance. The growth of three male pups is shown in Fig. 18.

The experiment was not very successful. Of the four cows captured only one produced a pup. The first captured was released after 3 days' confinement. Two others were kept for 11 and 13 days without

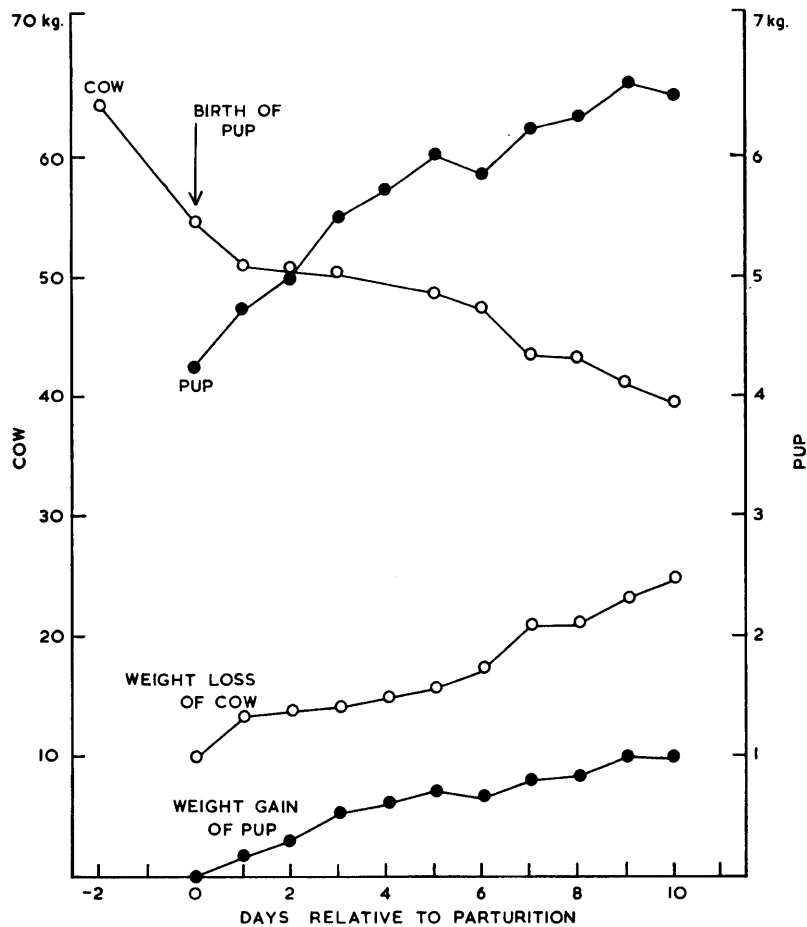


FIGURE 17

Weight changes of a caged cow (specimen 3) and her pup.

producing pups, although the normal interval between haul-out and parturition is 2 days (p. 55). One of these animals was sacrificed and the pregnancy confirmed by dissection. The foetus showed no sign of life and was thought to have been dead before the mother was shot. It was assumed that conditions were similar for the other cow. The remaining cow, specimen 3, produced a male pup after 2 days' confinement and it is on this specimen that the results are based. It is worth noting that all the cows apparently settled down extremely well in their cages (about 150 cm. \times 75 cm. \times 75 cm.). One of them (specimen 4) was of a rather nervous disposition and was disturbed by the attentions of a young adult bull which adopted the caged animals as a harem group for the duration of the experiment, but this disturbance was judged to be no greater than that often seen in normal harem groups.

Table IX and Fig. 19 show the daily weights of the cows kept in captivity. In each case, a sharp initial loss of weight was followed by a steady decline; it was greatest in specimen 3 which had a pup to feed. For the two cows which failed to produce pups the average loss of weight was 0.88 kg. per day. It may be assumed that this represents a normal loss for basal metabolism, and that the parturient specimen would have lost weight at the same rate had she not produced a pup. For the period between the birth of her pup and her release (11 days) this should have amounted to about 9.7 kg., but the actual weight-loss was 14.8 kg. and the difference, 5.1 kg., may be taken as the loss of weight consequent on milk production. In the same period the pup gained 2.3 kg., so that the efficiency of the transfer could be roughly estimated at about 45 per cent.

After oestrus and copulation the post-parturient cow abandons her pup and goes to sea on a feeding expedition. Thereafter, until weaning, maternal absence and attendance alternate. In one instance, a careful watch was kept on a white cow and her pup for a period of 90 days following birth. The cow was

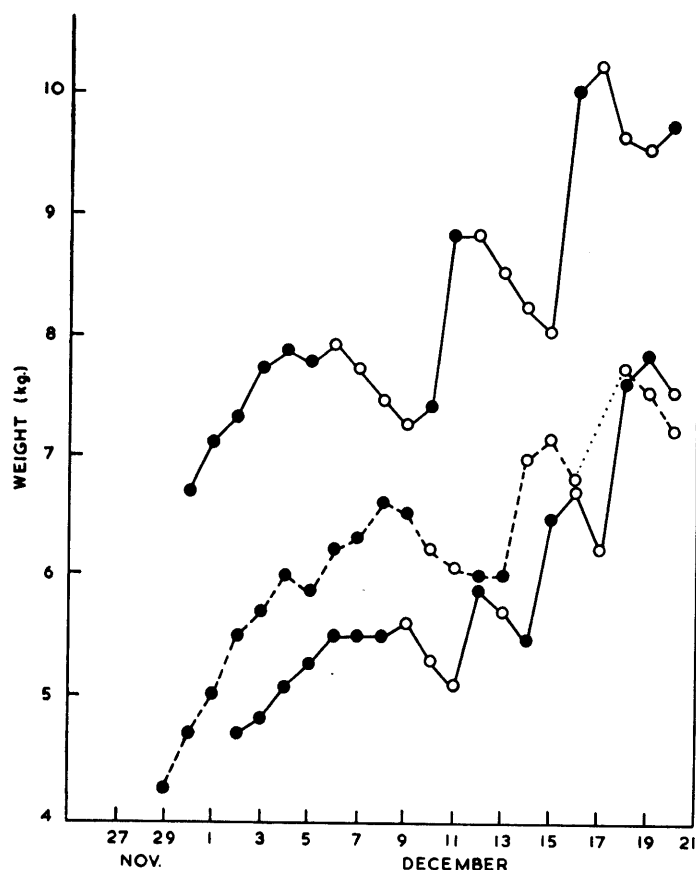


FIGURE 18

Growth of three male pups from birth.

- Weighings when the pup's mother was seen to be present.
- Other weighings.

conspicuous on the beach and was unlikely to have gone unnoticed when ashore, but the pup, being black, was more difficult to locate and it was frequently impossible to find it for weighing. Nevertheless, sufficient weighings were made to illustrate the pattern of the pup's growth (Table X). These showed that the general increase in weight was made up of a series of very sharp rises, associated with the return of the cow from foraging expeditions, each followed by a gradual decline, associated with the absence of the cow and caused by the utilization and excretion of the milk meals received. The record of the cow's attendance and the weight changes of her pup are given in Fig. 20.

For the 90 days of observation the cow was in attendance for a total of 40, i.e. about half the time. The duration of the periods of attendance remained fairly constant, averaging almost exactly 3 days. The periods of absence, on the other hand, increased from about 3 days for the first 4 weeks after the initial departure of the cow, to more than twice as long at the end of the period of observation. Bartholomew and Hoel (1953) found in *Callorhinus* that the duration of the cow's first trip to sea was 5 days and that the second and subsequent trips lasted 8 days; the duration of the stay ashore was 2 days or less.

The weight change of the pup on the return of the female is dramatic. Consecutive weighings made on days 48 and 49 showed an increase of 2.6 kg., i.e. 33 per cent in just over 24 hours. Rand (1956b) recorded a 20 per cent increase in an *Arctocephalus pusillus* pup, and concluded that even greater weight changes can take place when the herd is undisturbed. In the South Georgia fur seal the average gain in weight on the return of the cow amounted to 27.0 per cent. This is, of course, a measure of the amount of milk taken in, and a large part of the weight loss following the departure of the mother is caused by the elimination of water (apparently mostly in the faeces, which are very liquid) from this milk.

For the first 3 months of the pup's life (excluding the first 10 days when the mother is constantly

TABLE IX
DAILY WEIGHT CHANGES (KG.) OF THREE ADULT COWS
CONFINED IN CAGES

| Day | Specimen | | |
|-----|----------|-------|-------|
| | 2 | 3 | 4 |
| 1 | 53.4 | 64.1 | 57.0 |
| 2 | — | — | — |
| 3 | — | 54.4* | 51.5 |
| 4 | 48.4 | 50.9 | 50.5 |
| 5 | 46.9 | 50.6 | 51.0 |
| 6 | 47.4 | 50.1 | — |
| 7 | — | — | 50.0 |
| 8 | 46.4 | 48.6 | 49.0 |
| 9 | 46.4 | 47.3 | 46.5† |
| 10 | 44.4 | 43.4 | 48.0† |
| 11 | 43.9 | 43.3 | 45.0 |
| 12 | 43.4 | 41.0 | — |
| 13 | 42.4 | 39.6 | — |

* Specimen 3 produced a 4.3-kg. male pup prior to this weighing.

† Reading of doubtful accuracy.

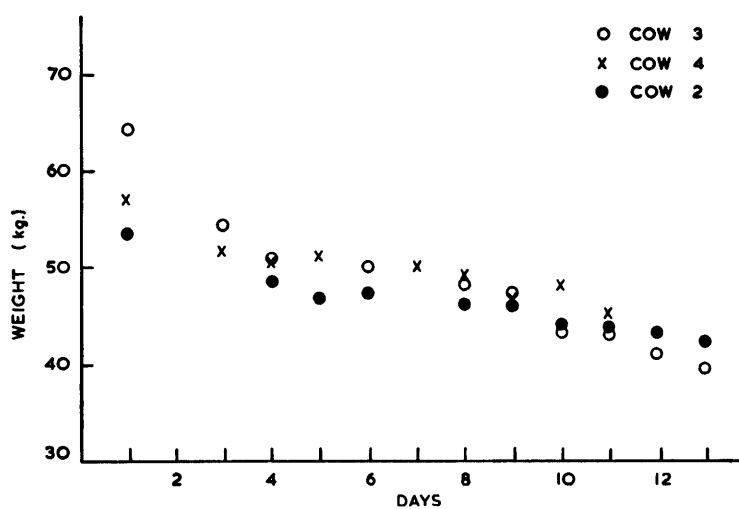


FIGURE 19
Weight changes of three caged cows.

TABLE X
WEIGHT CHANGES (KG.) IN PUPS

| Age in days | Males | | | Female |
|-------------|-------|-----|-----|--------|
| | 1 | 2 | 3 | |
| 1 | 6.7 | 4.3 | 4.1 | 5.6 |
| 2 | 7.1 | 4.7 | 4.8 | 6.1 |
| 3 | 7.3 | 5.0 | 5.1 | 6.0 |
| 4 | 7.7 | 5.5 | 5.3 | 6.3 |
| 5 | 7.9 | 5.7 | 5.5 | — |
| 6 | 7.8 | 6.0 | 5.5 | 6.7 |
| 7 | 7.9 | 5.9 | 5.5 | 6.7 |
| 8 | 7.7 | 6.2 | 5.6 | — |
| 9 | 7.5 | 6.3 | 5.3 | — |
| 10 | 7.3 | 6.6 | 5.1 | — |
| 11 | 7.0 | 6.5 | 5.9 | — |
| 12 | 8.8 | 6.2 | 5.7 | — |
| 13 | 8.8 | 6.1 | 5.5 | — |
| 14 | 8.5 | 6.0 | 6.5 | 7.6 |
| 15 | 8.2 | 6.0 | 6.7 | — |
| 16 | 8.0 | 7.0 | 6.2 | — |
| 17 | 10.0 | 7.1 | 7.6 | — |
| 18 | 10.2 | 6.8 | 7.8 | — |
| 19 | 9.6 | — | 7.5 | 8.2 |
| 20 | 9.5 | 7.7 | — | 8.2 |
| 21 | 9.7 | 7.5 | — | — |
| 22 | — | 7.2 | — | — |
| 23 | — | — | — | 8.3 |
| 53 | 12.2 | — | — | — |

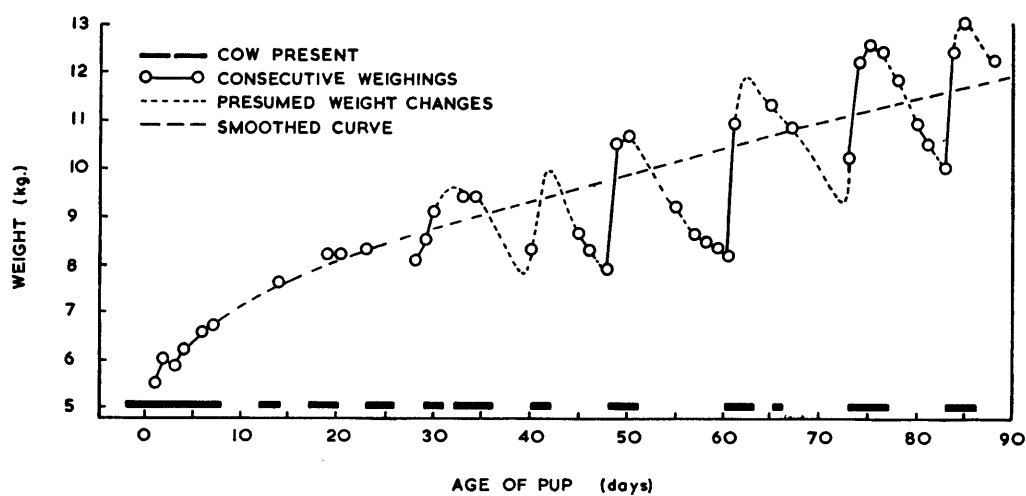


FIGURE 20

Attendance of the cow and growth of the pup.

present and the pup grows faster) its growth follows an almost linear curve, its weight increasing by 0.07 kg. per day. Rand found that in *A. pusillus* the pups' weight on the 7th day was doubled by the 84th day. The same is approximately true for *A. tropicalis gazella*, in which the birth weight is increased by 50 per cent in 25 days and doubled in 70 days. This may be compared with the elephant seal in which Laws (1953) found the corresponding ages to be 7 and 11 days, respectively.

The moult of the pup commences when it is between 50 and 60 days old, and hairs commence to loosen on the top of the head. By 70 days the moult is complete on the head and has started along the middle of the back and on the rump. At 80 days the back is free from the black puppy coat, and at 90 days the new coat is complete. Rand found that the onset of the moult in *A. pusillus* was at 60–65 days after birth, and that about 28–35 days were required to obtain the new coat.

No observations on marked animals are available to indicate the length of the lactation period. Lactating females are commonly seen at the beginning of March but there are none left by the middle of May, so lactation probably lasts about 100 days. Rand (1955) showed that lactation in *A. pusillus* may last till the birth of the next pup (or even beyond it if the cow loses her new pup), but this species is resident at its breeding grounds throughout the year.

The behaviour of the pup changes during the second stage of lactation, i.e. after the initial departure of the cow. Prior to this the cow normally stays within the territory of her harem bull or moves to adjacent harems only, usually remaining on the beach, and her pup stays near her. After the cow's departure, however, the pup tends to roam about, moving from territory to territory and even leaving the breeding area altogether. As the pup becomes hungry it begins to bleat for food and even to solicit strange cows to feed it, but it is unlikely that these attempts are ever successful. Cows bite savagely at strange pups that approach them and, because of this, the pups awaiting the return of their mothers tend to form themselves into small companies ("pods") at the back or landward side of the breeding beaches, especially where these are hemmed in by cliffs. Earlier in the season these pods show little activity, the members simply sleeping together, but the young males occasionally indulge in a little play-fighting. The pups at this stage show a preference for lying in contact with as much surface as possible, and assemble in rock crevices or small gullies. During the tagging operations it sometimes happens that seven or eight pups can be successively dragged out of a crevice barely wide enough to admit one of them. No doubt the pups receive some advantage from the mutual heat generated by lying together in groups, though no extra tendency to huddle was noticed in severe weather (Plate Vf).

As the pups grow older they become more adventurous. Water exerts a strong attraction for them and any puddle or streamlet is soon surrounded by pups. By the first week in January the older pups are already venturing into the sea, but they do not swim competently until about the beginning of March when the moult is complete.

On returning from a feeding excursion a cow will haul out in the vicinity of the beach on which she left her pup and will begin to call to it, often while still in the shallows. She advances up the beach, pausing to call at intervals of a few metres. Any hungry pups in the locality will answer, but all except her own pup are driven away or ignored. Periods of up to half an hour may elapse before her own pup answers; the cow moves towards it, confirming its identification by sniffing. The pup solicits for milk at once, but at the beginning of the season the cow will rarely feed it on the beach, as the bulls there are constantly scuffling and the cows show adverse reactions to newcomers. Instead, she leads it to the back of the beach or into the tussock, where she carefully selects a site before lying down and letting the pup feed.

This tendency of returning cows to feed their pups behind the beaches, particularly in the tussock, causes a gradual shift of population inland as the season progresses. Cows may travel considerable distances inland and ascend to a height of about 30 m. (100 ft.). In places where seals are numerous, the tops of the tussock clumps become flattened by nursing seals settling down on them to feed their pups (Plate IIIb).

G. BREAK-UP OF THE HAREM STRUCTURE

The rigid patterns of territorial maintenance and aggressiveness to other bulls, shown by the harem bulls, decline steadily as the breeding season passes. The bulls become more prone to move from their territories when scared, and apparently sometimes move spontaneously. In mid-January, one bull was noted to occupy three different territories in the course of a week. The nursing females tend to suckle their pups

away from the harem areas, often in the tussock, and this reduces the number of cows present in the original territories. Some of the harem bulls also retreat into the tussock, following the drift of the nursing females, while others stay on the beaches with the remaining cows. By the end of the second week in January there is a noticeable fall-off in the number of harem bulls present and in the number of cows in organized harems, though the total number of cows ashore remains much the same as at the height of the breeding season (Fig. 21).

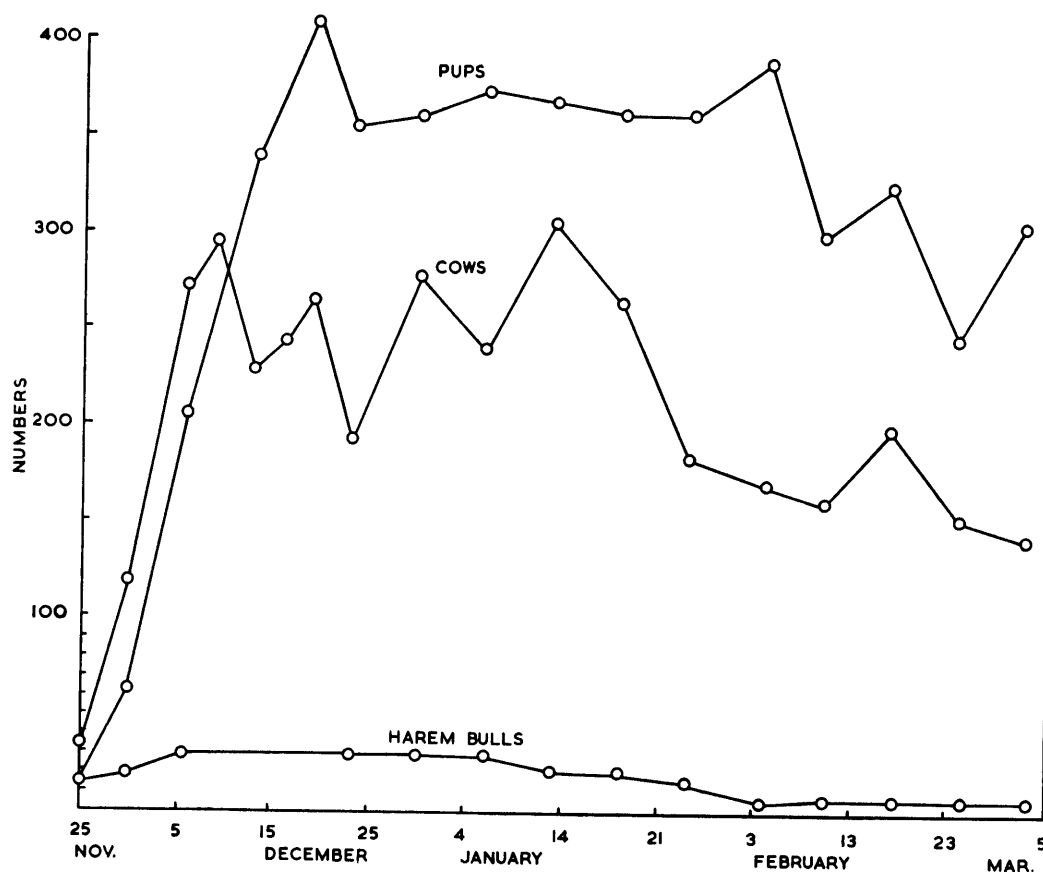


FIGURE 21

Population changes in Area 6, 1958-59.

The original owners of beach territories are gradually replaced by younger bulls which have taken no active part in territorial behaviour earlier in the season. No definite data are available concerning the period spent continuously ashore by the harem bulls, nor is it known whether the first departure of a harem bull from its territory is the final move or the preliminary to a short swimming or feeding excursion. Evidence collected by P. A. Cordall (private communication), to whom the author is indebted for many of the observations in this section, indicates that the latter may be the case. Cordall writes:

On 14th January [1959] as I walked along the shore of FWBW a harem bull about 20 yards ahead of me left his harem, entered the sea and slowly corkscrewed his way into the middle of the bay where I lost him. He left 7 cows and 3 pups on the beach. The following morning One-eye [another bull] was in charge here, vigorously defending his harem against all comers. In the evening One-eye was gone and a much larger bull than he was in possession. I cannot say whether or not he was the original owner but his reactions to my approach were those of a bull well used to our comings and goings. One-eye at this time was on "Stinker Cape"* lordling it over a single cow.

By mid-February the number of obviously mature bulls on the rookery begins to increase again, and the bulls which make up this increase are fat animals, with none of the loose folds of skin characteristic of the old bulls still keeping harems. Presumably, they are animals which have returned to shore after a feeding period at sea. Some of the returning animals merely lie about on the beach, but others oust younger

* Unofficial place-name.

bulls from the harems which they have acquired. Cordall reports that one bull returned to its harem (territory ?) after an absence of about 2 weeks. The new arrivals soon begin to moult, the first observation of this being on 11 February.

By the beginning of March, many harem groups are composed of young bulls with collections of nursing cows interspersed with juvenile females—both yearlings (i.e. about 15 months old) and two-year-olds. It is not known where these virgin females are impregnated, nor whether they are served by the young bulls in whose harem groups they are to be found. The number of juvenile females ashore represents only a small proportion of the class.

No observations are available for April, but in the middle of May the small number of adult bulls which remain ashore tend to behave in a territorial manner, spacing themselves out from their fellows on the beach. However, there are no harems as, by this time, all the breeding females have departed. It is probable that adult male fur seals, whenever ashore, will shun the company of their fellows and thus assume a territorial distribution, though this may have no permanent significance.

VII. BEHAVIOUR OF THE JUVENILES

JUVENILE seals are conspicuous throughout the season in the tussock areas behind the breeding beaches, and on neighbouring beaches. The majority of them are males. This is partly accounted for by the longer period required for the males to attain sexual maturity but, nevertheless, yearling and two-year-old females are definitely under-represented ashore. No adequate counts of the sex ratio of the juveniles ashore have been made, as it is impossible to sex the seals without capturing and examining them individually. Juvenile specimens killed included seventeen males and three females, but of the latter two were specially selected for killing after their sex had been determined.

Unlike *Callorhinus*, there is no tendency for the bachelor males of the South Georgia fur seals to congregate in large numbers at high density on particular beaches fringing the breeding areas. On the contrary, the seals seem to avoid each other's company, lying separately on the sward or cradled on the flattened head of a large tussock.

The harem bulls are intolerant of juveniles in their territories, and the younger seals gain access to the tussock areas mostly along well-marked corridors through the breeding territories. These corridors frequently follow minor water courses, as in Area 2 (Plate IIIa), where a temporary stream runs over the shingle of the beach after heavy rainfall. The small river which emerges in Freshwater Inlet is another important road to the interior. It is not certain whether these corridors are left free of harems because of the traffic of the juveniles (and a number of spare adult bulls), or whether they are used by the juveniles because they are unsuitable for breeding (as is clearly the case with the Freshwater Inlet river) and therefore empty. On densely populated beaches, such as Areas 2, 4 and 5, they are the only places where it is possible for a seal to land and cross the beach without interference from the harem bulls.

The juveniles tend to follow the stream beds inland, avoiding the very heavy going over the hummocky tussock, and may reach considerable elevations in the course of their wanderings. In the valley behind Freshwater Inlet they have been found at an altitude of about 90 m. (290 ft.). Those found inland are mostly seen sleeping, but they rouse readily at the approach of an observer. Occasionally, a pair are to be seen play-fighting or chasing each other across the tussock. Inland pools formed by damming of streams and the large pond on the headland between Jordan Cove and Ebermann Bay are always tenanted by numbers of young seals, and these display considerably more activity than those elsewhere.

Juveniles also congregate on the half-tide rocks fringing the breeding beaches (for example, in Area 2 and on the extra beaches), and many are to be seen playing in the shallows just off-shore.

It was not practicable to maintain continuous observation of the juveniles, but casual observations on white specimens indicated that they remain ashore for up to three days, at least. Juveniles killed ashore rarely contain the remains of recent meals in their stomachs. Examination of faeces indicated that fish forms an important part of the diet, and it may be assumed that they are feeding in fairly shallow water.

Most of the fur seals seen by casual observers away from the breeding areas are juveniles, because of the greater tendency of this class to wander. The seal taken in Smaaland Cove in 1915 was a young male, as was the animal photographed in the Bay of Isles in 1955 (Bonner, 1958a), and there are numerous records of young fur seals at Grytviken. So far as is known, apart from Cooper Bay and the other possible breeding

sites discussed earlier (p. 37), there are no records of adult fur seals being seen ashore other than at established breeding colonies. The tendency for juveniles to disperse more widely than the adults is not, of course, confined to fur seals.

VIII. POPULATION STUDIES

1. *Census area*

A. THE CENSUSES

It is unlikely that the number of fur seals in the South Georgia colonies in any particular year will ever be counted accurately. This is not only because the numbers involved are too great to handle precisely, but also because the various classes of seals are never all available for counting (i.e. hauled out on land) at the same time. The present study of population has been based on annual censuses of the pups, which make up about 25 per cent of the total. On this basis the herd, or herds, on Bird Island in the 1961–62 census (the last for which the author was responsible) numbered about 40,000 individuals.

As mentioned on p. 32, Jordan Cove and the neighbouring coastline were divided up into a number of units and the counts were based on these. In the early part of the season, counting is a relatively simple task. The observer takes up a vantage point on each section of beach and checks off the seals one by one on a mechanical hand tally counter. The use of hand tallies speeds up the process of counting very considerably and prevents the somewhat auto-hypnotic effect of counting verbally large numbers of similar objects. Tallies are not, of course, infallible and it was found that some tallies wore out quite rapidly and failed to register certain digits. Properly used and maintained, however, they represent a valuable aid. The total score of seals for each section was entered in a field notebook and later transferred to a permanent register.

Harem bulls, cows and pups were scored separately. A harem bull may be defined as an adult male holding territory containing one or more breeding females. However, this definition was extended in some later counts, to include any adult males which occupied positions on the breeding beach early in the season and appeared likely to acquire and retain breeding females subsequently. The other two classes are self explanatory, though undoubtedly on certain beaches a small proportion (probably less than 0.5 per cent) of the animals counted as cows were juvenile males.

This simple and direct method was perfectly adequate until cows began to arrive in large numbers and produce pups. The counting was then complicated not only by the increase in numbers to be counted but also by the very considerable difficulty of moving about the densely populated beaches. On certain beaches, Area 2 for example, the lack of suitable vantage points made it necessary for the observer to cross and recross the beach while counting, and as it was impossible for him to remove his gaze from the seals being counted there was considerable risk of coming too near an angry cow or bull. The situation was undoubtedly worst at Area 2 and the shingle patch and its environs of Area 8, where amorphous masses of seals or harem crowds made it very difficult to determine which animals had been counted and which had not. Areas 1 and 12 were crowded, but the risk of being bitten on either of these beaches was small as counting could be carried out in safety from cliff tops or from the shore below the level of the breeding seals.

A further complication occurred at about the peak of the breeding season; the numbers to be counted remained large and a considerable proportion of the pups whose mothers were away on feeding excursions left the beaches and hid in the tussock or under heaps of rock. It then became necessary to beat the tussock to reveal the pups concealed there and, owing to their gregarious nature, as many as half a dozen pups could be found in a single clump of tussock or in a crack in the rock from which the hind quarters of one pup were seen protruding. The eastern shores of Freshwater Inlet, the main bay of Jordan Cove and Evermann Cove, are all backed by large areas of tussock inhabited by seals and very difficult to examine properly.

Of the potential sources of error, undoubtedly the greatest was the undercount of pups in the tussock, either the progeny of mothers away feeding or, in recent years, of mothers who had initially pupped in the tussock. Errors due to miscounting visible seals were remedied by recounting the area (or part of it), both if an error were suspected and also occasionally as a routine check. In the case of pups concealed in the tussock, however, no check was possible, as those disturbed by the first counting would all find fresh hiding places and a subsequent count would be no more accurate than the first. Experience was of great assistance in guessing which hiding places would contain pups, and the use of binoculars at short range

(usually less than 10 m. (33 ft.)) helped in doubtful situations. Very careful sample counting of characteristic areas gave correction values which could be applied to routine counts, and these were arbitrarily applied to final values. In one or two cases where a consistent value could not be obtained by counting, a value was derived from the known previous population of that beach, by applying to it the ratio between the present and previous populations of another beach which was more easily counted. During the first two years, values were occasionally obtained by calculating from the number of cows present on the beach, but this is not a good method and it is no longer used.

The main object of carrying out the censuses was to determine the final total of pups present in the rookery at the end of the breeding season. This cannot be done by direct counting, as by the time the last pups have been born (in the second half of January) the older ones are beginning to take to the water for short excursions and to wander far up into the tussock where it is not always possible to find them.

The latest date in any season on which useful censuses of the whole rookery have been made is 19 December. Behavioural observations show that some pups are born after this date, but such late births form only a small fraction of the total crop. If serial counts are made over the entire breeding season, the results can be plotted and a characteristic curve drawn through them. This curve flattens off at a value 2–3 per cent greater than the value obtained for 19 December, and agrees well with observations. For purposes of calculation, the final height of the curve (taken at 28 December) has been accepted as being equivalent to the total number of pups in the census area in that year. The results of the counts are given in Tables XI and XII.

TABLE XI
GROWTH OF THE BIRD ISLAND COLONY, 1957–62

| Year | Census area† | | | Subsidiary beaches‡ | | | Entire herd | | |
|-------|--------------|----------|-------------------|---------------------|----------|-------------------|-------------|----------|-------------------|
| | Pup total | Increase | Increase per cent | Pup total | Increase | Increase per cent | Pup total | Increase | Increase per cent |
| 1957 | 5,100 | — | — | 230 | — | — | 5,350 | — | — |
| 1958 | 6,400 | 1,300 | 25·5 | 400 | 170 | 74·0 | 6,800 | 1,450 | 27·1 |
| 1959 | 7,500 | 1,100 | 17·2 | 797 | 397 | 99·3 | 8,300 | 1,500 | 22·1 |
| 1960 | 8,046 | 546 | 7·2 | 1,337 | 540 | 67·8 | 9,400 | 1,100 | 13·3 |
| 1961 | 8,257 | 211 | 2·6 | 1,653 | 316 | 23·6 | 9,900 | 500 | 5·3 |
| 1962* | 8,520 | 263 | 3·2 | 1,679 | 26 | 1·6 | 10,200 | 300 | 3·0 |

* 1962 data are from Vaughan, 1963.

† Areas 1–15.

‡ For definition see p. 69.

TABLE XII
PUP CENSUSES, 1957–62

| | 1957 | 1958 | 1959 | 1960 | 1961 | 1962‡ |
|------------------|-------|-------|-------|-------|-------|--------|
| Census area* | 5,100 | 6,400 | 7,500 | 8,046 | 8,257 | 8,520 |
| Extra beaches† | | | 180 | 309 | 372 | 390 |
| Johnson Cove | | | 304 | 394 | 493 | 554 |
| “Sound beaches”§ | 230 | 400 | 313 | 585 | 704 | 596 |
| “Cleft beach” | | | — | 49 | 84 | 139 |
| TOTAL | 5,330 | 6,800 | 8,297 | 9,385 | 9,910 | 10,199 |
| ROUND TOTAL | 5,350 | 6,800 | 8,300 | 9,400 | 9,900 | 10,200 |

* Areas 1–15.

† Area 16.

‡ 1962 data are from Vaughan, 1963.

§ The Bird Sound beaches.

|| Shoemaker Point beach (see p. 35).

The censuses that have been made vary in their accuracy. As it is easier to count smaller numbers, the counts made early in each season are more accurate than those made later and, as the breeding stock is increasing from year to year, the results for the earlier seasons are more accurate than those for the later ones. The census of 1957 (Bonner, 1958c) was of a very high degree of accuracy but, unfortunately, no counts were made after 13 December. In 1958, a series of counts was made from 25 November to 19 December and a curve plotted from them (Bonner, 1959). These gave what is believed to be the most accurate enumeration of the whole series; two people were available for making the count, and an accuracy of better than ± 2 per cent was estimated. The greatest total of pups counted in 1958 was 6,235.

In 1959, no assistance was available for counting and the census had to be performed single-handed (Bonner, 1960). Three counts were made—on 10, 12 and 14 December. Of these, only the last one covered the entire census area (Areas 1–15), the two earlier censuses applying to Areas 1–6 only. The 1958 counts showed that the proportion of pups present in the various parts of the rookery does not change significantly with the date. Hence it is possible to derive values for the entire census area from the two partial censuses by multiplying the pup totals of the partial censuses (Areas 1–6) by a factor derived from the number of pups in Areas 1–6 divided into the entire pup population at the time of a complete census. In the complete 1959 census (14 December) there were 2,504 pups in Areas 1–6 out of a total of 6,632, a proportion of 1 : 2·649, and values for the total pup population were therefore obtained by multiplying the partial censuses of 10 and 12 December by 2·649.

When compared with the 1958 totals for the same dates (10, 12 and 14 December), the three 1959 totals show the following increases:

| | |
|-------------|-----------------|
| 10 December | 18·30 per cent |
| 12 December | 17·04 per cent |
| 14 December | 17·38 per cent. |

These values are sufficiently similar to justify the assumption that the pattern of pup population build-up was similar in the two years, and therefore that the final total in 1959 must have been about 7,500. The accuracy of this derived total depends on the accuracy of the counts and though the highest 1959 count (6,632) is significantly greater than the highest 1958 count (6,235), it was obtained five days earlier in the season when counting is easier and there is no reason to doubt its validity. Supposing that the population curves for the two years are similar, the accuracy for the 1959 census is believed to be only a little lower than that of the 1958 census, i.e. 2–5 per cent.

In 1960, counting again had to be carried out single-handed (Bonner, 1961) and the results suffered in consequence. Three counts were made—on 6–7, 13 and 19 December. Of these, the first is believed to be accurate to within 5 per cent; the second is of a very low degree of accuracy, because of adverse weather conditions during counting, and has been rejected for further calculation; the third, which is for Areas 1–6 only, has an accuracy of 10–15 per cent. The census of 6–7 December gave (after 5 per cent had been added to correct under-counting in Areas 7–15) a total of 4,847 pups. On 19 December, Areas 1–6 gave a counted total of 2,572 pups to which a correction of 138 was added for pups missed (distributed beach by beach, as appropriate). Using the proportional method already described, this gives a total of 7,840 pups for the entire rookery on 19 December. Assuming that the pattern of population build-up was the same as in 1958, this gives a final total of 8,046 pups but with a low degree of accuracy comparable to that of the count of 19 December, i.e. 10–15 per cent. It should be noted that the probable errors are likely to be due to under-counting rather than over-counting.

In 1961, two observers were available for making the censuses but, half-way through, the more experienced was unfortunately injured and had to be replaced by an unskilled helper (Bonner and Vaughan, 1962). It was doubly unfortunate that the replacement took place when conditions were becoming most difficult. Thirteen censuses were carried out between 23 November and 19 December, complete and partial (Areas 1–6) censuses alternating. As is to be expected, some of the later values deviate quite markedly from the expected curve, but the value obtained for 19 December (8,058 pups) is consistent with the general trend; this is equivalent to a final pup total of 8,257 pups, with a probable accuracy of about 10 per cent.

In 1962, Vaughan (1963) carried out a modified census based on a careful and accurate count which was made, with the help of three observers, over the entire census area on 12 December; there were 6,743 pups. Subsequently, sample areas (Area 1 and a beach outside the census area, Shoemaker Point beach) were counted till all the pups had been born. Vaughan then applied the increase factor, obtained from the

sample areas, to his count of 12 December and the resulting total was 8,520 pups. The sample areas chosen were backed by high cliffs which prevented the loss of pups into the tussock, but even so the final estimate is likely to be low as Vaughan's last sample count (on 9 January) may have failed to record some of the pups born at the beginning of the season.

In a private communication, Vaughan states that the pup total for 1963 was of the order of 11,500, but gives no limits of accuracy.

2. Subsidiary beaches

In addition to the pups born in the census area, there is a further crop from several isolated beaches scattered around Bird Island (p. 35) and from a western extension of the census area, the "extra beaches". These localities, collectively known as the "subsidiary beaches", are areas of recent and active colonization. The yearly crops in these areas have been increasing at a consistently greater rate than those of the census area, and in 1959 showed the phenomenal increase of 99·3 per cent over the previous year. Such increases, of course, cannot be due to an endogenous increase of the population on the subsidiary beaches (Bonner, 1964); they must represent reinforcement from the crowded beaches of the main colony. The presence on the subsidiary beaches of breeding cows which had been tagged as pups in the census area confirms this.

In Table XII, collective totals are given for the subsidiary beaches prior to 1959, as the individual data are defective. (Shoemaker Point beach was not counted till 1960.)

B. HAREM SIZE

It is not possible to determine the size of the average harem by direct counting, as by the time the greatest number of cows are ashore the boundaries between many of the harems have become indistinct, the cows forming an amorphous clump—the so-called "harem crowd"—with the bulls scattered at intervals. As mentioned earlier, this is especially true of territories not defined by natural features (Plate IIIa).

Counts made early in the season (about 6 December) showed that the average harem consisted of between 6 and 11 cows. The larger harems occurred in rocky areas (Bonner, 1964), where the cows preferred to haul out. Table XIII shows comparative counts for areas of mainly rocky and mainly open beaches for 1958 and 1961.

As the final crop of pups born must equal the number of cows present on the rookery (not allowing for early pup mortality or multiple births), a value for the average harem size can be obtained by dividing the

TABLE XIII
COMPARISON OF HAREM SIZE AT VARIOUS DATES IN DIFFERENT HABITATS
IN 1958 AND 1961

| | 25 Nov. 1958 | | | 30 Nov.–1 Dec. 1958 | | | 5–6 Dec. 1958 | | |
|----------------|--------------|-------|--------------------|---------------------|-------|--------------------|---------------|-------|--------------------|
| | Bulls | Cows | Average harem size | Bulls | Cows | Average harem size | Bulls | Cows | Average harem size |
| Rocky beaches* | 57 | 209 | 3·667 | 91 | 654 | 7·189 | 123 | 1,209 | 9·827 |
| Open beaches† | 42 | 110 | 2·620 | 93 | 483 | 5·192 | 122 | 974 | 7·984 |
| TOTAL COLONY | 195 | 739 | 3·790 | 332 | 2,163 | 6·516 | 474 | 4,034 | 9·025 |
| | 25 Nov. 1961 | | | 29 Nov. 1961 | | | 4 Dec. 1961 | | |
| | Bulls | Cows | Average harem size | Bulls | Cows | Average harem size | Bulls | Cows | Average harem size |
| Rocky beaches* | 150 | 370 | 2·467 | 170 | 760 | 4·471 | 171 | 1,107 | 6·471 |
| Open beaches† | 197 | 410 | 2·081 | 217 | 946 | 4·359 | 256 | 1,476 | 5·767 |
| TOTAL COLONY | 574 | 1,286 | 2·241 | 638 | 2,691 | 4·219 | 694 | 4,244 | 6·116 |

* Rocky beaches comprise Areas 6, 8, 12 and 13.

† Open beaches comprise Areas 7 and 15.

maximum number of harem bulls present during the season into the final pup crop. This is the sense in which the term "average harem" has been used by Kenyon and others (1954). The term is not precise as, undoubtedly, the cows which arrive earliest leave the beach before the last arrive, and there is probably some replacement of harem bulls during the season. Table XIV shows values for this parameter for the years 1957–61, excluding 1959 when the harem bull count was incomplete.

TABLE XIV
AVERAGE HAREM SIZE

| | <i>Harem bulls</i> | <i>Final pup crop</i> | <i>Average harem</i> |
|------|--------------------|-----------------------|----------------------|
| 1957 | 411 | 5,100 | 12.41 |
| 1958 | 474 | 6,400 | 13.50 |
| 1959 | — | — | — |
| 1960 | 511 | 8,046 | 15.75 |
| 1961 | 718 | 8,257 | 11.50 |

The fall in average harem size in 1961 may be due either to an under-estimate of the number of pups born or, less likely, a miscount of the harem bulls. An increase in the size of harems is to be expected in a young, rapidly expanding population, as the females reach sexual and social maturity about five years before the males.

Bartholomew and Hoel (1953) have discussed harem size in *Callorhinus*. They found that the mean harem size in the area studied was 39, varying from 3 to 153, though less than half the breeding females were ashore at any one time. Kenyon and others (1954) supposed that 26 or 27 was the natural primitive size of the average harem in that species. It is generally accepted that *Callorhinus* represents the greatest development of polygyny in mammals, and it seems unlikely that the southern fur seals would naturally support such large harems. The average harem size for an undisturbed population of South Georgia fur seals is probably about 15. Paulian (1964) stated that the average harem size for *A. tropicalis tropicalis* on Ile Amsterdam was between 6 and 8, with a maximum of 14.

C. TAGGING

As part of the basic research on the fur seals, a pup-tagging programme was begun in the 1957–58 season and continued subsequently.

The tags used initially were a standard pattern of cattle ear tag made to order from Monel metal by the Ketchum Manufacturing Company (U.K.). Since 1962, a similar tag of slightly larger size, manufactured by the National Band and Tag Co., Newport, Kentucky, U.S.A., has been used. They are supplied in blocks of twenty-five mounted on cardboard formers.

The two types operate on the same principle. The tag is inserted between the jaws of a pair of tagging pliers, where it is retained by the springiness of the tag and a raised part of the anvil jaw of the pliers. The point of the tag is then placed over the target on the seal, and as the pliers are closed the point of the tag is driven through the skin and through the larger hole in the lower limb of the tag. The point then strikes the curved anvil on the pliers and is deflected up through the smaller hole in the tag (Fig. 22). When the pliers are released the tag falls free of the jaws (Plate IVa).

Following the findings of Scheffer (1950), tags were applied to the posterior border of the fore flipper near its junction with the body. In 1957–58, in addition to the tag on the fore flipper, 518 animals were tagged with a second tag in the interdigital web between the first and second digits of the left hind flipper. This double tagging was intended as a check on tag security, but it was discontinued as the hind tag was frequently torn out as it tended to catch in cracks in the rocks. Plate VIb shows an animal with an extensive tag scar caused by the tearing out of a hind flipper tag.

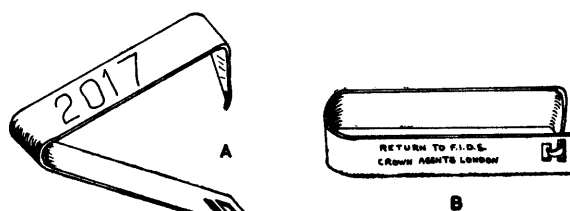


FIGURE 22

Standard seal flipper tag made in Monel metal.

A. Open.

B. Clinched.

Tagging seemed to cause the seals little distress; it is notable that they react only very slightly to stimuli that would be presumed to cause considerable pain. Bleeding was normally very slight though occasionally, presumably when the tag point perforated a vein, it was considerable. No cases of manifest suppuration about the tag were observed, although the surface of the rookeries is invariably filthy and tags were frequently obliterated by mud within a few moments of application. No mortality directly attributable to tagging was observed.

From 1959 onwards, besides inserting a tag, a $\frac{1}{4}$ -inch diameter hole was punched in the web on the hind flipper, using a leather punch.

Tagging was restricted to pups, and thus all animals bearing tags on Bird Island are of exactly known age. To facilitate field identification of juveniles of various ages, the side on which the tag and punch-hole were placed was alternated year by year: in odd years they were placed on the left and in even years on the right.

Tagging is most conveniently carried out in early January, as by that time the harem bulls are considerably less antagonistic to intruders and the pups have not yet become too active or heavy to handle conveniently. Owing to the broken nature of the ground in South Georgia, it is not possible to corral a number of pups and remove them one by one for marking. Each pup has to be captured and removed individually. A team of three, one tagger and two catchers, can apply about 100 tags in an hour (Plate VIe).

Table XV shows the number of tags successfully applied in the years 1957–62 and the estimated proportion of the pup population tagged. Only a few tags have been recovered as few specimens have been killed, but sightings have been very frequent in recent years. Vaughan (1963) lists 76 animals sighted in the 1962–63 season whose tag numbers could be read, including 6 animals which had been tagged in the

TABLE XV
TAGGING RESULTS, 1957–62

| <i>Season</i> | <i>Tags applied successfully</i> | <i>Percentage of pup population tagged</i> |
|---------------|----------------------------------|--|
| 1957–58 | 1,718 | 33 |
| 1958–59 | 1,185 | 19 |
| 1959–60 | 1,393 | 19* |
| 1960–61 | 1,193 | 14 |
| 1961–62 | 1,294 | 15 |
| 1962–63 | 823 | 8 |
| TOTAL | 7,606 | |

* Flipper-punching begun.

1957–58 season. In the 1963–64 season there were 285 sightings (Vaughan, personal communication). Many more tagged animals were seen, but the tag numbers were illegible, either because of distance or because the tag had slipped round in the flipper.

It is not possible to estimate the survival rate of the tags with these data. A larger killing programme would, no doubt, reveal many animals without tags but with tag scars or punch-holes. Some tag scars sighted in the field are large and conspicuous but the punch-holes usually heal, leaving an aperture about 1–2 mm. in diameter surrounded by a dense ring of scar tissue, and are consequently difficult to identify visually though easy to palpate on the dead specimen. At least one tag (applied to a male pup in January 1958) survived for six years. One feature of the recoveries, so far unexplained, is the lack of sightings of tags applied in the 1958–59 season. Of the 1,185 tags applied that year only one was sighted later. (It was among the 285 sightings referred to above.)

Tag data are held at Discovery House, South Georgia.

D. SEX RATIO

During the pup-tagging operations in the 1957–58 season, the sex of all but two of the pups tagged was recorded. As there was no selection for sex when catching for tagging, the data thus obtained can be used to determine the sex ratio of the seals. The tagging was carried out between 2 and 7 January when the mean age of the pups was about four weeks. 877 male and 832 female pups were tagged,* giving a ratio of 1.054 : 1 (51.34 per cent males). This is not significantly different from a unitary ratio ($\chi^2 = 1.19$; $P > 0.05$). Paulian (1964), in a small sample of *A. tropicalis tropicalis* from Ile Amsterdam, found 54 males and 75 females giving a ratio of 1 : 1.3, though this again does not differ significantly from unity ($\chi^2 = 3.42$; $P > 0.05$).

Kenyon and others (1954) found 52.7 per cent males in 1,172 foetal *Callorhinus*, and 50.5 per cent males in 1,000 living pups. Rand (1956b) found a ratio of 1.25 : 1 in favour of the male in *A. pusillus*. This has a very high degree of significance ($\chi^2 = 15.3$; $P < 0.001$). Coulson and Hickling (1964) found, in *Halichoerus*, sex ratios significantly in favour of the male (91.8 females to 100 males from a sample of 2,979), but suggested that this might be partly due to a seasonal effect. Hewer (1964) for the same species found 2,239 males to 2,205 females (though these figures include part of Coulson and Hickling's data). It seems that a slight preponderance of male pups is of common occurrence.

E. MORTALITY

No direct observations are available on the mortality of adult fur seals, but there is no doubt that most natural mortality occurs at sea. Although even the largest adult fur seal could be the subject of predation by killer whales, the latter are not specially common around South Georgia and the fur seals may be regarded as top predators. Hence, their natural mortality is caused either by senility or by disease.

No clearly marked pathological conditions likely to cause death have been noted. Parasitic infestations are well below the level noted in other seals (e.g. Weddell and leopard seals). The condition of mange referred to above (p. 11) does not in itself appear serious, though it may be the outward symptom of a more dangerous internal disorder. Three seals have been found with fibrous cysts of the abdominal viscera, but these were not of great size and were judged unlikely to be a potential cause of death. No seals have been seen which were clearly senile. Even the oldest bulls holding territory perform all the normal activities of territorial maintenance adequately, though they rely to a larger extent on bluff than do bulls in their prime. It is possible that senile seals do not come ashore in the breeding season.

1. Pup mortality

Table XVI sets out the number of dead pups found on various beaches in the season 1959–60, and the number of live pups at the same stations on 14 December 1959. When corrections are applied to the numbers of dead pups to allow for under-counting, and to the living to allow for the natural increase by the end of the season, it is found that the overall mortality is about 6 per cent. This value has not been found to vary much from year to year, though other counts of dead pups were less accurate than that of 1959–60.

* Seven pups tagged before 2 January are not included in this total.

TABLE XVI
PUP MORTALITY ON VARIOUS BEACHES

| <i>Area</i> | <i>Dead pups</i> | <i>Live pups 14 Dec. 1959</i> |
|----------------------------|------------------|-----------------------------------|
| 1 | 75 | 1,366 |
| 2 | 85 | — |
| 5 | 3 | 127 |
| 6 | 3 | 402 |
| 7 | 13 | 1,013 |
| 8 | 116 | 782 |
| 9 | 2 | 96 |
| 10 | 22 | 275 |
| 12 | 28 | 550 |
| 15 | 24 | 1,121 |
| TOTAL | 371 | 5,732 |
| 10 per cent under-count | 37 | — |
| 12·5 per cent increase | — | 716 |
| FINAL TOTAL | 408 | 6,448 |

The distribution of dead pups is very uneven. Mortality is highest on crowded beaches (e.g. Areas 2 and 8), and on beaches where there are rock gullies in which pups can be trampled without the possibility of escape (e.g. parts of Areas 12, 10 and particularly 8). It is lowest on beaches where the density of population is low (Area 9), where the harems form a single rank along the sea (Area 7), and where the pups can shelter under rocks and tussocks (e.g. Areas 7 and 6).

The principal cause of death of the pups is probably starvation, resulting from their losing touch with their mothers, coupled with their maltreatment by other cows from whom they solicit food. Direct trampling undoubtedly accounts for some deaths, but the animals are much more resistant to this form of maltreatment than might be believed at first sight. Some mortality, largely unmeasurable, is accounted for by drowning when storms flood the breeding beaches. A few pup carcasses are washed up after each heavy storm, but a pup's chances of survival seem good, even in quite heavy seas. Conditions are in no way similar to those on Ile Amsterdam, where Paulian (1964) records that 58 per cent of the pups die by drowning in bad weather.

The possibility of hookworm disease, which takes such a toll of the northern fur seal pups in the Pribilof Islands (Kenyon, Scheffer and Chapman, 1954), was not investigated.

Only once have remains attributable to a juvenile seal (i.e. one older than a pup but not sexually mature) been found ashore; the cause of death was not apparent as decomposition was far advanced. The animal appeared to be a yearling.

2. Adult mortality ashore

Adult mortality ashore in the breeding season shows very great fluctuations. In most seasons one or two bulls are found dead or dying behind the breeding beaches. Many of them bear the usual scars of territorial fighting, but some are almost unmarked. The physical condition of the seals at death is frequently good; one animal, examined just after death, weighed 160 kg. and had blubber 45 mm. thick

over its chest. Perhaps 10 per cent of the spare bulls behind the breeding beaches are moribund in appearance. The majority disappear after a day or so, probably to return to the sea where they either recover or die, while the remainder succumb where they lie. No cause of death is apparent, and it may be suggested, very tentatively, that the primary cause of death in these animals is stress. (The very low body temperature of one such animal has been referred to on p. 44.) This mortality of males reached a peak in 1959–60, when about 50 were found dead. In the following season only one dead bull was found ashore. Leaving the exceptional season 1959–60 out of account, the average number of bulls found dead in this way in any one season is about five.

It is much more rare to find dead cows, but 1959–60 was also a peak year for cow mortality and 29 were found dead. These cows had all died early in the season before observations started, and deaths were concentrated in Area 2 and to a lesser extent in the northern part of Area 1. These areas are characterized by open beaches, devoid of natural territorial boundaries, and are the scene of the most intense and continuous territorial fighting. The dead cows could have been fatally injured (perhaps during parturition) by fighting bulls or perhaps, as suggested for the bulls, these animals had succumbed to stress. No cow carcasses were found in a fresh enough state to allow an autopsy to be carried out.

An approximate estimate can be made of the cumulative mortality of the females from birth to breeding age by working from the census data. The years 1957–60 have been chosen, as reasonably accurate data are available for them. It is almost certain that the Bird Island stock is a closed population, i.e. not significantly affected by inward or outward migration, and, if this is so, the increase in the number of pups born in 1960 when compared with the 1959 total (an increase of 1,100) must be due to cows arriving to breed for the first time. For the purposes of this calculation it is assumed that all the primiparae are 3 years old. (2-year-old cows have been found to be virgin and two 3-year-olds examined were found to be pregnant.) The 1,100 new breeders of 1960 are, therefore, derived from the female pups born in 1957. The total pup crop in that year was 5,350, and as the sex ratio is unity there were 2,675 females of which 1,100 survived to breed. This gives a cumulative mortality from birth (actually from census time, which eliminates natal mortality) to breeding age of about 59 per cent. This calculation, however, has taken no account of the multiparous cows. Kenyon, Scheffer and Chapman (1954), in their study of the northern fur seal, assumed a yearly mortality for the adult females of 5 per cent from age 4 to 10 years, and thereafter a cumulative mortality of 12·5 per cent.

It is difficult to decide what mortality to postulate for the Bird Island breeding herd. As the stock is increasing a smaller proportion of the cows will belong to the older age groups, and it seems certain that the overall mortality must be less than for the northern fur seal. It will be assumed that a yearly mortality of 5 per cent can be applied to all the multiparae. Then, 5 per cent (about 400) of the 8,300 cows that pupped in 1959 must be replaced in 1960. Therefore, the real accession is 1,100 plus 400, i.e. 1,500, and the value of the cumulative female mortality from birth to breeding age is 44 per cent.

This calculation neglects the incidence of pup mortality before the pup crop is counted, though as differences are taken this will not be very significant. It also assumes that the entire 3-year class of females is pregnant, but this is unlikely as it has been shown that the age at which northern fur seal females reach sexual maturity can vary by several years. Both these factors will tend to give a mortality less than that indicated above (for if a considerable number of the females produce their first pup when they are 4 years old, then they must have been derived from the smaller stock existing in 1956), but within the limits of probable accuracy of the method neither of these factors is important.

If similar calculations are carried out for the census data for the years 1958–61 and 1959–62, the mortalities are found to be 63 per cent and 81 per cent, respectively. This apparent increase in the mortality of the females will be referred to later.

F. NEW COLONIZATION

1. *South Georgia*

For logistic reasons few observations have been made on newly established colonies of fur seals around the shores of South Georgia, apart from the newly colonized beaches of Bird Island itself.

On 21 December 1960, it was established that a minimal colony of fur seals composed of one harem bull, 3 cows and their pups was present in Elsehul, on the northern side of the north-western tip of South Georgia. It is of the greatest interest to find that so small a group should be stable to the extent of the

females pupping there and returning to feed their offspring, but the area has not been revisited at the appropriate time of year and so its subsequent history is not known.

On 23 January 1961, a small colony of 3 harem bulls, 19 cows and 12 pups, together with 11 spare bulls was found at Johan Harbour. This area was re-visited on 21 December 1961 and 8 harem bulls, 36 breeding cows and 29 pups were then counted. Although censuses made at such different times of the breeding season are not easily comparable, there is no doubt that this represents a very considerable increase.

In December 1960, 13 black pups were found at Undine Harbour, a small cove to the north-east of Johan Harbour, but again it was not possible to make any further visits to check on the subsequent progress of the colony.

2. Other islands of the Scotia Ridge

Fur seals sighted in the late nineteen-forties at the South Orkney Islands were the first seen on the islands of the Scotia Ridge (excluding South Georgia) for many years (Fig. 9). Breeding at this group was first confirmed on 6 December 1959, by Øritsland (1960) who found a group of adult fur seals with a single pup at Ellefsen Harbour, at the junction of Michelsen Island and Powell Island. By 17 February 1960, the fur seal population consisted of a single harem bull, 11 cows and their pups and non-breeding seals, totalling 111 animals. In 1962, Dollman (private communication) recorded a herd of 160–70 fur seals, apparently non-breeding animals, at Cape Geddes on Laurie Island, South Orkneys. On 4 December 1964, Vaughan re-visited Ellefsen Harbour and found 10 adult bulls, 2 adult cows and 4 sub-adult males but no pups. As Vaughan pointed out, a visit as early as 4 December is too soon to record pups, but the small number of mature females sighted suggests that no great increase, if any, had taken place since Øritsland's visit.

In the 1958–59 season, O'Gorman (1961) recorded a breeding community of one harem bull, a single cow and her pup (though a dead pup nearby indicated that at least one other cow had been present earlier) at Cape Shireff on Livingston Island in the South Shetland Islands. By late March 1959, 32 fur seals were counted in this locality.

The largest stock of breeding fur seals away from Bird Island are at the remaining island group of the Scotia Ridge, the South Sandwich Islands. About 400 breeding animals were seen on Visokoi Island in February 1960 (O'Gorman, 1961). This area was again visited in the middle of March 1962, and oblique aerial photographs were taken. Counts made from the photographs indicate a total of about 600 fur seals on the beach, but as the photographs were taken so late in the season some of the animals shown may be migrants from another colony. It is, unfortunately, not possible to identify the various classes of seal present.

A further visit to the South Sandwich group in 1963–64 by Vaughan (Baker and others, 1964) revealed the existence of several breeding colonies.

With such considerable stocks and a history of much slighter exploitation in the nineteenth century, it is quite possible that the South Sandwich stock is as ancient as the South Georgia one. It has been argued in a previous paper (Bonner, 1964) that the occurrence of white-coated specimens at the minor colonies of fur seals indicate a derivation from the South Georgia stock. This colour anomaly has not been reported from other populations of fur seals in the Southern Hemisphere, and it is unlikely to have originated in two separate localities on the Scotia Ridge. One of the animals photographed by Øritsland (1960, fig. 2) at the South Orkneys was white coated, and Vaughan reports sighting a white specimen at the South Sandwich Islands in 1963–64.

Although the sighting of white specimens may reveal a genetic relationship between various colonies, it does not, of course, indicate which one gave rise to the others. The South Georgia stock is assumed to be the parent one, on account of its superior size and the diminishing numbers of seals in the various colonies as one proceeds first eastwards and then southwards through the islands of the Scotia Ridge.

G. GROWTH OF THE COLONY

It is evident that the fur seal population of South Georgia is increasing. Although no reliable data are available until the first of the census counts in 1957–58, each successive count has shown an increase in the number of pups born at Bird Island. The annual increase over the previous year has declined steadily

from 27.1 per cent in 1958–59 to only 3.0 per cent in 1962–63 (Table XI). Rates of increase as high as those recorded in 1958–59 or 1959–60 (22.1 per cent) must be near the maximum possible, and it is surmised that 1957 was the peak of a population explosion. It is impossible to judge how long the population had been expanding at this rate, but it may be pointed out that if the stock had been expanding at a steady rate of 25 per cent per year the sightings of Rayner in 1933 and Marr in 1936, and the estimate of 1,000–3,000 fur seals given in 1950 by a sealing captain to Laws (1953*a*), fit very well. Taking 1958–59, when there were 6,800 pups, as a year of reference, the corresponding pup totals for 1950, 1936 and 1933 would have been 1,140, 56 and 29, respectively.

From 1960 onward, however, it is apparent that the stock was no longer increasing at anything like the maximum rate. The reasons for this fall-off are obscure, but it may be due to changes in the availability of food and breeding space. It is unlikely that the breeding stock of females (the only part of the population, other than the pups, sampled by the existing technique) was reduced by a sharp rise in mortality.

The quantity of food in the seas around South Georgia must be sufficient to support a far greater stock of fur seals than that at Bird Island. The very great reduction in the number of krill-eating whales in the last half-century must have led to a significant increase in the standing crop of krill and, in addition, historical evidence shows that the population was once many times as large as it is today. On the other hand, during the breeding season the females are necessarily concentrated about Bird Island in order to return to feed their pups. Nothing is known of the length of the excursion they may make during a feeding foray, but it may be that at the present size of the population the food resources in the effective feeding range of the nursing females on Bird Island are becoming strained.

That breeding space availability on Bird Island is becoming critical cannot be doubted. The spread of the breeding seals into the obviously less favoured tussock areas behind the beaches, together with the much greater rates of increase on the subsidiary beaches, indicates that the beaches of the census area are becoming saturated. Though the lack of suitable breeding space would affect the number of pups born at any particular station, it would not directly affect the number of juvenile females reaching breeding age. Once impregnated and bearing a full-term foetus, the females would have to come ashore to give birth, and if there was no room at the preferred site they would haul out at some suitable spot nearby. (The experiment with caged cows suggests that the cows might be able to postpone parturition.) In the northern fur seal, the females appear to have a tendency to return year after year to the same spot and to pup initially at the spot where they were born (Kenyon, 1960), and such tagging data as are available indicate that this is true of the South Georgia fur seal also. A nulliparous pregnant cow, deterred from hauling out at her natal beach because of crowding, might be expected to haul out nearby, and to some extent the rapid colonization of the extra beaches and the other subsidiary beaches confirms this.

Another possibility is that under conditions of crowding virgin females do not mate but, as the circumstances under which this class does mate are not known, it is not possible to suggest a mechanism which could cause their non-impregnation; presumably it would be a social factor. Nevertheless, a sudden large fall-off in the rate of increase is most easily explained by supposing that a complete year class, or a large part of it, had failed to breed. Breeding would not, of course, be postponed indefinitely and in a subsequent year the accession would be increased by the females that had failed to breed previously. So far, there is no evidence that this process has taken place at South Georgia.

Congestion at one breeding site need not check an increase in numbers if the population is sufficiently mobile. For the purposes of calculating rates of increase the Bird Island stock has been regarded as a "closed population", i.e. one which is not affected by inward or outward migration, but this is not strictly true. Without doubt, the minor colonies on the coast of the north-western tip of the mainland of South Georgia have been derived from the Bird Island stock. It is also thought that the Bird Island stock itself may have originated from a relict population on the Willis Islands, and it is possible—especially as the breeding site on the Willis group is probably saturated—that some migration towards Bird Island may still be taking place. But these movements and the amount of colonization away from Bird Island are very small and, on their own, seem insufficient to account for the decline in the rate of increase of the main stock.

One puzzling feature is the small amount of colonization that has taken place on the mainland of South Georgia. As would be expected, colonization of the islands of the Scotia Ridge seems to have taken place in inverse order of their remoteness from South Georgia, the South Shetlands (furthest from South Georgia) having the smallest population and the South Sandwich Islands (nearest to South Georgia) the

largest. It would also be expected that localities on the mainland of South Georgia, such as Antarctic Bay and the Bay of Isles, both known to have contained extensive colonies of fur seals in the past, should support populations of fur seals similar in size or larger than those from more remote localities, such as the South Sandwich Islands. As suggested in an earlier publication (Bonner, 1964), a possible explanation of this apparent anomaly of distribution is that the homing reaction of the seals may be intensified in the vicinity of their birth place. Thus if, as is likely, the ultimate mechanism of homing is by visual recognition, the seals within sight of known landmarks will continue to home until they land at their natal colony. Small displacements laterally along the coast, such as have occurred at the subsidiary beaches, would then be possible but colonization at intermediate distances would be less likely.

Another factor which could be of significance in the repopulation of the shores of South Georgia is the existence of the flourishing elephant seal population there. Unfortunately nothing is known of the distribution of the elephant seal and fur seal colonies in the unexploited population, and it would be interesting to know whether both species would have occupied the same cove or whether they would have occurred separately. Elephant seals begin their breeding haul-out in early September and continue on the breeding grounds till well into December, and so there is considerable overlap with the fur seal breeding chronology. The presence of elephant seals may make a beach less attractive to a wandering fur seal. It is noteworthy that the parts of the mainland at present colonized by fur seals, Elsehul, and Undine and Johan Harbours, have very small elephant seal populations, but it is likely that the elephant seals are a contributory rather than a main causative factor in restricting repopulation by fur seals.

It is not possible to forecast the future progress of the stock with any certainty, but unless much larger numbers of breeding cows are prepared to occupy sites in the tussock for parturition the capacity of Bird Island as a breeding station is unlikely to increase very much further. The fall-off in the rate of increase is an indication that the breeding grounds are almost saturated. The size of most animal populations tends to oscillate about a mean, and there may be a decrease in the Bird Island population in the future. It should be remembered, however, that as the rest of South Georgia is virtually untenanted by fur seals, saturation at Bird Island represents only a fractional usage of the food and breeding space resources of the locality as a whole. Under these circumstances, colonization of the mainland could continue until the population has been built up to the level existing before exploitation.

In an animal with such a marked homing instinct as the fur seal, any new colonization must represent anomalous behaviour. Young and potent bulls are probably widely dispersed, but the females are far less likely to haul out away from their natal rookeries. Even if an exceptional cow does so, she is unlikely to stay ashore unless her gregarious instincts are satisfied by the presence of other females. Nevertheless, the minimal breeding groups recorded at Elsehul and Livingston Island show that these events do occur. Whether such small colonies persist is doubtful. A female that has once pupped at a certain locality may tend to return there in future seasons, in which case the new colony may grow steadily, as the presence of some females would satisfy the gregarious instincts of newcomers. Pups born at a new colony presumably return there to breed, some of the females within three years. On the other hand, Fraser Darling (1951) has pointed out that in some species of animals there is a threshold of numbers below which breeding will not occur. It would be of the greatest interest to know whether copulations have occurred at these small colonies.

The critical size at which a colony of fur seals becomes self-sustaining and capable of maximum increase is not known. On the basis of the sightings and the postulated rate of steady increase of the Bird Island herd, a figure of about 50 breeding cows might be suggested very tentatively. There is no doubt that the breeding stocks at Bird Island, the Willis Islands and the South Sandwich Islands are large enough to be self-reproducing, and at least the Bird Island stock is capable of providing material for the colonization of other localities. Provided that the fur seals are left to increase, it is probable that the coming years will see an increase in the rate of colonization as the existing colonies are reinforced by new arrivals and by the return of new stock born *in situ*. It is possible that the original range of the species may become repopulated to approximately the same density as existed before the advent of the sealers.

An interesting fact whose significance, if any, is obscure, is the synchronization of increase in, or recovery of, fur seal populations in various parts of the world. *Arctocephalus forsteri* in the New Zealand region has in the last few years nearly doubled its population, while in 1954 the Guadalupe fur seal, *A. philippii townsendi*, which was thought to be extinct, was discovered to be breeding, with an estimated population of 300–400 (Hubbs, 1956).

H. EXPLOITATION AND CONSERVATION

Fur seals, like all other pinnipeds except the leopard seal, are at present rigidly protected in the Falkland Islands and their Dependencies, and in those areas the taking of seals is permitted only under licence. South of the latitude 60°S., the Antarctic Treaty prohibits the taking of seals for commercial purposes. Experience has shown, however, that large populations of mammals capable of yielding valuable products are rarely left unexploited, and the Antarctic fur seal, with a pelt second in value only to that of the northern fur seal, is capable of being regarded as a potential asset. Exploitation, provided that it is based on adequate scientific knowledge of the species, need have no deleterious effect on the population, as can be seen in the case of the northern fur seals on the Pribilof Islands. There, under scientific management, the herd has increased in number from about 200,000 in 1911 to a present value of about 1·5 million animals from which an annual crop of about 70,000 skins is taken.

While it is quite possible that the Antarctic stocks of fur seals may approach or even surpass the size of the Pribilof herd, the opportunity for commercial exploitation is not so favourable. The best skins for the furrier are those from animals 3–4 years old, and for conservation reasons it is logical to restrict the commercial kill to males, as the removal of even a considerable number of these will not upset the breeding structure of the herd. In the northern fur seal, the 3- and 4-year-old males have the convenient habit of hauling out in considerable numbers on beaches adjacent to, but not part of, the breeding beaches. From these hauling-out grounds groups of males, numbering several hundred, can be rounded up and driven off to be killed. The equivalent age classes in the South Georgia fur seal, however, are to be found scattered widely in the broken ground behind the breeding beaches. Here, under possible commercial exploitation, each seal would have to be individually hunted out, clubbed and skinned, which would add enormously to the labour of collecting the pelts. Other difficulties in the way of exploitation are the remoteness of the sealing grounds and the problems of navigating in unfamiliar waters.

This does not imply that exploitation of fur seals in the Antarctic will never be economically feasible. For a luxury product such as furs prices may rise without reference to the usual economic rules, so that although the Antarctic skins are never likely to be produced as cheaply as those from the Pribilofs they may, nevertheless, be worth harvesting.

It may be that a properly administered system of cropping would be the best way of protecting the stocks from the depredations of unlicensed sealers, as the presence of legitimate sealers at the rookeries during the breeding season would deter casual poaching. The necessary controls associated with rational cropping would also result in the amassing of considerable bodies of scientific data, but this work could be carried out without exploitation.

Finally, it is to be hoped that ethical considerations as well as commercial ones will decide the future use of the Antarctic fur seals, especially as this species has managed to re-establish itself in at least part of its old haunts, while elsewhere in the world mammal populations are fast disappearing.

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APPENDICES

APPENDIX I

WEIGHTS OF SOME PRINCIPAL VISCERA

| | Females | | | | Males | |
|--------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | FS 77 3-year | FS 80 4-year | FS 15 mature | FS 46 mature | FS 78 2-year | FS 17 mature |
| Body weight (kg.)* | 33·0 | 38·0 | 48·0 | 31·6 | — | 138·0 |
| Heart | 240 | 282 | 270 | — | 320 | 560 |
| Lungs | 330 | 393 | — | 600 | 390 | — |
| Stomach | 200 | — | — | — | 475 | — |
| Liver | 1,090 | 1,165 | 1,470 | 1,150 | 1,700 | — |
| Spleen | 27 | 71 | — | 62 | 110 | — |
| Kidney R. | 95 | 114 | } 305 | — | 158 | 255 |
| Kidney L. | 98 | 124 | | — | 165 | 265 |
| Pancreas | 59 | — | — | — | 75 | — |

* Body weights are in kg. All other weights are in g.

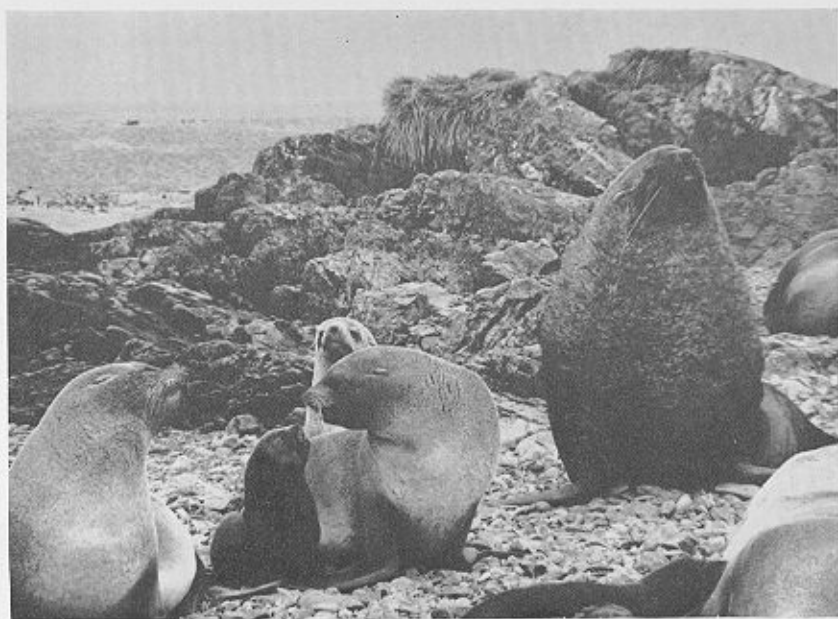
APPENDIX II
MEASUREMENTS OF FUR SEALS
(cm. and kg.)

| Specimen number | Status | Sex | Length | | R. fore flipper insertion-tip | | R. hind flipper insertion-tip | | | R. ear pinna | Longest vibrissa | Girth | | | Width | | | | Weight |
|-----------------|-----------------------------------|-----|-----------|------------------|-------------------------------|-------|-------------------------------|-------|--------|--------------|------------------|-------|------------------|-------------------|-------|------------------|-------------------|--------|--------|
| | | | Nose-tail | Nose-flipper tip | Ant. | Post. | Ant. | Post. | Spread | | | Neck | Ant. to flippers | Post. to flippers | Neck | Ant. to flippers | Post. to flippers | "Hips" | |
| FS 22 | Black pup, c. 2 days | ♂ | 66.0 | 80.5 | — | — | — | — | — | — | — | — | — | 43.0 | — | — | — | — | 5.9 |
| FS 33 | Black pup, 5-6 days | ♂ | 63.5 | 77.0 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 5.0 |
| FS 76 | Black pup, c. 3 weeks | ♂ | 80.0 | 95.0 | 24.5 | 23.0 | 18.5 | 17.5 | 12.0 | 3.55 | 7.95 | 38 | 50 | 51.5 | 9.0 | 17 | 16 | 13.0 | 10.6 |
| FS 64 | Moulted pup, c. 3 months | ♂ | 89.0 | — | — | — | — | — | — | — | — | — | — | 60.0 | — | — | — | — | 14.4 |
| FS 63 | Moulted pup, c. 3 months | ♂ | 90.0 | — | — | — | — | — | — | — | — | — | — | 55.0 | — | — | — | — | 15.8 |
| FS 82 | Yearling | ♂ | 100.0 | 124.0 | 31.5 | 31.5 | 25.0 | 24.5 | 13.5 | 3.70 | 9.60 | 47 | 63 | 59.0 | 13.0 | 24 | 21 | 17.0 | 17.3 |
| FS 68 | Yearling | ♂ | 101.0 | 121.0 | 32.0 | 28.0 | 25.0 | 24.0 | 16.5 | — | — | — | — | — | 14.0 | 24 | — | 14.5 | 17.6 |
| FS 78 | 2-year-old | ♂ | 118.0 | 144.0 | 38.0 | 31.0 | 30.0 | 27.0 | 18.0 | 4.00 | 14.50 | 51 | 86 | 84.0 | 15.0 | 34 | 28 | 16.0 | — |
| FS 69 | 2-year-old | ♂ | 119.0 | 142.0 | 39.0 | 35.0 | 30.0 | 32.0 | — | — | — | — | — | 75.0 | 12.5 | — | 33* | 18.5 | 36.6 |
| FS 31 | 2-year-old | ♂ | 122.0 | 149.0 | 37.5 | 40.0 | 29.5 | 29.0 | — | — | — | 60 | — | 70.0 | — | — | — | — | — |
| FS 73 | 2-year-old | ♂ | 143.0 | 179.0 | 45.0 | 42.0 | 35.5 | 36.5 | 22.0 | — | — | — | — | 75.0 | 17.0 | — | 39* | 23.0 | 53.5 |
| FS 57 | — | ♂ | 148.0 | — | — | 39.0 | — | — | — | — | — | — | — | 93.0 | — | — | — | — | — |
| FS 30 | — | ♂ | 163.0 | 202.0 | 52.5 | 50.0 | 45.0 | 44.0 | — | — | — | 81 | — | 106.0 | — | — | — | — | 86.0 |
| FS 55 | Adult bachelor bull | ♂ | 172.0 | — | — | 48.0 | — | — | — | — | — | — | — | 112.0 | — | — | — | — | — |
| FS 58 | Harem bull | ♂ | 172.0 | — | — | 46.0 | — | — | — | — | — | — | — | 128.0 | — | — | — | — | — |
| FS 56 | Adult bachelor bull | ♂ | 173.0 | — | — | 46.0 | — | — | — | — | — | — | — | 113.0 | — | — | — | — | — |
| FS 17 | Harem bull | ♂ | 174.0 | 207.0 | — | — | — | — | — | — | — | — | — | 130.0 | — | — | — | — | 138.0 |
| FS 59 | Harem bull | ♂ | 180.0 | — | — | 46.0 | — | — | — | — | — | — | — | 123.0 | — | — | — | — | — |
| FS 71 | Harem bull | ♂ | 183.5 | 224.0 | 51.5 | 49.5 | 45.0 | 40.0 | 28.5 | — | — | — | — | 129.0 | 26.0 | — | 52* | 29.0 | — |
| FS 49 | Adult (pre-breeding) | ♂ | 184.0 | — | — | — | — | — | — | — | — | — | — | 142.0 | — | — | — | — | — |
| FS 48 | Adult (pre-breeding) | ♂ | 185.0 | — | — | — | — | — | — | — | — | — | — | 140.0 | — | — | — | — | — |
| FS 84 | Harem bull | ♂ | 187.0 | 230.0 | 51.0 | 47.0 | 46.5 | 43.5 | 25.0 | 5.00 | 32.50 | 80 | 127 | 120.0 | 21.0 | 48 | 42 | 27.0 | 137.5 |
| FS 51 | Adult bachelor bull | ♂ | 189.0 | — | — | — | — | — | — | — | — | — | — | 136.0 | — | — | — | — | — |
| FS 23 | Harem bull | ♂ | 189.0 | 229.0 | — | — | — | — | — | — | — | — | — | 135.0 | — | — | — | — | 160.0 |
| FS 74 | Harem bull | ♂ | 191.0 | 232.0 | 54.0 | 53.0 | 43.0 | 42.5 | 23.0 | 6.20 | 37.20 | — | 134 | 116.0 | 31.0 | — | — | 25.0 | — |
| FS 60 | Harem bull | ♂ | 194.0 | — | — | 51.0 | — | — | — | — | — | — | — | 112.0 | — | — | — | — | 126.0 |
| FS 50 | Harem bull | ♂ | 194.0 | — | — | — | — | — | — | — | — | — | — | 132.0 | — | — | — | — | — |
| FS 67 | Harem bull | ♂ | 197.0 | — | — | — | — | — | — | — | — | — | — | 132.0 | — | — | — | — | — |
| FS 16 | Full-term fetus | ♀ | 58.0 | 69.5 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4.2 |
| FS 20 | Full-term fetus | ♀ | 62.5 | 76.0 | — | — | — | — | — | — | — | — | — | 35.0 | — | — | — | — | 5.4 |
| FS 25 | Black pup, 4 days | ♀ | 68.0 | 80.5 | — | — | — | — | — | — | — | — | — | 41.0 | — | — | — | — | 5.8 |
| FS 27 | Black pup, 6 days | ♀ | 62.0 | 75.5 | — | — | — | — | — | — | — | — | — | 40.0 | — | — | — | — | 5.1 |
| FS 83 | Yearling | ♀ | 100.0 | 124.0 | 31.5 | 31.5 | 25.0 | 24.5 | 13.5 | 3.70 | 9.6 | 47 | 63 | 59.0 | 13.0 | 24 | 21 | 17.0 | 17.3 |
| FS 29 | Yearling | ♀ | 104.0 | 126.0 | 31.0 | 32.5 | 25.5 | 25.5 | — | — | — | — | — | 63.0 | — | — | — | — | 20.0 |
| FS 52 | 2-year-old | ♀ | 113.0 | — | — | — | — | — | — | — | — | — | — | 66.5 | — | — | — | — | — |
| FS 53 | 2-year-old | ♀ | 113.0 | — | — | 28.0 | — | — | — | — | — | — | — | 64.0 | — | — | — | — | — |
| FS 70 | Primiparous breeding cow, 3 years | ♀ | 113.5 | 135.0 | 30.0 | 33.0 | 27.0 | 25.0 | 15.0 | — | — | — | — | 82.0 | 17.0 | — | 32* | 18.0 | 38.8 |
| FS 77 | Primiparous breeding cow, 3 years | ♀ | 116.5 | 140.5 | 35.0 | 31.0 | 25.5 | 29.0 | 15.0 | 4.50 | 13.0 | 50 | 77 | 74.0 | 17.0 | 30 | 25 | 17.0 | 33.0 |
| FS 79 | Adult breeding cow, 4 years | ♀ | 117.0 | 142.0 | 38.0 | 32.0 | 30.0 | 26.0 | 16.0 | 3.50 | 15.0 | 46 | 74 | 68.0 | 13.0 | 29 | 22 | 16.0 | 30.5 |
| FS 80 | Adult breeding cow, 4 years | ♀ | 120.0 | 146.0 | 37.5 | 33.0 | 31.0 | 27.5 | 17.0 | 4.00 | 14.5 | 50 | 79 | 83.0 | 14.5 | 29 | 25 | 14.0 | 38.0 |
| FS 47 | Adult breeding cow (moulter) | ♀ | 120.0 | — | — | — | — | — | — | — | — | — | — | 79.0 | — | — | — | — | 35.0 |
| FS 61 | Adult breeding cow | ♀ | 121.0 | — | 34.0 | — | — | — | — | — | — | — | — | 73.0 | — | — | — | — | 30.0 |
| FS 54 | Adult breeding cow | ♀ | 125.0 | — | 30.0 | — | — | — | — | — | — | — | — | 85.0 | — | — | — | — | — |
| FS 28 | Adult breeding cow | ♀ | 126.0 | 155.0 | — | — | — | — | — | — | — | — | — | 78.0 | — | — | — | — | 34.5 |
| FS 26 | Adult breeding cow | ♀ | 127.0 | 156.0 | — | — | — | — | — | — | — | — | — | 80.0 | — | — | — | — | 38.0 |
| FS 85 | Adult breeding cow | ♀ | 127.5 | 155.5 | 41.0 | 35.0 | 32.0 | 30.5 | 17.5 | 3.50 | 22.0 | 45 | 84 | 76.0 | 10.0 | 29 | 23 | 15.0 | 40.0 |
| FS 39 | Adult breeding cow | ♀ | 128.0 | 155.0 | — | — | — | — | — | — | — | — | — | 83.0 | — | — | — | — | 36.0 |
| FS 24 | Adult breeding cow | ♀ | 129.0 | 156.0 | — | — | — | — | — | — | — | — | — | 87.0 | — | — | — | — | 39.0 |
| FS 46 | Adult breeding cow (moulter) | ♀ | 129.0 | 165.0 | — | — | — | — | — | — | — | — | — | 75.0 | — | — | — | — | 31.6 |
| FS 76 | Adult breeding cow | ♀ | 131.0 | 155.0 | 35.0 | 32.0 | 30.0 | 30.0 | 18.0 | — | 20.0 | — | — | — | 15.0 | 27 | 25 | 17.0 | 45.0 |
| FS 42 | Adult breeding cow | ♀ | 132.0 | 164.0 | — | — | — | — | — | — | — | — | — | 84.0 | — | — | — | — | — |
| FS 18 | Adult breeding cow | ♀ | 133.0 | 162.0 | — | — | — | — | — | — | — | — | — | 80.0 | — | — | — | — | 37.3 |
| FS 15 | Adult breeding cow | ♀ | 135.0 | 163.0 | — | — | — | — | — | — | — | — | — | 87.0 | — | — | — | — | 48.0 |
| FS 45 | Adult breeding cow (moulter) | ♀ | 139.0 | 164.0 | — | — | — | — | — | — | — | — | — | 77.0 | — | — | — | — | — |
| FS 43 | Adult breeding cow | ♀ | 139.0 | 168.0 | — | — | — | — | — | — | — | — | — | 81.0 | — | — | — | — | — |
| FS 19 | Adult breeding cow | ♀ | 139.0 | 168.0 | — | — | — | — | — | — | — | — | — | 89.0 | — | — | — | — | 51.0 |
| FS 21 | Adult breeding cow | ♀ | 139.0 | 169.0 | — | — | — | — | — | — | — | — | — | 88.0 | — | — | — | — | 43.5 |

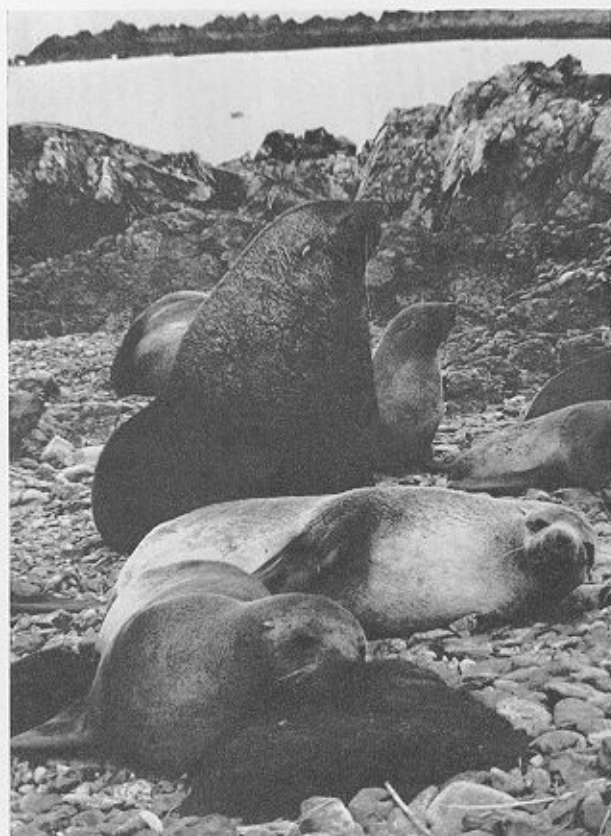
* Average value.

PLATE I

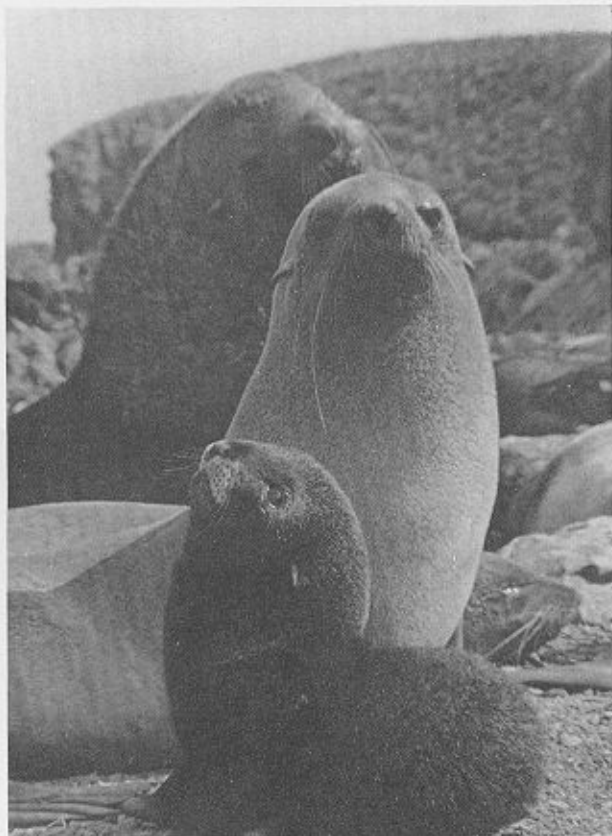
- a-c. Studies of fur seals. Note the disparity in size between the adult male and female.
In Plate 1c, note the white-tipped hairs about the head and muzzle of the pup.



a



b



c

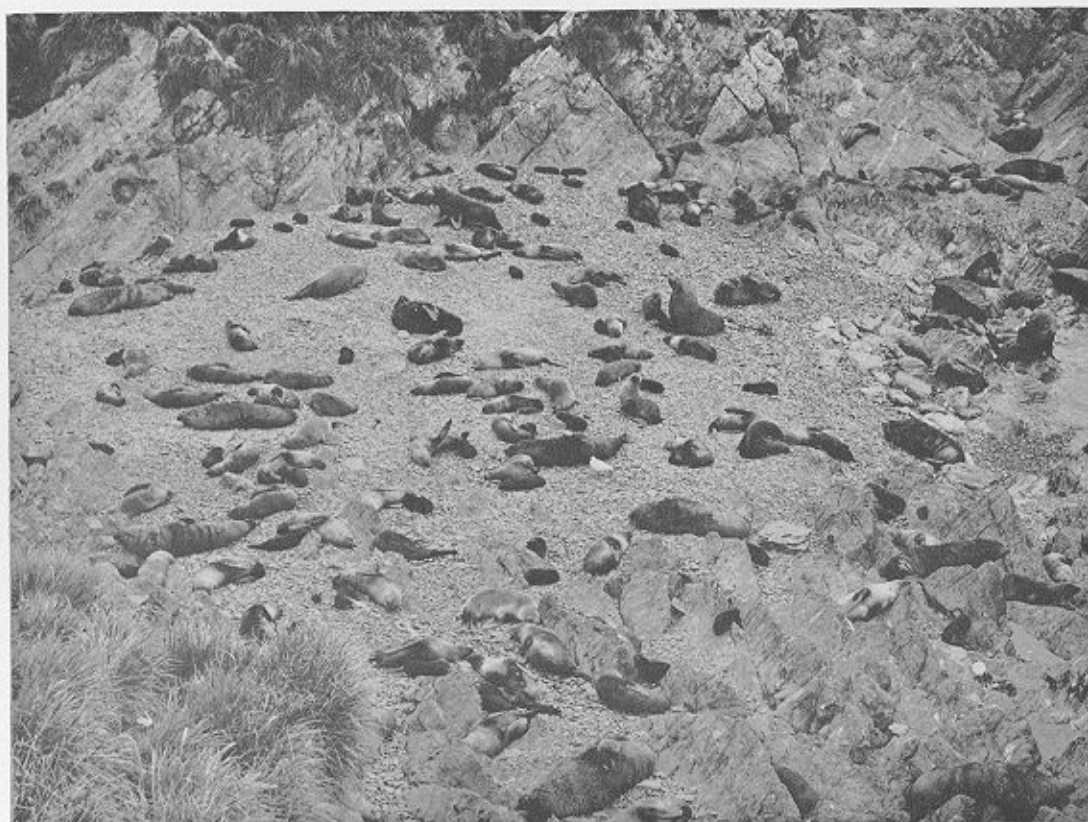
PLATE II

Breeding beaches used by fur seals. (See also Plate IIIa.)

- a. The extreme rocky type. Main Island, Willis Islands; January 1961.
- b. The rocky-cove type. Area 10 on the headland between Jordan Cove and Ebermann Bay; December 1961. The sea lies to the right and to the left; a narrow gully affords access to the tussock-covered inland region. The disposition of the cows in groups about the bulls can be clearly made out. The scene is unusually peaceful; the only harem-bull in the "alert position" (right centre) is next to a newly-arrived bull which has not yet accumulated any cows.



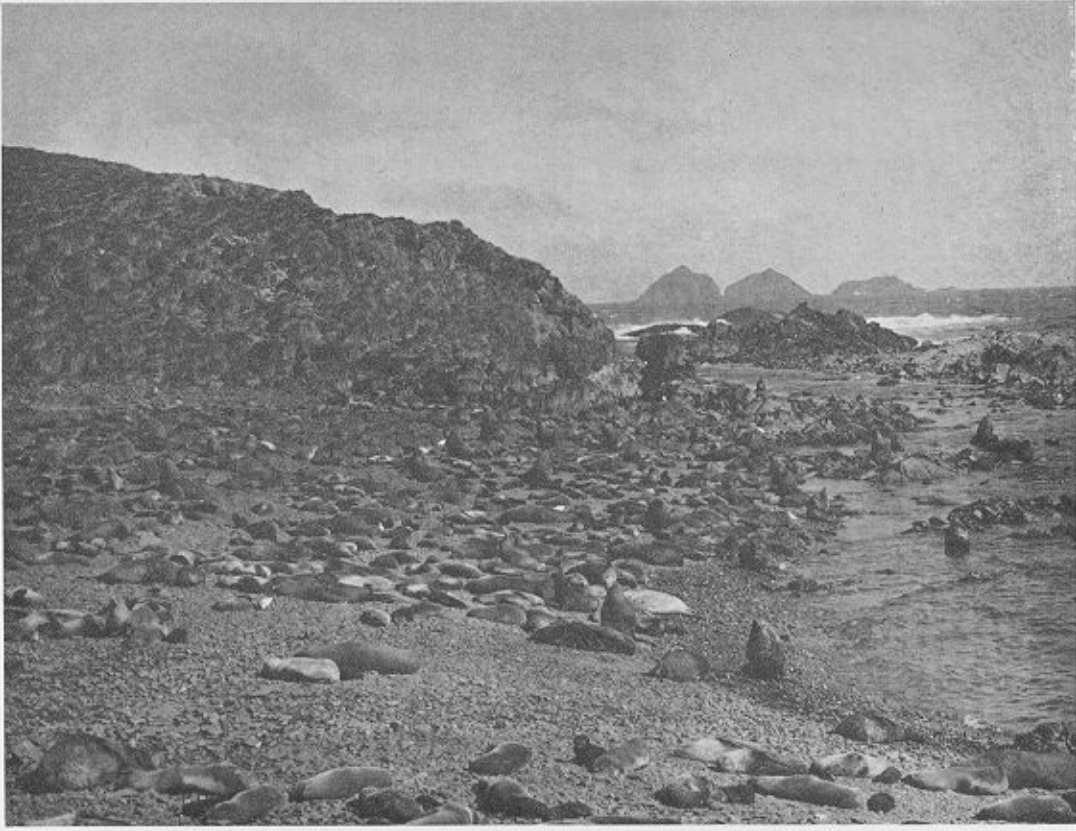
a



b

PLATE III

- a. The open beach type of breeding beach. Area 2 south-east of Freshwater Inlet, at high water; December 1960. As there are no natural barriers to separate the harems the cows form a "harem crowd". A number of spare bulls on intertidal territories can be seen. In the foreground is a corridor free from breeding seals down which there is a trickle of water.
- b. Cow seals feeding their pups in the tussock immediately behind the beach shown in Plate IIIa. Note the flattened condition of the tussock stools.



a



b

PLATE IV

- a. Yearling fur seals. The two in the foreground bear axillary tags.
- b. A white-coated 2-year-old male fur seal. Note the normally-pigmented eye and darker muzzle and ear.
- c. A mature cow seal affected on the rump by patches of "mange" (see p. 11).
- d. A mature cow seal infested with numbers of the barnacle *Lepas australis*. This is an unusually heavy infestation.
- e, f. Territorial disputes between harem bulls. In Plate IVf the lunging bull on the right has received a large wound just behind the ear, and blood is flowing freely from a wound lower down its neck. The plight of the pup between the fighting bulls is a common one on crowded beaches.



a



b



c



d



e



f

PLATE V

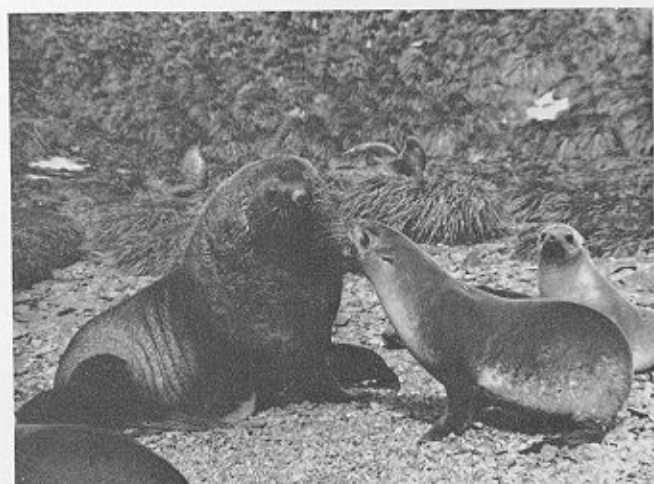
- a. The conclusion of a territorial dispute. The bulls turn inwards towards their own territories.
- b. The copulatory attitude. The bull is about to challenge the photographer.
- c. The "whisker-snapping" reaction of the cows. Note the apposition of the vibrissae of the cow and the bull.
- d. A cow suckling her pup. Note the strongly-erected nipple.
- e. A cow with two pups (see p. 56).
- f. A pod of pups at the back of a breeding beach. The mothers of these pups are away at sea on a feeding excursion.



a



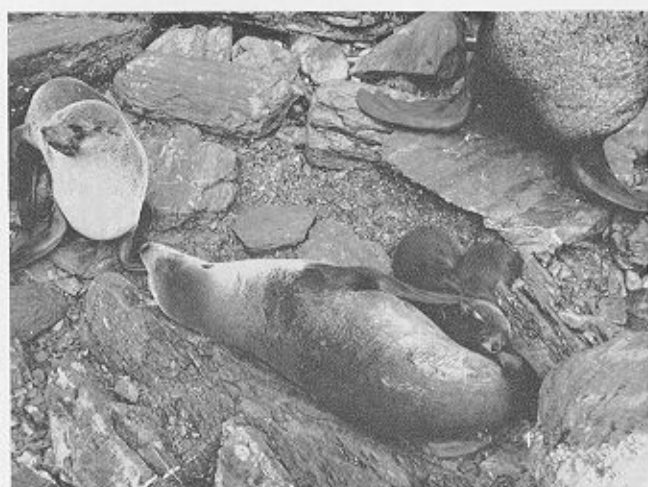
b



c



d



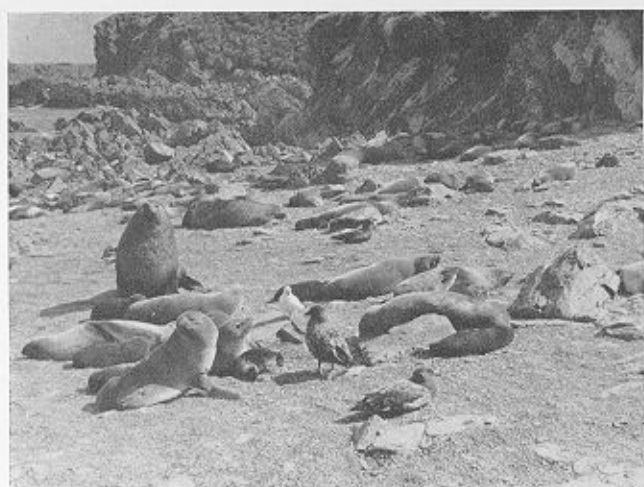
e



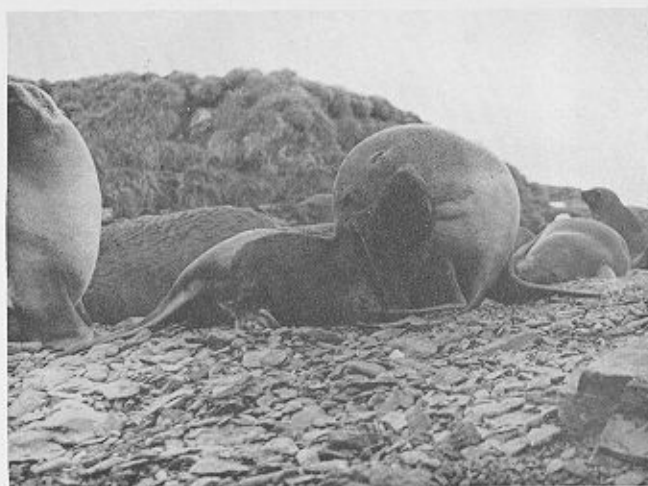
f

PLATE VI

- a. Harem group in Area 8. Note the pair of brown skuas and a sheathbill lurking by a new-born pup.
- b. Cow fur seal dragging her new-born pup towards her with her teeth. The placenta has not yet been delivered.
- c. Taking the rectal temperature of a lethargic bull fur seal (see p. 44).
- d. A harem bull in the sprawling attitude associated with heat stress. This attitude enables the seal to radiate heat away from the fur-free surfaces.
- e. Tagging fur seal pups. One operator (right) holds the pup steady while the other applies the tag. Note the metal tubes (in the foreground) which were used to fend off adult seals; light bamboo poles are now found more suitable.
- f. A 4-year-old male seal bearing an axillary tag. There is an extensive scar on the interdigital web of the left hind flipper where a duplicate tag has been torn out.



a



b



c



d



e



f