An analysis of the southern elephant seal *Mirounga leonina* breeding population at Kerguelen

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The spring 1979 breeding population of southern elephant seals Mirounga leonina *at Kerguelen (49°15'S, 69°30'E) numbered 2 993 bulls and 38 181 cows, with 36 291 live pups present during the census period. Mean harem structure (beachmasters : assistant beachmasters : challengers : bachelors : cows) was 1 : 0,43 : 2,98 : 1,54 : 76,13±111,55; harem sex ratio and overall sex ratio being 1:53,1 and 1:12,8 respectively. Significant differences in the overall sex ratio, harem structure and frequency distribution exist in comparison with previous surveys, particularly that of 1977. These differences may be related to the difference in the mean census dates of the different years, but were also accompanied by a continued decrease in both the cow and bull components, corroborating the slump noted since 1970. An analysis based on subdivisions of the study area into distinct regions, showed area specific increases and decreases in cow numbers, in spite of the net decrease in cow numbers. The linear regression of area specific percentage pup mortality on the density of cows was highly significant, which could explain the area specific fluctuation in cow numbers, elephant seal cows reputedly showing fidelity to their birthsites. This density dependent mechanism acts primarily through pup mortality as a function of the density of bulls active in and around the harems, bull numbers being positively correlated with cow numbers.*

Die 1979 lente-teelbevolking van suidelike olifantrobbe Mirounga leonina *te Kerguelen (49°15'S,69°30'O) se getalsterkte was 2 993 bulle en 38 181 koeie, met 36 291 lewende welpies teenwoordig gedurende die sensustydperk. Gemiddelde haremstruktuur (strandmeesters : assistent strandmeesters : uitdagers : vrygeselle : koeie) was 1 : 0,43 : 2,98 : 1,54 : 76,13 ±111,55; met harem geslagsverhouding en algehele geslagsverhouding respektiewelik 1:53,1 en 1:12,8. Betekenisvolle verskille in die algehele geslagsverhouding, haremstruktuur en harem frekwensieverdeling, bestaan in vergelyking met vorige opnames, in besonder dié van 1977. Hierdie verskille hou moontlik verband met die verskille in die gemiddelde sensusdatums van die verskillende jare, maar was ook deur 'n voortgesette afname in beide die koei- en bulkomponente vergesel, wat die plotselinge daling sedert 1970 staaf. 'n Ontleding gebaseer op onderverdeling van die studiegebied in duidelike streke, het gebiedsgebonde toenames en afnames in koeigetalle getoon ongeag die netto afname in koeigetalle. Die lineêre regressie van areagebonde persentasie welpiesterftesyfers op die digtheid van koeie was hoogs betekenisvol wat die areagebonde wisseling in koeigetalle kan verklaar aangesien olifantrobkoeie volgens bewering getrouheid aan hulle geboorteplekke vertoon. Hierdie digtheidsafhanklike meganisme funksioneer hoofsaaklik deur welpiesterftesyfers as 'n funksie van die digtheid van bulle wat aktief is binne en rondom die harems, met bulgetalle positief gekorreleerd met koeigetalle.*

Introduction

Since the cessation of intensive exploitation of the southern elephant seal *Mirounga leonina* during the nineteenth and early twentieth centuries, with a brief revival of sealing between 1958 and 1964 at Kerguelen (Pascal 1979), population size estimates for the Kerguelen archipelago varied between 100 000 (Laws 1960) and 210 000 (Pascal 1979). Accounts of the general biology of this population were given by Ring (1923), and Angot (1954). Van Aarde (1980 a & b) described harem sizes and harem structure with special reference to the influence of beach surface nature and breeding population size, and concluded that the *M. leonina* population at Kerguelen is stable but fluctuating based on analysis of published information since 1952 (Angot 1954, Bajard 1962, Pascal 1979). As the analysis based on subdivisions of the study area indicated an increase in the range of fluctuation in cow numbers as mean density increased and a change in the sex ratio in favour of cows, the present paper provides further information on the trend of this southern elephant seal population concentrating on a possible explanation for the density-related phenomenon in cow numbers. This study forms part of a cooperative mammal research programme between France (TAAF) and South Africa (SASCAR).

Descriptions of the study area at Kerguelen (49°15'S, 69°30'E), where most elephant seals breed along the southern and eastern coastlines of the Courbet Peninsula (Fig. 1), appear in Angot (1954).

Methods

Sexually mature adult bulls, adult cows and pups were counted directly by two observers on foot. Censuses were done from 15 – 25 October 1979 at breeding beaches along the Courbet Peninsula coastline from Point Molloy in the south to a point between Cap Digby and Cap Noir in the north-east (Fig. 1). Adult bulls were allocated to four social classes following Carrick, Csordas and Ingham (1962). Pups being suckled and those that were weaned were scored separately. This allowed a predicted assessment of the maximum number of cows that would have been ashore during the breeding haulout, using the quadratic equation $y = 26{,}4 + 307{,}6x - 4{,}57x^2$, where y = number of cows plus weaned pups, x = days of the season, day 1 being 19 September and day 60 being 16 November (Van Aarde 1980a). This adjustment to cow numbers had to be made, since the study area could not be covered within the one day period of the peak cow haulout (15 October). Weaned pups represented departed cows. In very large harems the number of pups being suckled could not be counted with reasonable accuracy and therefore their numbers were estimated using cow/unweaned pup ratios determined for harems of manageable size censused on that particular day(s). The

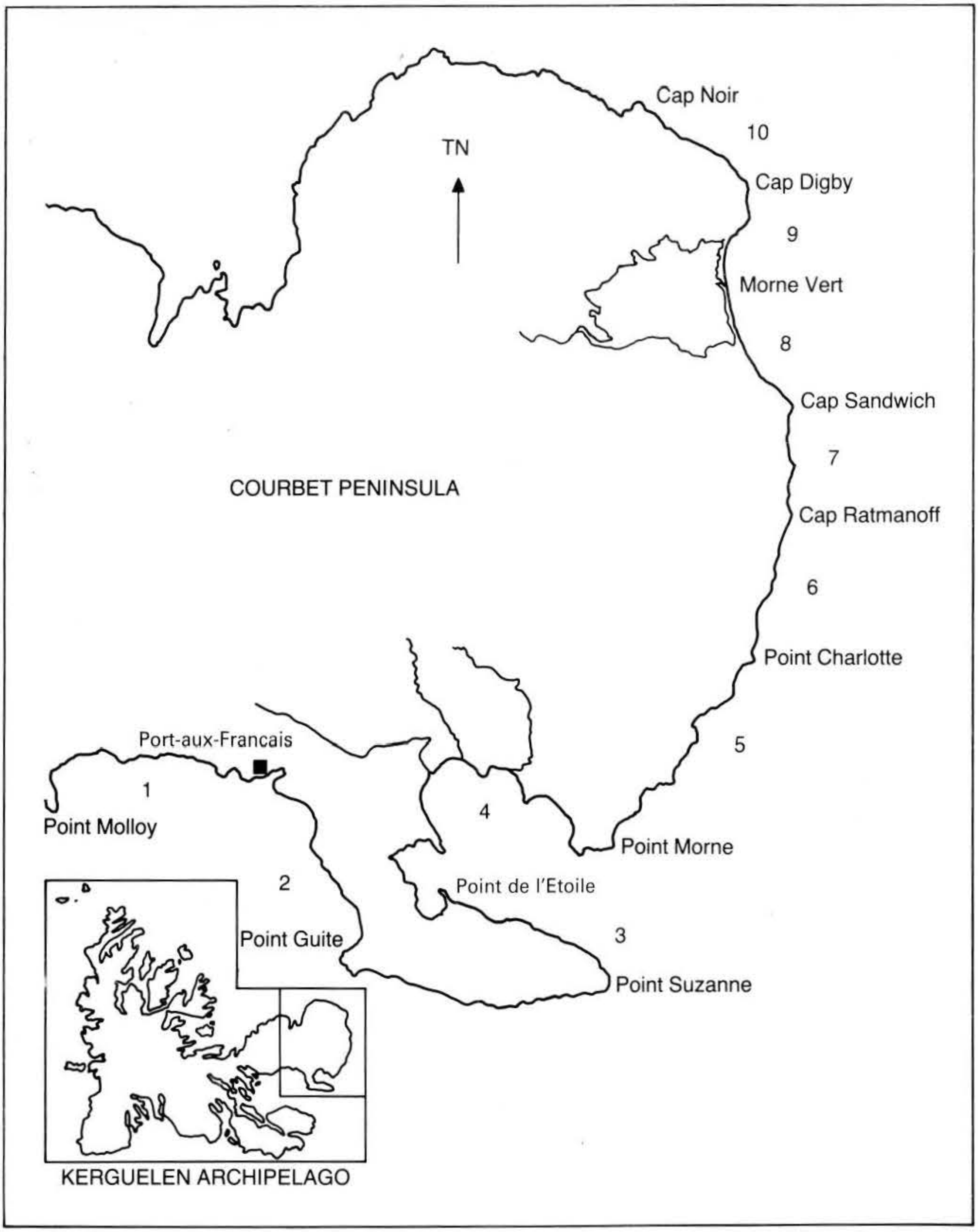

Fig. 1. Map of the Courbet Peninsula showing the extent and divisions of the study area. Area Codes (1 to 10) correspond with those in Table 1.

counts of bulls were not adjusted as Van Aarde (1980a) assumed their number present on any specific day during the mating period to be a reflection of the actual size of the bull component of the breeding population.

The analysis of population trends was based on an intrinsic rate of natural increase or decrease (r) contained in the exponential function $N_t = N_0e^{rt}$ as suggested by Caughley (1977), and applied for the Kerguelen elephant seal population by Van Aarde (1980a). To this end, and to make direct comparisons possible with published as well as raw data from 1977, the study area was divided into nine specified stretches of coastline (Cap Digby to Point Molloy), eight of these corresponding

Table 1
Census of *M. leonina* in the eastern sector of the Courbet Peninsula during the breeding season at Kerguelen.

Code	Censused areas	Date	Number of Seals						
			Bulls	Cows	(Adjusted)	Pups	WP*	DP**	Total
1	Point Molloy — Port-aux-Francais	23-10-1979	136	1 514	1 841	1 373	324	7	3 354
2	Port-aux-Francais — Point Guite	24-10-1979	163	1 676	1 992	1 518	307	6	3 670
3	Point Suzanne — Point de l'Etoile	25-10-1979	147	832	1 003	761	162	3	1 905
4	Point de l'Etoile — Riviere du Chateau	25-10-1979	270	2 453	3 160	2 256	678	18	5 675
	Riviere du Chateau — Point Matley	22-10-1979	218	3 132	3 679	2 793	547	25	6 715
	Point Matley — Point Morne	22-10-1979	199	1 947	2 222	1 736	275	13	4 170
5	Point Morne — Point de l'Etang	21-10-1979	124	1 100	1 221	1 027	121	11	2 383
	Point de l'Etang — Point Charlotte	21-10-1979	144	1 142	1 216	1 066	73	10	2 435
6	Point Charlotte — Cabane l'Estacade	17-10-1979	398	6 702	7 390	5 678	554	199	13 531
	Cabane l'Estacade — Cap Ratmanoff	16-10-1979	345	6 185	6 622	4 735	260	139	11 664
7	Cap Ratmanoff — Cap Sandwich	15-10-1979	334	5 103	5 485	3 992	178	80	9 687
8	Cap Sandwich — Morne Vert	18-10-1979	239	3 396	3 673	2 737	236	54	6 662
9	Morne Vert — Cap Digby	19-10-1979	261	2 811	3 082	2 476	253	41	5 842
10	North of Cap Digby	19-10-1979	15	188	198	166	9	3	381
	TOTAL		2 993	38 181	42 784	32 314	3 977	609	78 074

*Weaned Pups **Dead Pups

with the 1977 division (Van Aarde 1980a). The area from Point Suzanne to Point de l'Etoile (Fig. 1), however, had not been included in previous surveys, and is included when reference is made to the extended census area. Area specific density estimates for 1977 were based on raw data provided by Van Aarde (in litt.).

Harems, which are social units each composed of a variable number of cows, their pups and a small number of bulls of varying social rank, one of which is dominant to all others (Le Boeuf & Briggs 1977), were assumed when two or more cows were found together with an adult bull (beachmaster) or bulls (beachmaster and assistant beachmaster(s)) in attendance.

In the text, harem size = number of cows, while harem density and cow density were number of harems and cows per km coastline respectively. Harem length was the greatest distance across a harem and was estimated by measured steps in a straight line parallel to the longest axis of a harem.

Table 2
Relationship between the mean number of cows per harem (each containing one beachmaster) and the number of assistant beachmasters

Number of Assistant Beachmasters	Number of Harems	Number of cows per harem	
		$\bar{x}$ S.D.	Range
0	401	37,73 ± 36,26	2 – 280
1	49	142,84 ± 64,14	43 – 360
2	22	210,27 ± 93,74	88 – 440
3	7	269,43 ± 108,88	154 – 420
4	5	394,00 ± 132,55	213 – 573
5	5	463,80 ± 99,26	350 – 549
6	2	647,00 ± 130,11	555 – 739
7	4	601,00 ± 99,39	498 – 730
8	2	605,00 ± 1,41	604 – 606
	497	76,13 ± 111,55	2 – 739

Results

Population size

Observed totals of 2 993 bulls, 31 181 cows, 32 314 suckled pups, 3 977 weaned pups and 609 dead weaned and suckled pups were counted in the study area (Table 1). The density of adults, expressed as the number of adults per km of coastline, was 397 per km for the extended census area.

The predicted number of cows (Table 1) for the various stretches of coastline using the quadratic model suggested by Van Aarde (1980a) gives a figure of 42 784, which is 12,1 per cent higher than the observed total. Area-specific numbers differed significantly from that observed ($t = 5{,}95$; $df = 9$; $P<0{,}001$) (Table 1).

The estimated minimum population size calculated from the pup count times 3,2 (Laws 1960) is 118 080. For the comparable (less extensive) census area, figures for 1979 (this study) and 1977 (Van Aarde 1980a) are 115 117 and 117 739 respectively.

Social structure of the breeding population

Beachmasters (BM) and assistant beachmasters (ABM) accounted for 23,8 per cent (n = 712) of all bulls counted, of which 49,5 per cent (n = 1480) were classified as challengers (CH) and 26 per cent (n = 801) as bachelors (B). The majority (n = 37 836; 99,1%) of cows occurred in 497 harems with a range of 2 to 739 and mean of 76,1 ± 111,6 ($\bar{x}$ ± S.D.) cows per harem. The remaining cows (345) were either found singly with an attending bull (classified here as a challenger; n = 34) or in varying numbers of 1 to 20 ($\bar{x} = 1{,}94 \pm 2{,}18$; n = 146) without bulls in attendance.

The harem structure and relationship between the number of assistant beachmasters and harem sizes for the extended census area are shown in Table 2. Harems of less than 43 cows never contained an assistant beachmaster, although a beachmaster could, at least temporarily, be in exclusive control of harems of up to 280 cows. Based on the ratio between breeding bulls (beachmasters and assistant beachmasters) and the number of cows in harems (712 : 34 836), beachmasters appeared to allow an assistant beachmaster(s) into the harem when harem size exceeded 53 cows.

Mean harem structure was 1 : 0,43 : 2,98 : 1,54 : 76,13 ± 111,55 (BM : ABM : CH : B : Cows), and harem sex ratio and overall sex ratio were 1 : 53,1 and 1 : 12,8 respectively. Overall sex ratio, using adjusted cow numbers, was 1 : 14,3. A significant linear relationship between the number of cows and the number of breeding bulls (BM + ABM) per harem exists

($r = 0{,}89$; $P<0{,}001$; $n = 497$) in spite of the large overlap in harem sizes (Table 2), with the number of cows per harem representing the dependent variable. Harems of known length ($n = 42$) ranging from 21 to 620 cows ($\bar{x} = 229{,}8 \pm 157{,}9$), were also linearly related to the number of breeding bulls ($r = 0{,}95$; $P<0{,}001$; $n = 42$) this relationship being better than that between cows and bulls for these harems ($r = 0{,}85$; $P<0{,}001$; $n = 42$). A partial regression analysis in which the effect of cow numbers was excluded showed that 79 per cent of the change in bull numbers can be ascribed to changes in the length of the harem.

Approximately 60 per cent of harems contained 50 cows or less, although harems of up to 739 cows were found. Overall harem density was 4,76 harems/km coastline, while the mean harem density for the specified stretches of coastline was 5,44 ± 2,20 ($n = 9$) per km, compared with the figure of 4,45 ± 1,76 ($n = 8$) obtained for 1977.

Population trend

Estimated minimum total population (pup population × 3,2) decreased at an intrinsic rate of 1,0 per cent per year between 1977 and 1979. Adjusted figures for the cow population showed a similar decrease while the bull component increased at a rate of 6,0 per cent per year over the same period. Bull numbers did not differ significantly ($\chi^2 = 0{,}023$; $df = 1$) from those suggested through extrapolation of the overall rate of decrease between 1958 and 1977 ($r = -0{,}019$; Van Aarde 1980a). On the other hand the adjusted cow population was significantly lower ($\chi^2 = 8{,}93$; $df = 1$; $P<0{,}005$) than expected through a similar extrapolation ($r = -0{,}006$; Van Aarde 1980a). The cow and bull populations, moreover, decreased at rates of 3,2 and 5,0 per cent per year respectively between 1970 and 1979.

Using adjusted cow figures, the overall sex ratio in the present study differed significantly from that found in 1977 ($\chi^2 = 33{,}02$; $df = 1$; $P<0{,}001$) and 1970 ($\chi^2 = 41{,}14$; $df = 1$; $P<0{,}001$) respectively. The frequency distribution of harem sizes for 1977 and 1979 also differed significantly ($\chi^2 = 42{,}9$; $df = 21$; $P<0{,}005$) and was accompanied by a significant change in harem structure ($\chi^2 = 61{,}4$; $df = 3$; $P<0{,}001$) as shown by a 2 × 4 contingency table analysis, when the number of assistant beachmasters and challengers were lumped together (see Discussion).

In dividing the study area into eight sectors as in 1977 (Van Aarde 1980a) area specific mean rate of change in the adjusted number of cows was positive for all beaches from Point Molloy to Point Morne ($r = 0{,}090$), negative for Point Morne to Point Charlotte ($r = -0{,}037$), positive for Point Charlotte to Cap Ratmanoff ($r = 0{,}047$) and negative for Cap Ratmanoff to Cap Digby ($r = -0{,}116$). Mean adjusted cow densities for these areas in 1977 and 1979 did not differ significantly ($t = 0{,}86$; $df = 7$: $P>0{,}10$) but area specific rates of change in average harem sizes were positively related to the rates of change in cow numbers ($r = 0{,}92$; $df = 6$; $P<0{,}01$).

Pup mortality

Minimum pup mortality was 1,65 per cent and no relationship between the number of dead pups per harem and the number of cows per harem existed ($r = 0{,}25$; $n = 497$), in contrast to the significant 1977 relationship ($r = 0{,}66$; $P<0{,}001$; $n = 375$) demonstrated by Van Aarde (1980b).

During 1979 (present study) the number of dead pups, expressed as a function (percentage) of the number of pups born in each area, increased linearly with an increase in cow densities ($r = 0{,}94$; $df = 6$; $P<0{,}001$). This relationship was not significant for the 1977 results ($r = 0{,}35$; $df = 6$). On the other hand the relationship between the percentage mortality of pups and the density of bulls in and around the harems (BM, ABM and CH) per specified area was linear and significant ($r = 0{,}96$; $df = 6$; $P<0{,}001$). The regression line is described by the function $y = 0{,}03x + 0{,}32$ where x = the density of bulls and y = the percentage mortality of pups (Fig. 2). This relationship was also linear, although not significant using 1977 data ($r = 0{,}68$; $df = 6$).

Discussion

Estimates of population size for 1979 (present study) and 1977 (Van Aarde 1980a) at the same study areas were similar, with the overall decrease in population size continuing. The mean date of census during 1979 (20 October ± 3,2 days) and 1977 (17 October ± 2,4 days) differed significantly ($t = 4{,}25$; $df = 7$; $P<0{,}005$) and these later counts would be biased towards high bull numbers as bachelor bulls increase towards the end of the breeding season (Carrick *et al.* 1962). Consequently the overall sex ratio, which differs significantly from that of 1970 and 1977 (Van Aarde 1980b), should be viewed with caution, but corroborates the change in sex ratio since 1952 (Angot 1954) in favour of the cow component as described by Van Aarde (1980a). This suggests a change in sex ratio associated with the selective removal of older bulls ascribed by Laws (1973) to an increase in environmental mortality factors acting on bulls during their aquatic phase (Van Aarde 1980b). Since the observed bull population for 1979 was not significantly different from that expected, it would appear that these environmental mortality factors are still depressing the bull population. The cow population (adjusted) on the other hand, was significantly lower than expected, although area specific cow densities did not differ significantly from 1977. The cow population of 1979 indicated a continued decrease after the slump from 1970 to 1977. The overall increase in harem density from 1977 to 1979, the decrease in harem size (102,3 ± 135,4 in 1977 to 76,1 ± 111,5 in 1979) and the significant change in harem structure are presumably brought about by the reduced number of cows. This change at least partly results from the later census dates of 1979, when cow numbers ashore were past the peak and cows increasingly started to leave. It could, however, also be interpreted that in spite of an overall intrinsic rate of change of 1,0 per cent from 1977 to 1979 in the cow component, harem structure (BM : ABM + CH : B : Cows) is not a constant for a specific area, but rather a variable which changes as a result of changes in other population parameters (i.e. density). The better relationship between a spatial variable (i.e. length of harems) as opposed to harem size and the number of assistant beachmasters seems to support this. However, on Macquarie Island (Carrick *et al.* 1962) and Marion Island (Condy 1978), harems of more than 50 and 60 cows respectively included an assistant beachmaster, as in the present study (53 cows on average). These figures differ considerably from those of 1977 at Kerguelen (30 cows on average — Van Aarde 1980b). The latter figure probably resulted from challengers on the periphery of the harem amongst the cows being erroneously classified as assistant beachmasters, as for example, two assistant beachmasters in a harem of eight cows (Table III — Van Aarde 1980b), is inconceivable. This would also account for the high percentage of breeding bulls (BM + ABM = 51,78%; $n = 1280$) during 1977 (Van Aarde 1980b) compared with 1979 (BM + ABM = 23,79%; $n = 712$), and the statement that in *M. angustirostris* less than a third of the bulls copulate (Le Boeuf 1974).

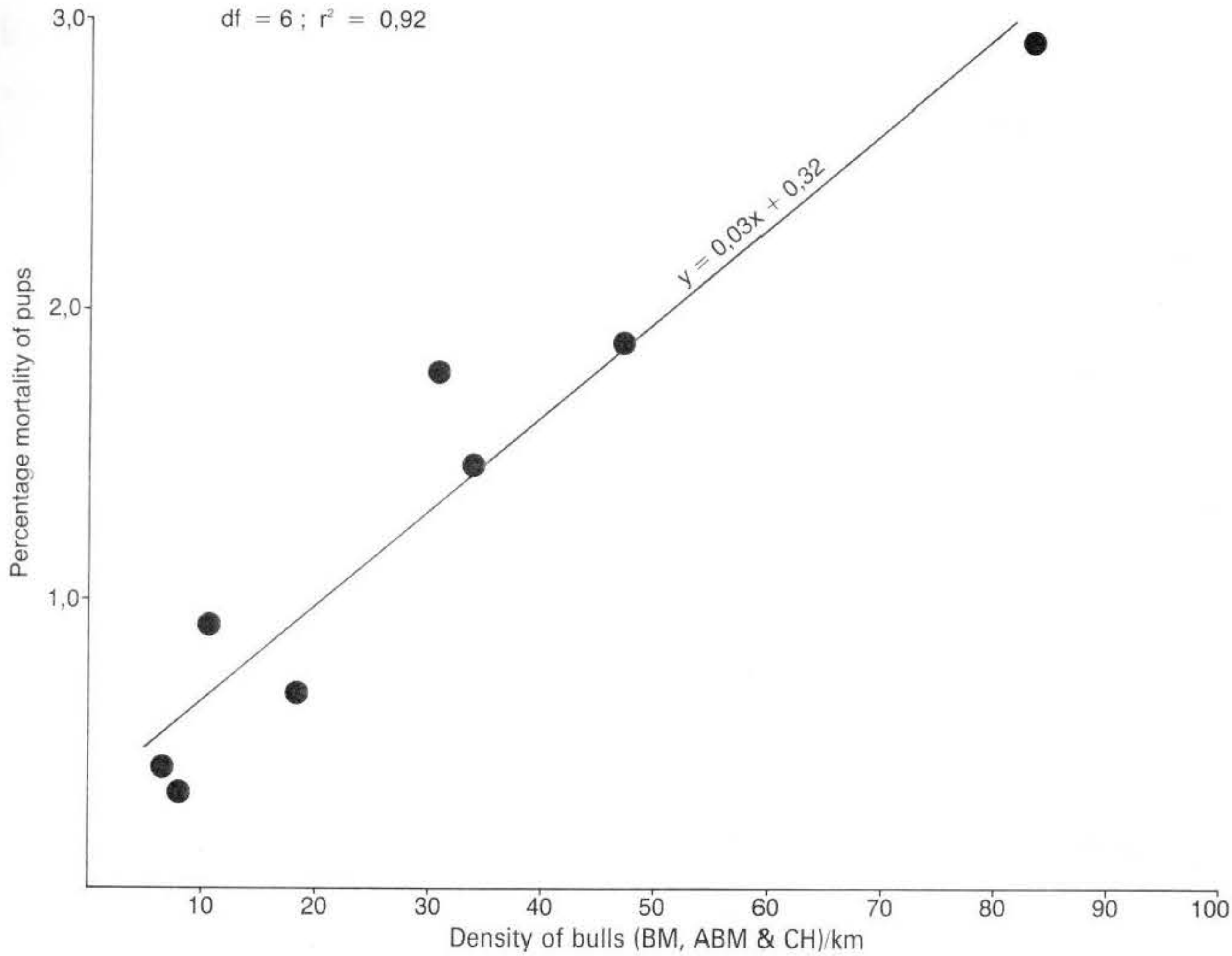

Fig. 2. Correlation between percentage pup mortality and density of bulls active in and around the harems.

Compared with 1977, cow numbers on the southern part of the study area increased, while cow numbers generally decreased on the northern part. Since elephant seal cows reportedly show a strong fidelity to their birthsite (Nicholls 1970) and all the tagged breeding cows resighted ($n = 17$) in the present study were found in the approximate vicinity of their birthsites, it would seem unlikely that the observed area-specific increases/decreases are the result of a change in the relative distribution of cows in the study area. This indicates that intrinsic population factors responsible for area-specific fluctuations in cow numbers (e.g. increased/decreased pup mortality) would ultimately affect recruitment to the breeding cow component for any particular area. The opposing results obtained for 1977 and 1979 when correlating pup deaths with the number of cows per harem does not, however, support this hypothesis. Similarly, when correlating the percentage pup mortality in the specific areas ($n = 8$) with cow densities for these years, no relationship for the 1977 results could be found, although 1979 results were highly significant. Since the area-specific density of cows did not differ significantly between 1977 and 1979 ($t = 0{,}86$; $df = 7$), the failure to establish a correlation for 1977 probably relates to the low number of dead pups counted. During 1979 approximately 82 per cent more dead pups were found than during 1977. This suggests that the good relationship between pup mortality and cow densities of 1979 was a function of the later census dates. Presumably the number of dead pups would increase later in the season since density dependent factors operating during the peak in cow numbers would have more time to take effect, the key event leading to pup deaths presumably being cow-pup separation as in *M. angustirostris* (Le Boeuf & Briggs 1977). Similarly, onshore density dependent pup mortality in the grey seal *Halichoerus grypus* results from starvation subsequent to the separation of the cows and their offspring (Bonner 1975).

Although cow-pup separation occurs more readily in large harems where cow-pup reunion is less likely through the large number of bodies present (Le Boeuf & Briggs 1977), the density of cows per unit harem area, whether large or small, remains fairly constant since individual distances between elephant seal cows are maintained seasonally and annually (Le Boeuf & Briggs 1977). Therefore yet another factor appears to be more important in density dependent pup mortality. Since male-induced trauma through trampling is a main source of injury to pups (Carrick & Ingham 1962; Le Boeuf & Briggs 1977), the linear relationship between pup mortality and the density of bulls active in bull:bull competition in and around the harems during both 1977 and 1979, implies that density dependent effects on pup mortalities involve bulls rather than cows. This would not only result from direct trampling of pups, but inter-male conflict would presumably also increase the level of arousal within the harem, which would be conducive to cow-pup separation (Le Boeuf & Briggs 1977).

Although the observed area-specific fluctuation in the breeding cow population at Kerguelen can therefore be ascribed to a density dependent regulatory mechanism that acts through pup mortality as a function of bull densities, the reasons for the overall decrease in elephant seal numbers at Kerguelen, Marion Island (Condy 1977) and Possession Island (Barrat & Mougin 1978) remain speculative (Van Aarde 1980a, Pascal 1982, Skinner & Van Aarde *in press*). At both Kerguelen (Van Aarde 1980a, this study) and Marion Island (Skinner & Van Aarde *in press*) the selective removal of bulls during their aquatic phase is, however, implicated. The decreasing trend in the cow component and the decline in the annual pup crop at Marion Island is ascribed to a possible malfunction of a mechanism ensuring pregnancy due to scarcity of bulls (Skinner & Van Aarde *in press.*).

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