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ZOOLOGY

The Seasonal Reproductive Cycle of the Female Elephant Seal — *Mirounga leonina,* Linn. — at Heard Island

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INTRODUCTION

Biological history. Although the southern elephant seal *Mirounga leonina*, Linn. has been known and exploited commercially since early in the last century, surprisingly little accurate information is available on its life history and physiology. The reasons for this are, first, that the elephant seal inhabits one of the least populous and one of the most rugged parts of the globe; secondly, that only about half of its life is spent on shore, where observation is possible; and thirdly, that any form of controlled experimentation on it is impracticable because of its large size and amphibious habits.

The companies which exploited the seals for their blubber on most of the subantarctic islands left few biological records of any importance. Most early records were made by amateur naturalists and untrained observers.

The first full accounts on the natural history of the elephant seal are those of T.P.A. Ring at Iles de Kerguelen (1923) and L. Hamilton Matthews at South Georgia (1929). Both accounts have been subsequently shown to be inaccurate in many details, particularly by Sorenson (1950) working at Campbell Island, and A.N.A.R.E. biologists working at Heard and Macquarie Islands (1948—).

If literature on the natural history of the elephant seal is scarce, that on its physiology is even more so. To date the writer knows of only two workers in this field, neither of whom has published his results.

This report, then, is an attempt to correlate some preliminary work on the sex physiology of the female elephant seal with its natural history.

Material and methods. The present report is based on the examination of 36 female elephant seals killed at Heard Island in 1952, and on general observations made there since 1949; all field observations refer to Heard Island unless otherwise stated. Original records and preserved organs are in the possession of the Antarctic Division, 187 Collins Street, Melbourne.

Throughout the 1952 breeding season daily visits were made to South West and West Bays where elephant seals were in abundance. Counts were made of the total numbers of seals; totals of each category (harem bulls, bachelor bulls, cows, pups and weaned pups); and the composition of individual harems. Many seals were marked with paint in order to study individual behaviour and notes were taken of activities within the harem from day to day.

All seals killed were shot with a .303 rifle and, after a straight length measurement had been taken from the tip of the snout to the tip of the tail, the abdomen was opened. It will be noted that the Heard Island measurements are decidedly smaller than those given by Laws (1953) but, as Laws' measurements were taken along the curve of the spine, the two sets are not precisely comparable. An examination was then made of the organs *in situ* in order to determine the relative sizes of the two horns of the uterus and of the ovaries. The whole sexual apparatus was then removed and taken back to the laboratory where the ovary capsules were opened and notes taken of the size of each ovary, the numbers of visible ovulation scars, and the external appearance of corpora lutea, corpora albicantia and developing follicles. The ovaries were then excised and placed in 5% formalin to harden for a few days. After hardening, most ovaries were sliced with a scalpel at 2 mm. intervals (special care being taken to cut through surface scars) and the resultant sections examined and drawn. Some were brought back to Australia for microscopic sectioning.

The fresh uterus and vagina were carefully split open from the ventral side and a close inspection made of their contents. In some cases vaginal and uterine smears were made.

SPRING—BREEDING AND MATING

Field observations. In the last week of August the first cows begin to haul out for the annual breeding season. At first they are solitary and usually return again to sea; but by the beginning of September permanent beach residents establish themselves, congregate together and finally form harems. Once a harem is established a bull takes control of it and the surrounding area of beach, maintaining his rights by frequent encounters with neighbouring bulls.

Under the protection of a bull the harem quickly grows by the recruitment of newly arrived cows until, by mid October, the harem is at maximum strength.

The harems begin to form first on the most popular beaches, and on these the peak population is reached slightly earlier than on the less favoured beaches. Fig. 1 is a graph showing the population of cows and pups during the breeding season at West Bay, for which the most complete data are available. The rookery here is a compact group, dominated by one or two bulls, and is particularly well situated for accurate observation. The fact that the pup curve never equals that of the cows is due to pups leaving the harem after weaning, to pup mortality and to the fact that in

a big harem it is virtually impossible to make a complete count of pups: some are always missed. Harems range in size from a few cows to more than two hundred but the average size is between forty and fifty.

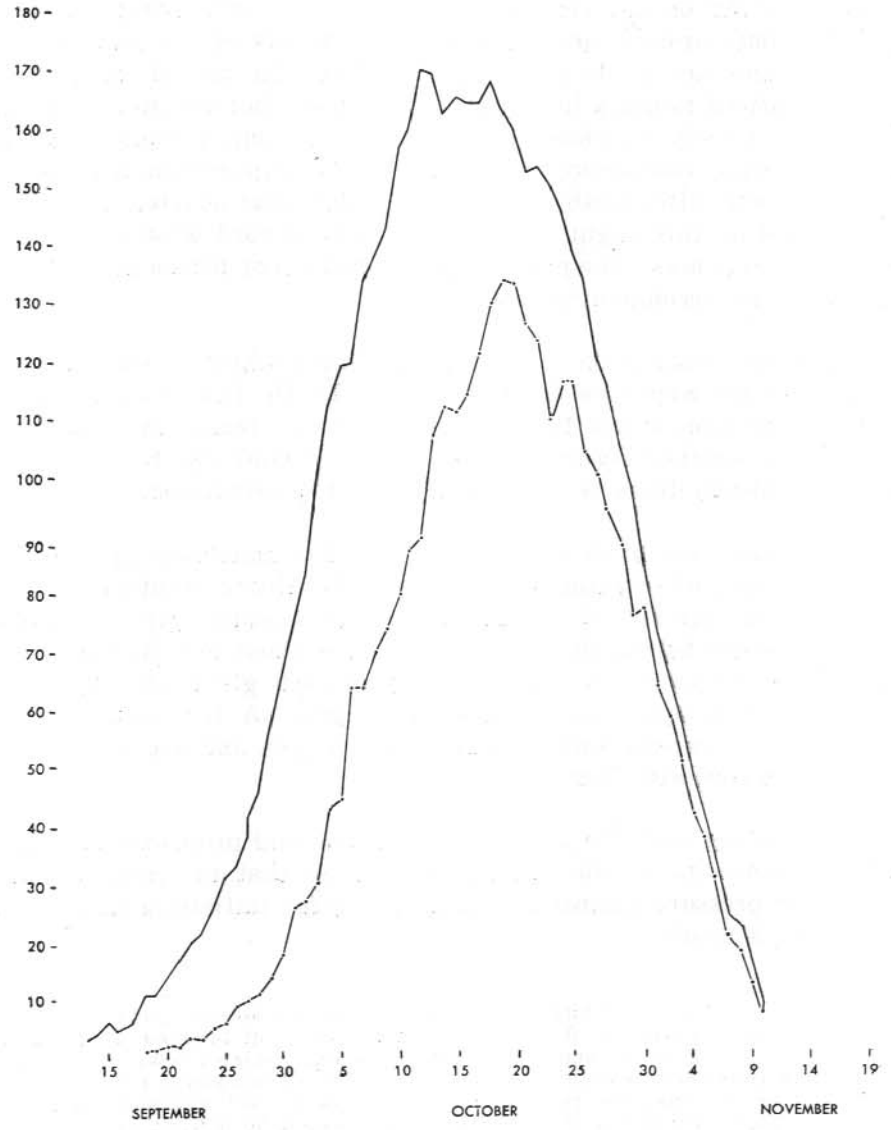

Fig. 1.—Graph of total population of cows and pups in the West Bay rookery during September and October, 1952. The first two weaned pups were noted on 11 October, and by 19 October eleven weaned pups were known to have left the harems.

The average cow lies ashore for about five days before giving birth to her single pup[1]. Only three births were actually witnessed by the writer but verbal descriptions of twelve others seen on Macquarie Island by Dr. Z. Soucek confirm all the main features of the following description.

The cow lies on her ventral side making very little movement apart from occasional upward and sidewards movements of the hind flippers. Uterine spasms are easily seen and soon force the tail of the pup out. For about fifteen minutes little progress is made, but the spasms become increasingly strong. Gradually the pelvis of the pup is worked out and a final maternal contraction expels the whole pup within a matter of seconds. Shortly after birth the cow swings her hind quarters away from the pup, and on this slight strain, the umbilical cord breaks at a point of apparent weakness. The placenta is expelled ten or fifteen minutes later with almost no accompanying bleeding.

The above description is of a breech birth which is the only kind witnessed by the writer on Heard Island, or by Dr. Soucek on Macquarie Island[2]. Sorenson states that presentations are facial, an observation borne out by another observer on Macquarie Island (R. Kenny, unpublished). Evidently there is some variability in presentation.

Very soon after birth suckling begins. The mammary apparatus of the female elephant seal consists of two glands situated ventrally beneath the blubber on each side of the umbilicus. These glands extend about six inches before and behind the nipple, and each is about four inches wide by half an inch deep. A net-work of ducts in each gland converges on a main duct which opens on a retractable nipple. A few instances have been noted of cows with one supernumerary nipple, and one instance was recorded of a cow with four nipples.

When giving suck the cow lies on her side and protrudes the nipple. The pup pushes its muzzle against her side so that the combination of sucking and pressure against the mammary gland initiates a flow of milk into the pup's mouth.

[1] No cases of multiple birth have been recorded on Heard Island. In 1954, at Macquarie Island, Dr. A. Gourin noted two cases of probable twin births at the beginning of the pupping season. Both were isolated cows at least thirty yards from their nearest neighbours, and both had two young pups of identical age; in one case the pups were only just born, still wet and bloodstained. Dr. Gourin comments in his notes that it would be difficult to notice twins later in the season when the beaches are crowded with thousands of cows and pups.

Laws (1953) states that twins are rare, but has not yet published any details.

[2] A birth witnessed by Dr. Gourin in 1954 was again tail first.

The milk is a creamy, slightly viscous fluid, which tastes oily and unpalatable. Its richness is vouched for by the extraordinary growth of the pups for whom it is the sole diet. The quantity of milk secreted at different stages of lactation is not known, but it is believed that the greatest quantity is produced towards the end. Laws (1953), at Signy Island, found the average weight at birth to be about 100 lbs., and that of weened pups to be almost 400 lbs.[1]. Furthermore, the rate of growth accelerates up to the time of weaning, arguing a differential lactation rate, and this is borne out by the different quantity of milk in the mammary ducts of seals killed soon after pupping and towards the end of the lactation period.

The cow suckles her pup at frequent intervals during the day for twenty-two days, during which time the pup loses the umbilical cord (five to eight days) and undergoes a post-natal moult of its black puppy fur. Finally it leaves the mother and wanders away from the harem to join groups well away from the water's edge. It is certain that the departure of the pup is not caused by the failure of the mother's milk supply, since cows have been killed several days after the departure of the pup and found to be still lactating freely.

By the end of lactation the cow is terribly emaciated because, during her thirty days on shore, she cannot feed and all the nourishment for herself and her pup has to be derived from the thick layer of blubber below her skin.

The time at which cows are inseminated is variable. Cases are known of cows receiving the bull while still suckling very young pups; others towards the end of suckling; and others after the pup has left. Observation, however, has convinced the writer that the majority are inseminated during the last week of suckling. But at whatever period it occurs the onset of oestrus is dramatically sudden. Prior to it the cow can easily thwart the attempts of a bull to copulate by moving her hind quarters rapidly from side to side. During heat, however, her behaviour is radically changed. She makes no attempt to struggle free of the bull's clasp, but raises her hind quarters clear of the ground and slightly spreads the hind flippers. Sometimes oestrus behaviour is even more marked than this. One bull who was already in coitus was approached by another cow. She

[1] The only pup weights available from Heard Island are three birth weights, all between 60 and 70 lbs. (60 lbs., Gilchrist, 1948; about 65 lbs., length 47 inches, Gibbney 1952; 65-70 lbs., length 50 inches, Gwynn, 1953; this was taken from a very large cow killed before the pup was born; field notes state that it seemed a very large pup). This gives further support to the suggestion that the Heard Island elephant seal may be a smaller animal than that at the South Orkney Islands.

nuzzled around his shoulder emitting characteristic falsetto distress cries and savagely bit the object of the bull's attention.

Copulation lasts about five minutes, during which time the bull remains passive while the cow maintains a gentle writhing of the whole body. Occasionally she may playfully bite at the bull's neck and frequently she gives voice to crooning noises.

Shortly after mating the cow leaves the harem and goes to sea for two or three months of intensive feeding.

The female reproductive system. Seven harem cows were killed during the 1952 breeding season at Heard Island. Table 1 summarises the results of the examination of their sexual organs.

An examination of the table suggests that a series of related changes occurs in the sexual organs during lactation. These are:

(a) *The healing of the placental scar.* In the earlier specimens the mucosa was dark red and rough in appearance, like an unhealed wound. A small quantity of watery fluid was found in such uteri and was presumed to be an exudate from the wound. In later specimens, although the colour of the area was still deep red, the rough appearance was lost and the newly grown mucosa was plainly visible. In the last seals killed (Ma24 and Ma26) the area was definitely healed over and the colour had changed from deep red to deep brown.

(b) *A decrease in size of the corpus luteum due to atrophy.* The invasion of the corpus luteum by connective tissue was plainly visible even on macroscopic examination of fresh selections.

(c) *A rapid development of the follicles in the ovary opposite to the one containing the corpus luteum.* In each case several follicles were enlarged but only one had reached maximum development. When fully formed it could easily be seen in the uncut ovary as a slightly bulging area, usually marked with small blood vessels. Internally, the follicle was supported by several lines of thickened tissue forming buttresses similar to those described for the northern fur seal (*Callorhinus ursinus*) by Enders, Pearson and Enders (1946).

All follicles remained small in the ovary containing the corpus luteum.

(d) *A change in the consistency of the liquor folliculi.* In follicles up to about 12 mm. in diameter the liquid was jelly-like in consistency. Above this size it changed to a watery state with a slightly greenish tinge. This change in other mammals, including man, is a sign of approaching ovulation.

The two seals killed after copulation (Ma23 and Ma24) present three interesting features. Neither seal had ovulated before insemination, suggesting that in the elephant seal ovulation may be induced by the act of copulation. The cow leaves the harem very soon after copulation occurs, indicating a very short duration of heat which is "especially true of species with induced ovulation" (Adsell, 1946, p. 16).

Secondly, no great quantity of semen was found in the vagina although one of the seals (Ma24) was killed ten minutes after the event and examined within an hour. The writer had previously dissected the testis of an adult male but had failed to find an ejaculatory mechanism such as is present in other mammals. Again, it was observed that during copulation, the bull remained quite passive and did not appear to experience any climax. It is possible that no orgasm occurs for the bull, his emission consisting of a continuous flow of sperm in a small amount of fluid.

The third point of interest is that the sperm reach the upper tracts of the uterus very rapidly. In the case of Ma24 uterine smears were taken within an hour of copulation and mobile sperm were certainly present throughout the uterus.

SUMMER—MOULTING

Field observations. Following the mating season harem females return to the sea to feed and replenish their reserves of blubber which have been sadly depleted by lactation. They then come ashore for the annual moult, which consists of the gradual shedding of the outer epidermis and hairs and the growth of a new pelt. The moult takes two or three weeks to complete during which time the animals migrate from the beach to areas of tussock grass which provide better conditions for rubbing off the moulting skin, or to mud wallows which seem to soothe the irritation caused by moulting.

A rough sequence of age groups has been noticed as the moulting season advances.

The first groups to come ashore in late November and early December are animals up to three years of age. Such groups are readily identifiable at Heard Island because of the high proportion of branded animals among them. Branding experiments were instituted at Heard Island in 1949 and only newly weaned pups were branded. Since then a proportion of each year's pups was branded so that at the time of observation (November

TABLE I

Examination of Genitalia from Seals Killed in the Breeding and Mating Seasons (1952) at Heard Island.

Catalogue Number	Date Killed	Uterus		Right Ovary		Left Ovary		Character of Liquor Folliculi
		Right Horn	Left Horn	Corpus Luteum	Largest Follicle	Corpus Luteum	Largest Follicle	
A	Oct. 20	Healing placental scar 2"	—	14 mm.	—	—	7 mm.	Jelly
B	Oct. 20	Unhealed placental scar	—	16 mm.	—	—	4 mm.	Jelly
Hz/52/Ma27[1]	Nov. 11	—	Healing placental scar 1½". Watery exudate.	—	12 mm.	14 mm.	—	Jelly
Hz/52/Ma25[1]	Nov. 2	—	Healed placental scar. Watery exudate.	—	12 mm.	11 mm.	—	Watery
Hz/52/Ma23[1][2]	Oct. 23	—	Unhealed placental scar. Watery exudate. Motile sperm.	—	13 mm.	10 mm.	—	Watery
Hz/52/Ma24[2]	Nov. 2	—	Healed and fading placental scar. Motile sperm.	—	15 mm.	10.5 mm	—	Watery
Hz/52/Ma26	Nov.11	Healed and fading placental scar	—	10.5 mm	—	—	—	Watery

[1] Still suckling pup.
[2] Seen mating shortly before being killed.

1952), all branded seals were either adolescents or, as later evidence will suggest, three-year-old cows which had ovulated for the first time in the recent breeding season[1].

From about 20 December, true adult females begin to arrive in large numbers. The age of mature females is not easy to judge by simple inspection, but the degree of tooth wear could be used to some extent as a rough guide to relative age. It was noticed that among the earlier arrivals the majority had quite sharply pointed teeth, indicating that they were relatively young. As the moulting season progressed (mid-January) more cases were noted of worn teeth, and towards the end (February) several of the seals killed had canines which were worn down almost to the gums.

Towards the end of February the exodus of moulting cows is in full swing and by the beginning of March the moulting season can be considered as ended, except for the bulls.

From the point of view of obtaining early foetal material this period appeared to be ideal and therefore about 25 large females were shot between 1 December, 1952, and 1 March, 1953.

[1] The writer's belief that females normally ovulate for the first time when three years old is confirmed by the sightings of branded seals during the 1953 season. In 1952 the writer failed to find any branded cows in harems, the oldest branded animals being three years old. In 1953 six four-year-old branded cows were located in the harems, five of which were known to have pups, but no three-year-old cows could be found, though at other seasons sightings of seals of the 1950 class were much more frequent than those of the 1949 class. In the 1954 breeding season nine four-year-old and two five-year-old cows were located, but again no three-year-olds could be found. It is fairly easy to pick out the young cows in the smaller harems and check them for the presence of brands. Laws (1953) mentions one very exceptional case of a seal which pupped when two years old, but believes that the first pup is normally born when three years old. Either there is an important difference between the Heard Island seals and those in South Georgia and the South Orkneys, or Laws' pregnant third year seals represent a minority which pup at three years of age.

TABLE II

1. Seals Killed during Period of Moult.

Catalogue No.	Date	Length	Right Ovary	Left Ovary	Uterus
Hz/52/Ma28	26 Nov. '52	8′ 3″	No corpus luteum	No corpus luteum	No placental scar
Hz/52/Ma29	1 Dec. '52	7′ 2″	Corpus luteum 15 mm. dia.	Unscarred	No placental scar. Free blastocyst right horn.
Hz/52/Ma32	22 Jan. '53	8′ 2″	Corpus luteum 17 mm. dia.	Surface scars only	No placental scar
Hz/52/Ma37	4 Feb. '53	8′ 2″	Functional corpus luteum	Degenerating corpus luteum	Placental scar left horn. Early implantation site right horn
Hz/52/Ma40	25 Feb. '53		←	See text	→

2. Seals Killed in Autumn.

Hz/52/Ma3	19 Apr. '52	6′ 7″	Unscarred	Unscarred	No sign of pregnancy
Hz/52/Ma4	21 Apr. '52	8′ 2″	Corpus albicans 5 mm. dia.	Corpus luteum 21.5 mm. dia.	286 mm. foetus in left horn
Hz/52/Ma6	9 May '52	8′ 7″	Corpus luteum 24 mm. dia.	Corpus albicans 4-5 mm. dia.	325 mm. foetus in right horn.
Hz/52/Ma9	30 May '52	8′ 5″	Corpus luteum 8.5 mm. dia.	Two small corpora albicantia	No foetus

3. Seals Killed in Winter.

Hz/52/Ma12	23 July '52	9′ 0″	Corpus luteum 19 mm. dia.	Corpus albicans 8 mm. dia.	Fresh placental scar right horn
Hz/52/Ma13	25 July '52	7′ 9″	Unscarred	Corpus albicans 6 mm. dia.	No foetus
Hz/52/Ma14	28 July '52	8′ 10″	Two corpora lutea 13 mm. and 7 mm. dia.	See notes	Fresh placental scar right horn
Hz/52/Ma16	15 Aug. '52	8′ 0″	Corpus luteum 16 mm. dia.		950 mm. foetus right horn
Hz/52/Ma17	14 Aug. '52	8′ 4″	See notes	Corpus luteum 8 mm. dia.	Macerated foetus left horn

The ovaries. With three exceptions, listed in Table II, all ovaries followed the same pattern:—

In one ovary was a fresh, vascular looking corpus luteum of between 16 and 18 mm. in diameter. In most cases the corpus luteum showed the same lobed appearance as described for the northern fur seal (Enders, Pearson and Enders, 1946). Follicles in this ovary were all 4-5 mm. in diameter.

In the other ovary of the pair there was an obviously degenerating corpus luteum which had been invaded by connective tissue. The extent of invasion and the size of the corpus luteum varied with the time of killing. Thus, seals killed in late December showed a discrete corpus luteum of about 10 mm. in diameter. In late January the invasion had progressed so that the clear outline was partly lost and specks of white scar tissue were clearly visible. Size was reduced to about 7-8 mm. In February the structure was mainly scar tissue and the rounded form was entirely lost. Follicles in this ovary were 7-8 mm. diameter (as compared with 15-16 mm. for a fully mature follicle).

The presence of an atrophying corpus luteum in one ovary indicates that all these females had given birth to pups in the previous September to October pupping season. The functional corpus luteum in the other ovary indicates a subsequent ovulation and is strong evidence that there is an annual alternation of ovulation between the ovaries. It also suggests that these seals were pregnant, since it would be expected that a corpus luteum, unaccompanied by pregnancy, would atrophy in a matter of a week or ten days.

Of the three exceptions, Ma28 was a medium-sized cow with no evidence of past or present pregnancy. Ma29 was a three-year-old seal bearing a 1949 brand. The left ovary was typically virgin in character, the largest follicle being only 2-3 mm. in diameter. There can be no doubt that this seal had ovulated for the first time in the breeding season just past, and that the corpus luteum in the right ovary was developed from that ovulation. In another branded third-year cow (Ma3) killed at the age of thirty months, both ovaries were unscarred and there was no evidence of maternity. Ma32 had a typical functional corpus luteum in the right ovary, but in the left there was no sign of any atrophying corpus luteum. Numerous surface scars on both ovaries suggested many previous ovulations, and hence that this seal was comparatively old, but it had not pupped in the 1952 season.

The uteri. The uteri of all seals taken in the moulting season were first examined externally; then both horns were opened from the ventral side and a careful examination made of the mucosa.

Like the ovaries, the majority of uteri conform to a definite pattern. In the horn on the same side as the atrophying corpus luteum, there was found a more or less well defined area of discolouration about midway between the junction of the two horns and the fallopian tube. This area—about an inch wide—formed a band lining the lumen and representing the attachment area for the placenta of the last pregnancy. Like atrophying corpora lutea these "placental scars" exhibited a progressive loss of colour and definition correlated with the time which had elapsed since the breeding season. Such scars in females taken in late December were very red in colour and had a clearly marked border. Through January and February the colour tended more and more towards the pink hue of a normal mucosa, while the extent of the scar became less and less well defined. In late February a careful examination was needed to locate it at all.

The two seals with no previous pregnancy (Ma28 and Ma29), of course, bore no placental mark and the other seal (Ma32) which had no atrophying corpus luteum, also carried no placental mark on this side.

The horn on the same side as the functional corpus luteum was minutely examined in all cases since it was on this side that early embryos should theoretically be implanted. Despite this examination the only sign of activity observed prior to 4 February was a reddish swelling about the size of a pea lying well down the uterine horn of Ma32. This was at first thought to be an early implanted foetus, but subsequent sectioning revealed it as a vascular angioma.

In seals killed after 4 February, however, a curious phenomenon was observed. Almost without exception each lumen was found to be enlarged at a point at about halfway along its length into a sort of pocket filled with fluid. The mucosa here was highly vascular and its folds much more complex. The watery fluid contained in the pocket must have been under slight turgor since it spurted when an incision was made. Despite careful cutting, no sign of an enveloping membrane was discovered and it is thought that the pocket was formed by the constriction of the lumen in two places and its expansion between.

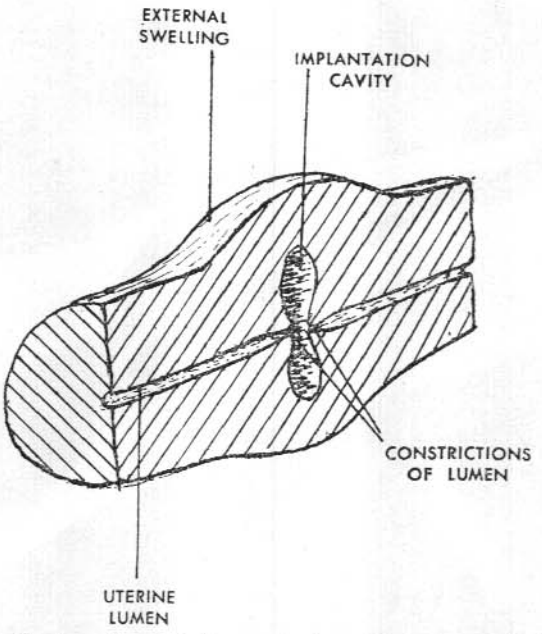

Fig. 2.—Diagrammatical section of the central portion of one horn of an implanted uterus.

Six such uteri were examined between 4 February and 26 February when the writer embarked for return to Australia. In the seal killed on 4 February the enlarged lumen was not apparent on examining the uterus externally. In two killed on 10 and 12 February, although nothing was visible externally, a definite lump could be felt. In three out of four killed on 25 February a definite swelling in that area could be seen.

Embryo and blastocyst. Three uteri from this period were serially sectioned in Australia at 15 micron intervals.

(a) The first (Ma29 killed on 1 December) was a three-year-old known branded seal. There was no macroscopic indication of any implantation site in the fresh uterus, but a piece was taken from midway along the horn on the side whose ovary contained the corpus luteum. Sectioning at right angles to the lumen disclosed 28 sections of an unimplanted blastocyst. It lay in a narrow fissure between folds of

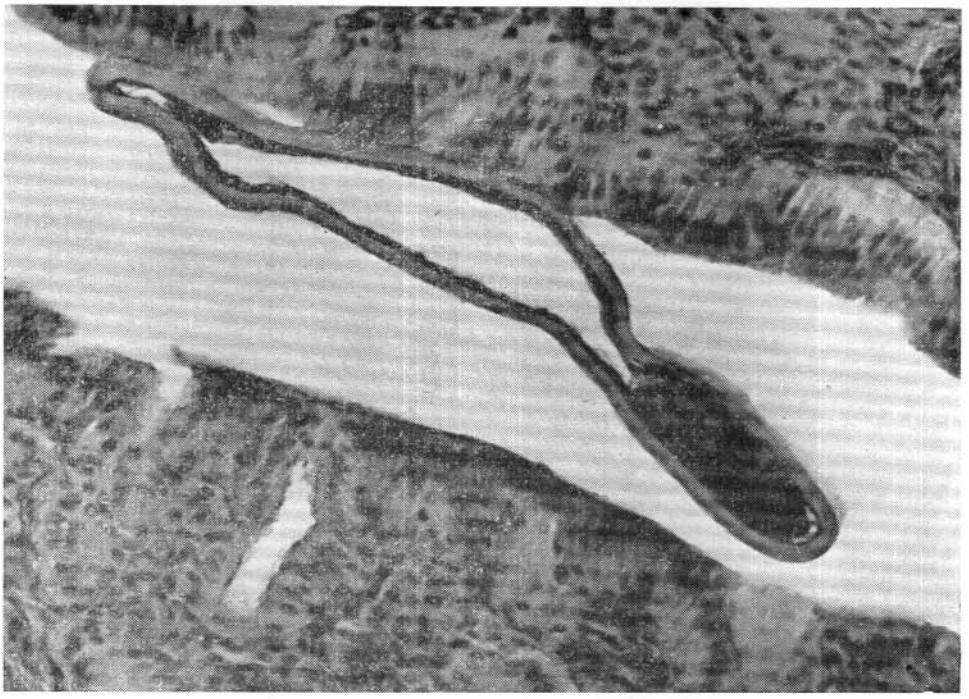

Fig. 3.—Unimplanted blastocyst from seal Ma29.

undifferentiated mucosa and appeared to be closely adherent, though not attached to each side of the fissure. It was made up of an outer zona pellucida averaging 8.25 microns in thickness and broken in places, probably due to stresses during fixation. This was lined by a single layer of cells which thickened to a cellular knot at one end. Mitotic figures were recognisable within this knot. Overall dimensions of the blastocyst were:—

Maximum length .. .. .. .37 mm.
Maximum width .. .. .. .047 mm.

The mucosa showed no particular specialisation in the region of the blastocyst. It was not highly vascular but was notable for the large number of gland openings.

(b) The second uterus sectioned was Ma37 killed on 4 February and showing the first—and smallest—implantation site. The sections were horizontal and longitudinal with respect to the lumen. Although no embryo or blastocyst was discovered, the sections were not without interest because of the conditions of the mucosa, which showed a transitional stage between that of Ma29 and the third uterus, Ma40. It was much more vascular than Ma29; less so than Ma40. Also the number of gland openings was about 50 per cent. less per unit area than in Ma29. The endothelium was unbroken in all sections.

(c) The third uterus (Ma40) from a seal killed on 25 February was again sectioned at right angles to the lumen. In about thirty of these, roughly lateral horizontal sections of a 1.5 mm. embryo were found between folds of the mucosa. The following structures could be easily identified:—

(i) Spinal cord and cerebro-spinal canal.
(ii) Cranial flexure.
(iii) Enlarged forebrain.
(iv) Eight or nine myotomes.

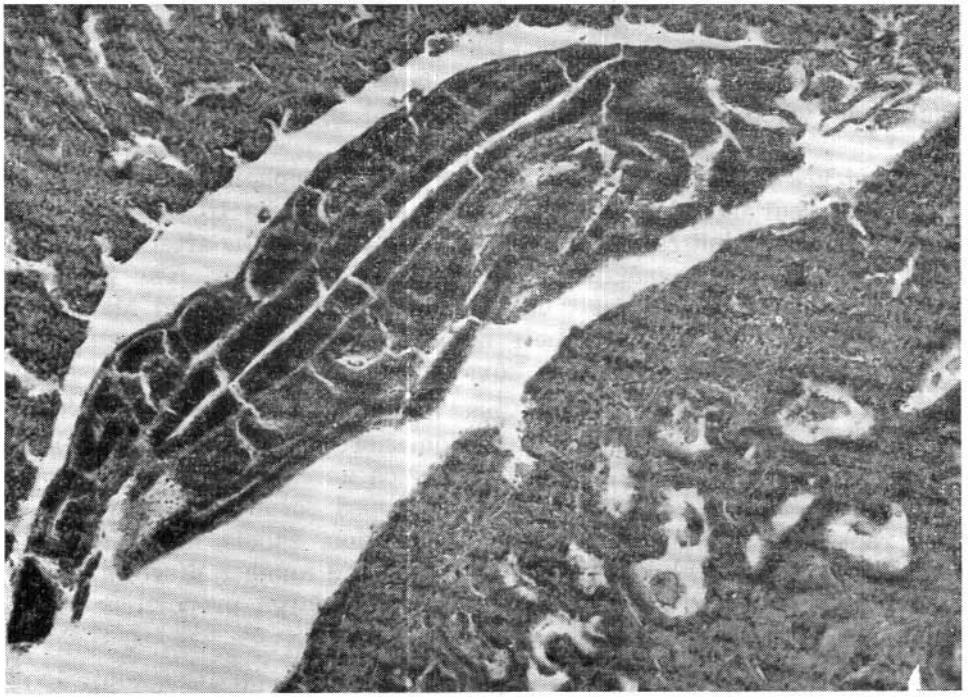

Fig. 4.—Developing embryo from seal Ma40.

Two cellular layers lined the lumen of the uterus. First, there was a single layer of squamous epithelium which could only be identified here and there, but whose widespread occurrence suggests that it was actually a delicate continuous layer damaged either when the uterus was first examined or later during sectioning. This may possibly be foetal endoderm. Secondly, a columnar trophoblast was observed continuous with the tissues of the embryo and underlying the foetal endoderm. It appeared to have replaced the uterine endothelium throughout the implantation site except for a small region immediately dorsal to, and slightly longer than, the embryo.

The trophoblast had also invaded the endometrium through the stroma and into the superficial glands, whose ducts were thus blocked by a glandular symplasma. All these superficial glands appeared much enlarged and all contained plentiful secretions—probably "embryotrophe"—for the nourishment of the embryo. Capillaries were numerous throughout the area.

The whole structure described above suggests the beginnings of a yolk-sac (chorio-vitelline) placenta such as occurs in the initial placentation of carnivores before the true (chorio-allantoic) placenta is formed.

One other interesting feature of the endometrium was that each gland appeared to have shrunk away from the surrounding stroma and seemed to lie in quite a large vacuole. Thread-like structures connected the stroma to the glandular epithelium. Whether this was due to a fault in fixation or whether it has some physiological significance is not known.

Evidence for delayed implantation. In the elephant seal, mating is known to occur only in a restricted season, viz., from 10 October to 15 November. Yet adult cows, killed as much as two months after the season was ended, showed no macroscopic evidence of pregnancy. The writer is not alone in noting this fact; other biologists at Heard and Macquarie Islands have recorded it in their notes on seals killed and examined. There are two possible interpretations of these facts:—

(a) That pregnant seals do not haul out to moult during their pregnancy, and that those seals killed on shore after the mating season are cows which have failed to conceive. Such an explanation is unlikely; first because of the presence of well-developed corpora lutea which, if they represent an ovulation without conception, should have atrophied within about three weeks; secondly because the number of cows ashore during the moulting season represents a very large proportion of the numbers ashore in the breeding season.

(b) That there is a delayed implantation. The evidence for this is:—

(i) At least a fortnight after the end of the mating season a free blastocyst was discovered.

(ii) Almost every mature cow killed up to the end of January had a functional corpus luteum but no other macroscopic sign of pregnancy. It is presumed that a free blastocyst was present in the uterus of each of these seals.

(iii) After 4 February highly vascular areas strongly suggestive of implantation sites were found in almost every uterus.

(iv) At least three months after the mating season a 1.5 mm. embryo was discovered in one of these implantation sites.

Two distinct varieties of delayed implantations are known.

Physiological delay of implantation occurs in some rodents, e.g., mice and rats; insectivores (*Sorex araneus, Sorex minutus,* etc.) and in at least one species of marsupial—the Rottnest Island wallaby (*Setonix brachyurus*). Such a delay occurs when impregnation happens during lactation. The blastocyst will not implant until lactation is completed. This type of delay can hardly apply in the case of the elephant seal, because lactation lasts for only three weeks and is normally completed a few days after copulation.

Natural delayed implantation is known to occur in a number of diverse mammals—the roe deer (*Capriolus*), the armadillos (*Dasypus*), and the Mustelids.

Among the Pinnipedia natural delayed implantation is not unknown. Nansen (1928, quoted by Bertram), working on the harp seal, suggests a pause in growth on the evidence of embryos only 2½ inches long after four months. Bertram also quotes similar suggestions in the case of the hooded seal (Høst) and the bearded seal (Chapsky and Kovelev, 1938).

Enders, Pearson and Enders (1946) have found free blastocysts in the northern fur seal two to three weeks after copulation. This taken in conjunction with the fact that adult females show no macroscopic signs of pregnancy two to three months after copulation strongly suggests a delay.

In some of these animals at least, the cause seems to be environmental. Hansson (1947) working on the mink, showed that there was a connection between implantation and the daily amount of sunlight. Work on the American pine marten (*Martes americana*), too, shows that the delay can be reduced by exposing pregnant females to artificial light during the winter (Pearson and Enders, 1944). These instances indicate a pituitary activation and Hansson suggests that when the amount of light reaches a certain threshold, the pituitary secretes the substance luteotrophine which stimulates the corpus luteum to secrete progesterone. This in turn brings on the changes in the endometrium necessary for implantation.

The influence of light on implantation in the elephant seal was not investigated by the writer since it is impossible to do experimental work on this species, but general considerations suggest that some such factor must operate as the governing mechanism.

AUTUMN

Field observations. Figure 5 shows the changes in the seal population at four Heard Island beaches over a period of about 18 months. It will be noticed that there are three periods (Peak A, Peak B, and Peak C), when seals are ashore in abundance.

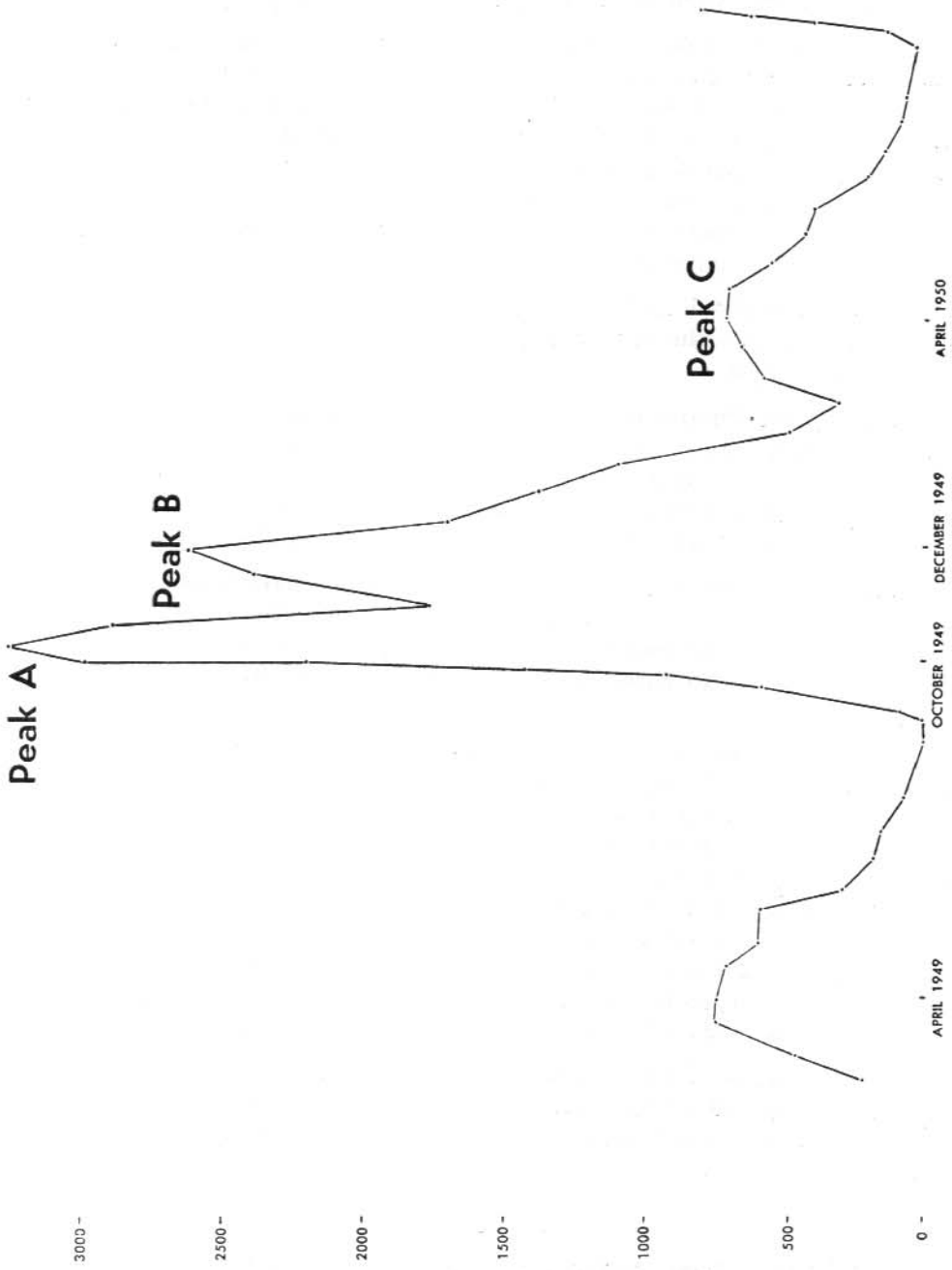

Fig. 5.—Fluctuations in the seal population in the "Four Bays" area, Heard Island, March, 1949-September, 1950.

Peak A is the breeding and mating peak. The population consists of comparatively few adult and near adult bulls, huge numbers of adult cows and a rather smaller number of pups.

Peak B is the moulting peak when the immature seals and cows come ashore.

Peak C covers a period from the beginning of March to the end of May. Its composition is complex, since each age group has its own particular cycle, but in general it consists very largely of immature seals, which at this period spend a good deal of time resting ashore. This intervenes between a period of feeding at sea after their moult, and their final departure for the winter at sea. Unlike breeding and moult, this period ashore does not appear to fulfil any widespread physiological need, since the numbers ashore are in no way comparable to the other peaks.

At the beginning of March the seals ashore are very mixed, including a few late moulters of various categories. Most of the bulls moult during March and they form an important element of the population in this month. The changes in the composition of the population ashore during these three months are illustrated by the following counts made in 1953. (Figures are the combined totals for Corinthian Bay and South West Bay, data supplied by Gwynn.)

Date	20 March	22-23 April	21-23 May
Bulls	36	26	—
Cows	2	2	3
5th and 6th year	1	12	127
4th year male	8	41	36
4th year female	—	4	12
18 and 30 month seals	176	234	54
Pups	40	58	58

The classification into age groups was inevitably arbitrary, especially after the third year, but was facilitated by the presence of branded animals up to three and a half years old, and it is claimed that with experience a considerable degree of accuracy can be attained. The main criterion is size. The fourth year females (i.e. $3\frac{1}{2}$ years old) present most difficulty, but can be distinguished from old cows by size and by their relatively unscarred coats. They are more easily confused with third year females, as there is a considerable overlap in size. Two branded females of this age-group were sighted during May, at least one of which was pregnant, as it gave birth to a pup the following October. As only about 1% of any age group are branded, this is valuable confirmation of the impression that fourth year females are not uncommon ashore in May. Undoubtedly others were included in the third year group. It will be seen that very few old cows come ashore during this period. In the count of 21-23 May all males over four years old were placed together, and the total included a few older animals, but they were nearly all obviously sub-adult immature seals (see Laws, 1953, Fig. 22d).

The female reproductive system. Three adult females were killed during this period (see Table II).

Ma4: The right ovary contained a 5 mm. corpus albicans, very yellow in colour and heavily invaded with connective tissue. The follicle measured up to 4 mm. in diameter.

The left ovary was considerably larger than the right, over half its bulk consisting of a functional corpus luteum. Fourteen follicles were found, ranging in size from 0.5 mm. to 8 mm. in diameter. At least four were over 6 mm. All follicles contained jelly-like liquor folliculi.

Only the left horn of the uterus was examined. It was very much larger than the right horn and contained a small living foetus. The foetus was 286 mm. in length (curved measurement, tip of snout to tip of tail), and weighed 1 lb. 5½ oz. It was male and even at this early stage was identical in shape and proportions with a normal adolescent seal. There was no hair except the vibrissae of the snout and "eyebrows". A small aperture on each side of the head represented the external ear opening. Visible tooth buds were absent but "finger nails" and "toenails" were well developed. The colour was salmon pink.

The placenta formed an annular band 3½-4 inches wide around the lumen of the uterus and almost exactly halfway along the horn. It was easily stripped from the uterus by the insertion of the fingers at its edge, and this resulted in very little bleeding. Blood vessels were plainly visible in the foetal membranes which contained about 950 ccs. of amniotic fluid (SG 1.006).

A piece of placenta attached to the uterus was sectioned in Australia.

Ma6: The right ovary was much larger than the left due to the presence of a 24 mm. diameter corpus luteum. Twenty-six follicles were counted. Most were small (about 2 mm.) but three of them were 4-5 mm.

The left ovary contained a 4-5 mm. corpus albicans which was almost entirely connective tissue. The follicles were all small.

Only the right horn of the uterus was examined, as it was of much greater size than the left and obviously contained a foetus. The foetus which was male was 325 mm. in length and weighed 1 lb. 13 oz. It was identical in appearance with Ma4. The placenta was 4½ inches wide and the quantity of amniotic fluid was 1100 ccs.

Ma9: The right ovary contained an 8.5 mm. corpus luteum and a few follicles, the largest of which was 5 mm. diameter. The corpus luteum retained its lobed appearance and there seemed to be very little invasion by connective tissue.

The left ovary contained two corpora albicantia consisting of very small areas of whitish scar tissue.

The uterus was not examined except to verify the absence of a foetus.

The mating season lasts roughly one month (from about 10 October to 15 November). Therefore the Ma4 foetus was between 5 and 6 months; and the Ma6 foetus between 6 and 7 months old. The size of these foetuses when compared with the birth size (about 1 metre) either indicates that the foetal growth rate is slow initially and becomes more rapid, or gives further support to the evidence for delayed implantation, that is, that actual growth of the foetus occurs only during 8 or 9 months of the pregnancy.

The corpora lutea of Ma4 and Ma6 were the largest found by the writer in any ovaries and it is probable that about 24 mm. is the maximum size attained during pregnancy.

It is interesting to note that even at this stage the previous year's corpora lutea are still recognisable as such, and have not entirely degenerated to scar tissue.

The corpus luteum of Ma9 presents a problem. In size and degree of degeneration it seems comparable to those found in seals which have recently pupped, e.g., Ma23 and Ma24. No foetus was found in the uterus and unfortunately no close examination of the endometrium was made to establish the presence or absence of a placental scar. It is, however, thought possible that this seal had had a miscarriage perhaps a month previously, and that this could account for her presence ashore so late in the season. Only two other possible explanations have occurred to the writer:—

(a) That the cow ovulated at the normal time but failed to conceive. This seems most unlikely, since such a corpus luteum should have developed and almost completely degenerated in the seven months which had elapsed since the breeding season.

(b) That the ovulation had occurred recently. The hypothesis of ovulation outside the normal season also seems unlikely since it is probable that a particular set of environmental factors determine the time of ripening of the follicles, and it is thought that ovulation itself is induced by copulation. In this case, then, the cow would have had to ripen the follicle in autumn instead of spring and acquire the services of a bull again out of season.

Since the approximate time of implantation (early February), the lengths of four foetuses (Ma40, Ma4, Ma6, and Ma16) and the average

length at birth (4 feet) are known, it is possible to get a tentative idea of the foetal growth rate, though the data are inadequate to construct a growth curve. For ease of reference these measurements are repeated below:

	Date	Length	Weight
Ma40	25 February	1.5 mm.	—
Ma4	21 April	286 mm.	1.34 lbs.
Ma6	9 May	325 mm.	1.8 lbs.
Ma16	15 August	950 mm.	40 lbs.
Pup	October	About 1200 mm.	65-70 lbs.

WINTER

Field observations. After the moulting season the adult females go to sea to feed, in order to recuperate from the strain of the breeding and moulting seasons, to supply the ever increasing demand of growing foetuses, and to build up reserves of blubber for the next period ashore. Except for a few cases they remain at sea from late February to late August. Little is known about their movement and habits at sea; in fact very few records exist of elephant seals being sighted at sea. It is thought that they move north into warmer waters and that their chief food is cuttlefish.

A few do come ashore again in the March-April peak and an occasional one may be seen on the beaches later in the winter. The writer intended to take as many of these stragglers as possible during the winter but events prevented him from doing so before mid-July. However, five seals were killed between 25 July and 15 August and provided some interesting material.

The female reproductive system.

Ma12: About 100 yards from this seal were found portions of the skeleton of a foetus which had been picked clean by birds. Some flesh still adhered to the bones and from this it was judged that the foetus had been there only a few days.

The right ovary contained a 19 mm. diameter corpus luteum.
The left ovary contained an 8 mm. corpus albicans.

The right horn of the uterus was almost three times the size of the left and, on being opened, a fresh unhealed placental scar was revealed.

Ma13: The right ovary appeared never to have carried a corpus luteum since there were no small masses of scar tissue such as are found in the ovaries of most adult seals denoting previous ovulations. A few follicles in both ovaries were 4-5 mm. in diameter.

The left ovary contained a well marked 6 mm. corpus albicans, hard and whitish in appearance.

The uterus showed no sign of pregnancy.

There are two possible explanations of the corpus albicans:—

(a) That it represents an ovulation in the last breeding season, but the cow failed to conceive.

(b) That conception occurred but was soon followed by a miscarriage.

No decisive evidence is available for either possibility. The virgin character of the right ovary suggests that in either case it was a first ovulation.

Ma14: The right ovary contained two corpora lutea, one 13 mm. and one 7 mm.

The left ovary contained one small mass of scar tissue from past ovulation and ten follicles, the largest 6.5 mm. in diameter.

The right horn of the uterus was about twice the size of the left, and when opened revealed a placental scar which was beginning to heal over. Healing scabs in the region of the cervix may indicate a difficult miscarriage. No foetal remains were discovered in the vicinity.

Ma16: The right ovary contained a 16 mm. corpus luteum.

The right horn of the uterus was tremendously distended and contained a 950 mm. female foetus weighing 40 lbs. Short fur was developed all over the body and tooth buds were easily visible. The placental width was 7 inches and the quantity of amniotic fluid was 3,500 ccs.

Ma17: The right ovary contained one small mass of scar tissue from past ovulation and follicles up to 6 mm. in diameter.

The left ovary contained an 8 mm. corpus luteum.

While removing the uterus from the body of the seal a hard object was felt in the body of the uterus. On examination this proved to be the decomposing anterior half of a foetus. The posterior half (umbilicus to tail) was still in the left horn in the normal foetal position; the placenta had lost its connection with the endometrium and lay loose in the lumen. The two halves of the foetus were placed roughly together and its length measured (approximately 230 mm.). This suggests that the foetus had died about April (cf. Ma4).

The five females listed above constitute practically the whole late-winter adult female population of a section of coast which at the peak

of the breeding season harbours about 1500 cows. Of these five, only Ma16 was carrying a live foetus and appeared to be normal. The remainder had been either unable to carry through a normal pregnancy, or had failed to conceive; in either case a physiological or anatomical defect was present. Ma9 may be cited as another case in point. The number of cases of abnormality justify the hypothesis that pregnant seals return to shore only when a pregnancy is about to be, or has been, terminated. Ma12 and Ma14 came ashore to abort, and healthy pregnant seals normally come ashore only when parturition is very close.

Among the small number of seals seen ashore during June and July immature males over three years old are the commonest category, most of the remainder being pups and other young seals under three years old, males predominating. The behaviour of Ma9 and Ma13, which had failed to conceive, or miscarried early (as seems more likely, from the size of the corpus albicans) therefore resembles that of other seals which do not have to build up their reserves in preparation for the breeding season.

The cause for the miscarriage in the case of Ma12 and Ma14 is thought to have been senility. Both these were large cows, with well-scarred coats. The ovaries of both seals were sectioned and it was discovered that extensive deposits of calcium were so heavy in places that the microtome blade was extensively chipped. Calcified arteries in other animals are usually associated with old age and there is no reason to suspect other causes in the case of these seals.

The presence of multiple corpora lutea may also have a bearing on the miscarriage. In Ma12, killed within a few days of the expulsion of the foetus, the 19 mm. corpus in the right horn was evidently the one associated with the pregnancy which had just terminated. The 8 mm. corpus which was heavily invaded by connective tissue in the opposite ovary seems too large to have been derived from the previous season's pregnancy, and the possibility of a twin pregnancy, involving both halves of the uterus, must be considered. If this were so, the foetus in the left horn must have aborted some time previously.

In Ma14, the presence of two corpora in the one ovary as far as the writer knows is the first case of this nature recorded in the literature of the elephant seal, and is no doubt a rare abnormality. It is obviously suggestive of a twin pregnancy.

Unfortunately, no microscopic sections were made of the ovaries of Ma17 and the reason for the death of the foetus is not known. It was evidently broken in half during an attempted expulsion. There was no sign of multiple ovulation.

SUMMARY

1. The reproductive history of the female elephant seal is described for four significant periods in the annual cycle, namely the breeding and mating season in the spring, the moulting season in summer, and autumn peak ashore, and the winter.

2. Right and left ovaries function alternatively, and the embryo is implanted in the uterine horn of the same side as the functional ovary.

3. The corpus luteum develops rapidly up to 15 mm. in diameter a fortnight after ovulation. It reaches maximum size (about 24 mm.) in early May. It begins to regress prior to parturition. It slowly atrophies throughout lactation, and is still present as a discrete body three or four months later.

4. The follicle begins to develop at parturition and continues to swell throughout lactation. Its jelly-like liquor folliculi liquifies just prior to copulation and this change may coincide with the onset of oestrus. It is thought that ovulation is induced by copulation.

5. The placental scar is a product of parturition. It decreases in width with the involution of the uterine horn. The endometrium heals over; the red colour slowly fades and the definition is gradually lost but it is still recognizable three or four months after parturition.

6. It is concluded that natural delayed implantation is the rule. Copulation occurs during October-November and implantation takes place in early February.

7. Placentation is initially chorio-vitelline which is replaced by chorio-allantoic to form a zonary type placenta.

8. Cases of miscarriage are recorded and suggestions advanced as to their cause.

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