HAREM STRUCTURE OF THE SOUTHERN ELEPHANT SEAL *MIROUNGA LEONINA* AT KERGUELEN ISLAND

by R.J. VAN AARDE
Mammal Research Institute, University of Pretoria, Pretoria 0002

The social organisation and breeding behaviour of the Southern Elephant Seal *Mirounga leonina* has previously been described in detail by Angot (1954), Laws (1956), Carrick and Ingham (1960) and Carrick, Ingham and Csordas (1962). Spontaneous gregariousness of adult cows during the onset of the breeding season results in the formation of a breeding rookery which, when under control of a bull, is defined as a harem. The term "harem", when used to describe the social organisation of this species, does not imply that one male keeps a fixed group of females, nor that he herds them, but refers to a social unit comprising a variable number of adult cows and a few mature bulls, one of which is dominant. A social hierarchy amongst bulls, established through threats and fighting, determines the access which a bull will have to a group of cows. Although bulls do not have an important role in harem formation, their experience and dominance are of importance to the continuance and growth of a harem (Carrick *et al.*, 1962).

The present paper provides information on the harem structure of a population of elephant seals which has not been exploited during the past 12 years. Previous accounts of the general ecology of this population were published by Ring (1923), Arctas (1951) and Angot (1954). Pascal (1979) indicated that the breeding population increased from 1952 to 1970 by an estimated 20 per cent, and Laws (1960) stated that this population was probably the second biggest in the world.

As part of a long term investigation on several ecological aspects of elephant seals at Kerguelen, conducted under the auspices of the Director of Scientific Laboratories, Terres Australes et Antarctiques Françaises (TAAF), this study was carried out at the

invitation of TAAF during the austral summer of 1977, forming part of a cooperative mammal research programme between the French and South African (SASCAR) scientific authorities controlling their respective Antarctic programmes.

METHODS

Data on numbers of cows and bulls of different social categories were obtained from ground counts, conducted at the time when the number of cows hauled out was at a maximum. Pascal (1979) indicated that the date did not differ at different localities or in different years, and that the peak occured on 15th October. Le Boeuf and Briggs (1977) indicated that the size of a specific harem is variable, except at a specific time during the breeding season, and that the most important time to describe harem size was when it contained the maximum number of cows. Due to practical limitations this survey could not be conducted within one day, and thus information on harem size and structure was obtained for the population breeding along 79 km of coastline (from Pointe Molloy to Cap Noir), from 13-22 October 1977. Adult bulls were assigned to one of the four social classes described by Carrick *et al.* (1962).

STUDY AREA

Kerguelen Island archipelago (49°15'S, 69°30'E), in the south Indian ocean, comprises approximately 300 islands and islets, all volcanic in origin, with a total area of approximately 7,200 km², and a coastline of 3,000 km. The triangular-shaped main island (" Grande-Terre ") is approximately 6,600 km² in area, and is characterized by numerous peninsulas, large bays and a coastline deeply indented with fjords. The climate is typically oceanic with a mean annual temperature of 4.4°C and persistent westerly winds, often of gale force. Rainfall is evenly distributed over 250-300 days of the year. The archipelago is on the Antarctic Convergence, and is therefore a mid-range breeding ground for elephant seals, and the population represents a major part of one of the three world stocks of southern elephant seals (Laws, 1960).

The largest part of this population breeds along the south and eastern coastline of the Courbet Peninsula (Angot, 1954). Four different breeding areas could be distinguished : (a) sandy beaches, (b) pebble beaches, (c) cobble beaches, and (d) vegetated humps behind the beach line.

RESULTS

At the time of the census 38,625 adult cows and 2,541 mature bulls, in 375 harems, were counted. Some of the bulls (69 ; 2.72 per cent) were observed in the water well away from the breeding rookeries, and it was not possible to categorise them. Beachmasters and assistant beachmasters (bulls observed within the harems) accounted for 51.78 per cent (1,280) of all the bulls counted, 19.58 per cent were classified as challengers and the remaining 28.64 per cent as bachelors.

Of all the cows counted only 0.7 per cent (362) did not occur in harems. The harem sex ratio was 1 ♂ : 29.97 ♀♀ and for all animals counted the sex ratio was 1 ♂ : 15.20 ♀♀.

Table I shows harem structures on the four different breeding areas. Mean number of cows for the total study area was 102.3 ± 135.43 (range 5 to 1,350 ; n = 375). However, harem size seems to be influenced by the surface structure of the breeding area. Harems located on sandy beaches were nearly treble the size of those on pebble beaches, which in turn were over twice as large as those on vegetated areas behind the actual beachfront. Harems on cobble beaches were considerably smaller that those on any of the other areas.

Considerable variation exists in the frequency distribution of harem sizes on the different breeding areas, as indicated in Figure 1. With the exception of sandy beaches, harem size classes with the highest frequency were below the calculated mean harem sizes.

The total number of animals per km of coastline, and the number of harems per km of coastline for the different surface types are given in Table II.

Mean harem density (number of harems per km coastline) for the study area was 4.75 harems per km coastline, with the highest density on sandy beaches (5.85) followed by vegetated humps (5.15), pebble beaches (4.98) and cobble beaches (1.11). Although the number of harems per km coastline did not vary greatly (cobble beaches excluded) the tremendous differences in harem size on different breeding areas (Table I) resulted in big differences in the number of adult animals per km coastline of different breeding areas, as indicated in Table II. However, the number of animals per km coastline in the total study area was estimated at 520 adults per km coastline.

The mean harem structure (beachmasters : assistant beachmasters : challengers : bachelors : cows) was 1 : 2.54 ± 4.03 : 1.29 : 1.89 : 102.3 ± 135.43. Since challengers and bachelors tended to move about within a specific area, bulls in these cate-

TABLE I

Mean number of cows and bulls of each social category per harem for four different beach types on Kerguelen Islands.

Beach type	Number of cows	Mean number of animals per harem				
		Adult * females	Beach-masters	Assistant * beachmasters	Challengers	Bachelors
Cobble beaches	10	22.1 ± 21.58	1	0.90 ± 0.88	0.70	2.70
Vegetated hillocks	134	37.9 ± 29.07	1	0.87 ± 1.19	1.20	2.13
Pebble beaches	152	84.6 ± 83.18	1	2.23 ± 3.43	1.28	1.17
Sandy beaches	79	253.5 ± 202.71	1	6.11 ± 5.78	1.53	2.75
Total area	375	102.3 ± 135.43	1	2.54 ± 4.03	1.29	1.89

* Mean ± Standard deviation

TABLE II

The influence of surface structure on harem size.

Surface structure	Distance of coastline (km)	Number of harems	Number of harems per km coastline	Number of adults per km coastline
Cobble beaches	9.0	10	1.11	30.33
Vegetated humps	26.0	134	5.15	220.72
Pebble beaches	30.5	152	4.98	449.45
Sandy beaches	13.5	79	5.85	1,550.85
Total area	79.0	375	4.75	520.20

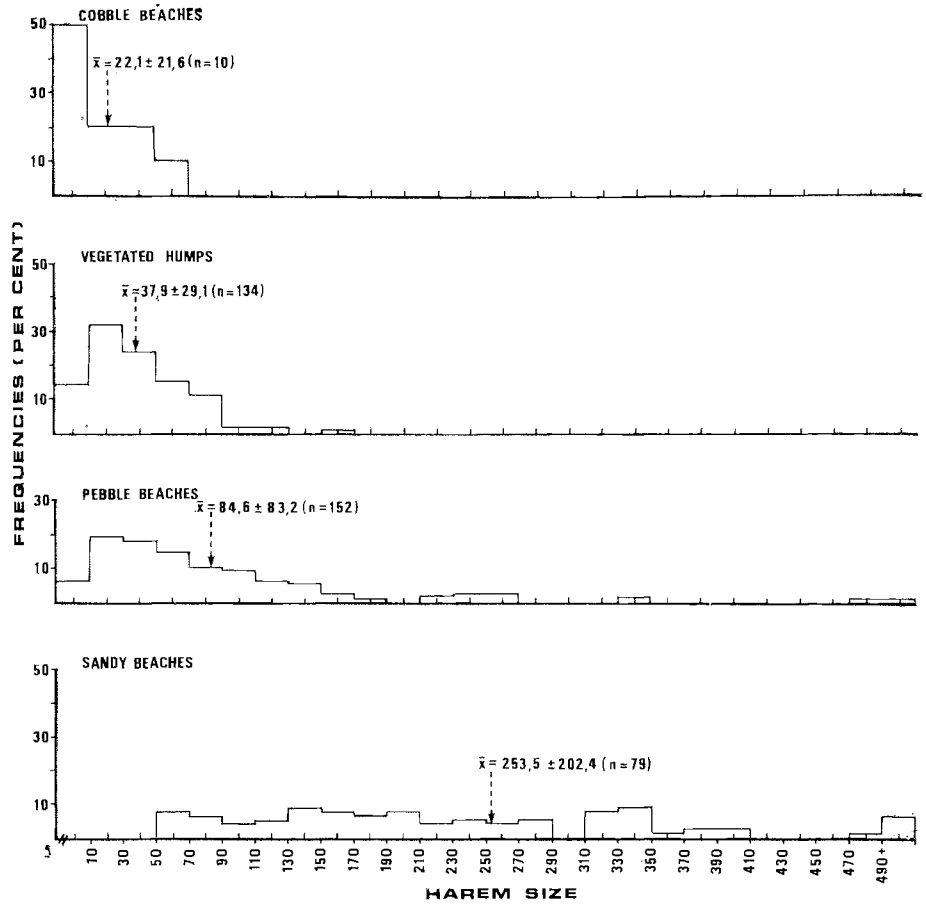

Fig. 1. — Frequency distribution of harem size related to surface structure of breeding areas.

gories were not allocated to specific harems, and therefore standard deviations for these categories could not be calculated.

The relationship between the number of assistant beachmasters and harem size is shown in Table III. It seems that harems with less than 33 cows do not have an assistant beachmaster.

TABLE III

Relationship between the number of assistant beachmasters and the mean number of cows per harem.

Number of beach-masters	Number of assistant beachmasters	Number of harems	Number of adult cows per harem		
			$\overline{X}$	S.D.	range
1	0	135	33.50	27.04	5 - 132
1	1	69	51.26	36.37	7 - 196
1	2	51	59.75	40.05	8 - 176
1	3	36	126.97	71.87	37 - 334
1	4	23	145.52	51.39	33 - 247
1	5	12	161.92	88.98	45 - 338
1	6	12	229.67	85.18	68 - 343
1	7	10	253.10	91.85	69 - 399
1	8	7	280.57	96.68	127 - 402
1	9	4	301.75	65.15	244 - 373
1	10 - 15	6	365.17	87.68	219 - 487
1	16 - 34	10	637.80	317.07	346 - 1,350
		375	102.3	135.43	5 - 1,350

Information available on the relationship between harem size and pup mortality indicated an increase in the number of dead pups with an increase in harem size (Table IV). In spite of tremendous variation a highly significant relationship ($r = 0.66$; $P < 0.001$; $n = 375$) between the number of cows per harem and the number of dead pups per harem exists. This relationship approximates a straight line described by the equation $y = 0.008\ x + 0.022$, where $y =$ number of cows per harem and $x =$ the number of dead pups per harem. A significent relationship ($p < 0.001$; $r = 0.64$) between the number of bulls per harem and the number of dead pups per harem has also been observed.

By extrapolating the information on harem structure published by Angot (1954) and by comparing this with the information obtained during this survey for the same part of the coastline, an evaluation of changes in harem structure with changes in population size was possible (Table V). During 1952, 15,830 females in 284 harems were counted along the coastline from

Pointe l'Etoile to Cap Ratmanoff, giving a mean harem size of 55.7 cows per harem. For the same area counted in the same week of 1977, 21,103 females occurred in 214 harems, with a mean harem size of 98.6 cows per harem.

TABLE IV

The relationship between surface structure, harem size and pup mortality.

Surface structure	Number of harems	Mean number of cows per harem	Mean number of live pups per harem	Mean number of dead pups per harem	Percentage pup mortality per harem
Cobble beaches	10	22.1	2.1	0.10	0.48
Vegetated humps	134	37.9	37.5	0.22	0.59
Pebble beaches	152	84.6	81.3	0.86	1.06
Sandy beaches	79	253.5	236.9	2.25	0.95
	375	102.3	96.8	0.90	0.93

Altough the cow population increased the number of harems decreased, especially in the area from Pointe Charlotte to Cap Ratmanoff (sandy beaches) where the cow population increased by 8.34 per cent while the number of harems decreased by 74.4 per cent and mean harem size increased by 322.93 per cent. On the coastline surrounding Norwegian Bay (Pointe l'Etoile to Pointe Morne) the increase of 159.9 per cent in population size was accompanied by an 138.0 per cent increase in the number of harems. For the total area a 33.3 per cent increase in the cow population was accompanied by a 24.7 per cent decrease in the number of harems.

Although the cow population and the number of harems on the coastline of the Norwegian Bay increased, the mature bull population in this area decreased by 23.1 per cent (from 745 to 573), resulting in a marked decrease in the number of bulls per harem as well as a dramatic change in sex ratio — from 1 ♂ : 3.60 ♀♀ in 1952 to 1 ♂ : 12.6 ♀♀ in 1977.

In the case of the area from Pointe Charlotte to Cap Ratmanoff however, a 30.3 per cent decrease in the bull population as well as a decrease in the number of harems resulted in an increase in the number of bulls per harem as well as a change in sex ratio — from 1 ♂ : 13.91 ♀♀ in 1952 to 1 ♂ : 21.67 ♀♀ in 1977. For the

TABLE V

An evaluation of changes in harem structure with changes in population size.

Area surveyed	Number of harems		Number of adult cows		Number of adult cows/harem		Number of adult bulls/harem	
	1952	1977	1952	1977	1952	1977	1952	1977
Norwegian Bay	50	119	2,680	6,966	53.6	58.54	14.9	4.82
Pnte Morne → Pnte de l'Etang	19	22	930	1,235	48.9	56.14	6.6	4.14
Pnte de l'Etang → Pnte Charlotte	47	30	1,460	1,245	31.1	41.5	6.3	7.73
Pnte Charlotte → Cap Ratmanoff	168	43	10,760	11,657	64.1	271.1	4.6	12.53
	284	214	15,830	21,103	55.7	98.6	4.9	6.7

Data for 1952 extrapolated from Angot (1954).

total area under consideration sex ratio changed from 1 ♂ : 11.35 ♀♀ in 1952 (Angot, 1954) to 1 ♂ : 11.77 ♀♀ in 1970 (Pascal, 1978), to 1 ♂ : 14.71 ♀♀ in 1977.

DISCUSSION

Limited terrestrial mobility in combination with a tendency to form aggregations results in breeding taking place under extraordinarily congested circumstances in the phocids (Bartholomew, 1970). This certainly holds true for elephant seals on Kerguelen (Table II), as 520 elephant seals occurred per km coastline over 79 km during the breeding season. Gregariousness is a characteristic that pinnipeds share with many other vertebrates, and a number of environmental factors influence the extent of gregariousness. Information obtained during the present study indicated that surface structure has an important influence on harem size. This in turn influences the number of bulls per harem, as well as the proportion of bulls in the different social categories. For example, 67.2 per cent of mature bulls that hauled out on breeding areas with a sandy surface were either beachmasters or assistant beachmasters, while 34.6, 32.3 and 56.1 per cent of all bulls on cobble beaches, vegetated areas behind beaches, and pebble beaches respectively belonged to these social categories.

A significant correlation between harem size in terms of the number of adult cows per harem and pup mortality has been observed. This is similar to the situation described by Le Boeuf and Briggs (1977) for the Northern Elephant Seal, *Mirounga angustirostris*. Since beach surface structure influenced harem size, it should therefore also have an indirect influence on pup mortality. In the northern species at least 60 per cent of pup mortality resulted from injuries inflicted by adult seals during conflicts of interest between adults attempting to maximize their reproductive success (Le Boeuf and Briggs, 1977). Trampling and crushing was an important cause of pup mortality in the Southern Elephant Seal at Macquarie Island (Carrick and Ingham, 1962) and Marion Island (Condy, 1977), resulting mainly from bull : bull aggression, and where harem size was the greatest, the incidence of bull competition increased, causing a density dependent increase in pup mortality. Although quantitative information on the causes of pup mortality for the population at Kerguelen in this respect has not been obtained, it is of interest to note that a significant relationship between the number of bulls per harem and the number of dead pups per harem has also been observed.

The overall ratio of cows to bulls on different islands where elephant seals breed does not vary much ; at Kerguelen their ratio was 11 : 1 in 1952 (Angot, 1954), at Macquarie Island 11 : 1

in 1960 (Carrick and *et al.*, 1962), in a protected area on South Georgia 13 : 1 and on exploited beaches on the same island 30 : 1 (Laws, 1956), at Marion Island 11 : 1 in 1974 (Condy, 1977), at Kerguelen 11 : 1 in 1970 (Pascal, 1979) and during the present survey 15 : 1. Laws (1973) indicated that an increase in sex ratio is associated with selective removal of older bulls, resulting in the harems being larger and the bulls in control of it younger and more inexperienced. During the years 1958-1964 approximately 12,000 adult bulls were removed from Kerguelen (Pascal, *pers. comm.*) but since the sex ratio during 1970 did not differ from unexploited populations, this commercial operation does not appear to have had much effect on the sex ratio of the population. However, since no bulls were artificially removed from this population between 1970 and 1977, and since an increase in sex ratio is associated with selective removal of older bulls, the increased sex ratio observed in 1977 could only be ascribed to an increase in environmental mortality factors acting on bulls during the aquatic phase of their life.

In the Northern Elephant Seal (allopatric to the southern species) less than one third of the bulls in residence will copulate (Le Bocuf, 1974). On Kerguelen the ratio of actual breeding bulls to cows was high (1 : 30) and although considerable variation exists, this indicates that when harem size exceeds 30 cows the dominant bull will allow another bull into the harem. This ratio differs considerably from that found by Carrick *et al.* (1962) for the population at Macquarie Island, where harems consisting of less than 50 cows never contained more that one breeding bull. Condy (1977) indicated that for the population at Marion Island harems consisting of more than 60 cows included an assistant beachmaster and those containing 130-150 cows included two assistant beachmasters, showing a pattern very similar to the Macquarie Island situation.

At Kerguelen the pattern varied considerably (Table III), particularly with respect to surface nature of the beach. In addition, the beach line extending nearly continuously over 79 km enabled elephant seals to occupy this whole area, whereas at Marion Island the beaches were separated from each other by geographical barriers and coastal cliffs, thus preventing large aggregations of elephant seals. On Kerguelen it is therefore more difficult for a beachmaster to maintain exclusive control over a group of cows than it is at Marion Island, resulting in the differences in the number of cows per bull.

Although great variation in the number of cows per bull occurred on Kerguelen Island (Table III), the general trend is that as harem size increases the number of assistant beachmasters per harem also increases. Although the ranges of harem sizes with different numbers of assistant beachmasters overlap considerably,

the relationship between the number of breeding bulls (beachmaster and assistant beachmasters) and the number of cows per harem approximates a straight line described by $y = 30.34\ x - 5.91$ (where x = number of breeding bulls per harem and y = number of cows per harem) with a coefficient of determination (r^2) of 0.81.

Mean number of cows per harem is greater at Kerguelen (102.3 ± 135.4) than at South Georgia, where average harem size was 24 for Darmouth Point Reserve, 46 at Hestesletten and 52 at Maiviken (Laws, 1960). At Macquarie Island Carrick *et al.* (1962) indicated that medium sized harems of 100-300 and large harems of 300-600 cows, as well as one enormous harem of more than 1 000 cows occurred. Condy (1977) indicated that harem sizes on Marion Island were much smaller than on Macquarie Island, and he calculated mean harem size at 45.3 ± 43.8. Angot (1954) found a mean harem size of 55 cows per harem, ranging from 10 to 190, at Kerguelen in 1952.

Carrick and Ingham (1960) stated that if certain favoured beaches became too crowded on Macquarie and Heard Islands harems coalesced into a continuous mass of cows and pups, with beachmasters dispersed among and around them. This is similar to the situation at Kerguelen Island, where a slight increase (8.34 per cent) in the cow population on the densely populated (1,551 adults per km coastline) coastline from Pointe Charlotte to Cap Ratmanoff resulted in a large decrease (74,4 per cent) in the number of harems and a 323 per cent increase in mean harem size. However, on the less densely populated coastline (450 animals per km coastline) of the Norwegian Bay an increase in population size resulted in a similar increase in the number of harems and a small change in mean harem size. As indicated above, an increase in harem size will result in an increase in pup mortality. Furthermore, Le Boeuf (1974) indicated that a higher percentage of resident mature bulls begins to mate as breeding beaches become more crowded, which will influence reproductive success of males and females.

It can be concluded that an increase in harem size, coupled to an increase in population size, can/will have a negative influence on pup survival as well as reproductive success and therefore must be regarded as a density dependent regulatory factor in population size.

SUMMARY

Information obtained during the austral summer of 1977 on the harem structure of the Southern Elephant Seal *Mirounga leonina*, breeding on Kerguelen Island is presented. Harem sex

ratio was 1 ♂ : 29.97 ♀♀ while the overall sex ratio for mature animals was 1 ♂ : 15,2 ♀♀. Mean harem structure (beachmaster : assistant beachmasters : challengers : bachelors : adult cows) was 1 : 2.54 ± 4.03 : 1.29 : 1.89 : 102.3 ± 135.43 for 375 harems occurring along a 79 km stretch of coastline. Harem size as well as harem structure were influenced by the surface structure of the area where animals breed — the largest harems occurring on sandy beaches, followed by pebble beaches, vegetated humps and cobble beaches. While the tremendous increase in population size on a moderately inhabitated stretch of coastline did not result in a significant change in harem size, a slight increase in population size on a densely populated coastline, resulted in a tremendous increase in harem size and a decrease in the number of harems. A significant density dependent relationship was found between harem size and pup mortality.

RESUME

L'auteur présente des données quantitatives sur les harems de l'Eléphant de mer des Kerguelen *(Mirounga leonina)* obtenues pendant l'été austral 1977. Le sex-ratio dans les harems était de 1 ♂ pour 29,97 ♀♀, alors que dans la population adulte générale il était de 1 ♂ pour 15,2 ♀♀. La structure des harems était en moyenne la suivante : 1 « maître-mâle » ; 2,54 ± 4,03 « assistants » ; 1,29 « challengers » ; 1,89 « célibataires » et 102,3 ± 135,43 femelles adultes (taille de l'échantillon : 375 harems observés sur 79 km de côte). La taille comme la structure des harems sont influencées par la superficie de l'aire de reproduction, les plus grands harems étant observés sur les plages sableuses, et les plus petits sur celles de gros cailloux. Alors que l'énorme augmentation de la population sur une côte modérément accueillante depuis 1952 n'a pas entraîné de changement significatif dans la taille des harems, une faible augmentation de population sur une côte déjà densément peuplée a abouti à une forte augmentation de la taille des harems et à une diminution de leur nombre. Une relation statistiquement significative a été mise en évidence entre la taille des harems et la mortalité des jeunes éléphants de mer.

ACKNOWLEDGEMENTS

I am grateful to the Director of the Scientific Laboratories of TAAF for permission to undertake this survey and providing logistical support while living on the island. Financial support were provided by the University of Pretoria and the South African Department of Transport. The programme was carried out under the auspices of the Mammal Research Institute of the University of

Pretoria. I wish to thank the Director, Prof. J.D. Skinner for his encouragement and support, for his comments on the manuscript and for Dr. P. Condy and Dr. N. Fairall for reading the manuscript and to Prof. J.A. Nel and Dr. M.N. Bester for their advice. The field assistance of Mr. D. Lincoln and members of the 27th mission to Kerguelen are greatly appreciated.

REFERENCES

ANGOT, M. (1954). — Observation sur les mammifères marins de l'archipel de Kerguelen - avec une étude détaillée de l'éléphant de mer, *Mirounga leonina* (L.). *Mammalia,* 18 : 1-111.

ARETAS, R. (1951). — L'éléphant de mer (*Mirounga leonina* L.). — Etude biologique de l'espèce dans les possessions françaises australes (archipel de Kerguelen). *Mammalia,* 15 : 105-117.

BARTHOLOMEW, G.A. (1970). — A model for the evolution of pinniped polygyny. *Evolution,* 24 : 546-559.

CARRICK, R. and INGHAM, S.E. (1960). — Ecological studies on the southern elephant seal, *Mirounga leonina* (L.) at Macquarie Island and Heard Island, *Mammalia,* 24 : 325-342.

CARRICK, R., CSORDAS, S.E. and INGHAM, S.E. (1962). — Studies on the southern elephant seal, *Mirounga leonina* (L.) IV. Breeding and development. C.S.I.R.O. *Wildlife Research,* 7 : 161-197.

CONDY, P.R. (1977). — *The ecology of the Southern Elephant Seal* Mirounga leonina (*Linnaeus 1758*), *at Marion Island,* D. Sc. Disertation, University of Pretoria, Pretoria, 146 p.

LAWS, R.M. (1956). — The Elephant Seal (*Mirounga leonina* Linn.) II. General, social and reproductive behaviour. *Sci. Rep. Falkland Isl. Dep. Surv.,* 13 : 1-88.

LAWS, R.M. (1960). — The Southern Elephant Seal (*Mirounga leanina* Linn.) at South Georgia. *Norsk Hvalfangst-Tidende,* 49 : 466-476 and 520-542.

LAWS, R.M. (1973). — Effects of human activities on reproduction in the wild. *Journal of Reproduction and Fertility,* 19 : 523-532.

LE BOEUF, G.A. (1974). — Male - male competition and reproductive success in Elephant Seals. *American Zoologist,* 14 : 163-173.

LE BŒUF, B.J. and BRIGGS, K.T. (1977). — The cost of living in a seal harem. *Mammalia,* 41 : 167-195.

PASCAL, M. (1979). — Essai de dénombrement de la population d'éléphants de mer (*Mirounga leonina* L.) des îles Kerguelen (49° S, 69° E). *Mammalia,* 43 : 147-159.

RING, P.A. (1923). — The elephant seals of Kerguelen's island. *Proceedings of the Zoological Society of London,* 29 : 431-443.