Marion Island elephant seals: the paucity-of-males hypothesis tested

I.S. Wilkinson and R.J. van Aarde

Abstract: The southern elephant seal, *Mirounga leonina*, population at Marion Island has declined since the start of research activities there in 1973, as have populations at other Indian Ocean breeding sites. One suggested mechanism for the decline at Marion Island is a shortage of males, resulting in low insemination rates. We tested this "paucity-of-males" hypothesis by looking at (*i*) adult sex ratios, (*ii*) male sexual activity, and (*iii*) the relationship between levels of sexual activity and the probability of a cow pupping in the following season. Sex ratios were similar to those at other sites where populations are either stable (South Georgia) or increasing (Peninsula Valdes). Dominant bulls monopolised mating opportunities, achieving 98.1% of 629 observed copulations over three seasons. Of the 138 cows coming ashore, only 4 (2.9%) were not seen mating and 89% copulated with only one bull; dominant bulls copulated with all but 1 of the 134 (99.3%) cows that did mate. Cows were mated more frequently than at sites with stable and increasing populations. There was no difference in the observed level of sexual activity between cows seen pupping in the following season and those who failed to pup. This indicates that bulls monopolising harems are capable of inseminating all the cows. Such findings refute the paucity-of-males hypothesis.

Résumé : La population d'éléphants de mer, *Mirounga leonina*, dans l'île Marion a diminué depuis le début des activités de recherche en 1973, à l'instar d'autres populations aux sites de reproduction dans l'océan Indien. Une hypothèse avancée pour expliquer le déclin dans l'île Marion est une pénurie de mâles qui entraîne un taux réduit de fécondation. Nous avons testé cette hypothèse de « rareté des mâles » par évaluation (*i*) du rapport mâles : femelles, (*ii*) de l'activité sexuelle des mâles et (*iii*) de la relation entre le degré d'activité sexuelle et la probabilité de mise-bas de la femelle au cours de la saison suivante. Les rapports mâles : femelles sont semblables à ceux enregistrés à d'autres sites où les populations sont stables (Géorgie du Sud) ou en croissance (péninsule de Valdes). Les mâles dominants monopolisent les chances de s'accoupler et ils ont été responsables de 98,1% des 629 accouplements observés au cours de trois saisons. Seulement 4 des 138 femelles (2,9%) qui ont gagné la terre ferme n'ont pas été observées en train de s'accoupler, 89% se sont accouplées à un seul mâle et les mâles dominants se sont accouplés à toutes les femelles sauf une sur les 134 (99,3%) qui se sont accouplées. Les femelles de l'île Marion se sont accouplées plus souvent qu'à des sites où les populations sont stables ou en croissance. Nous n'avons pas observé de différence dans l'importance de l'activité sexuelle chez les femelles qui ont mis bas au cours de la saison suivante et celles qui n'ont pas eu de petit. Cela indique que les mâles qui monopolisent des harems sont capables de féconder toutes les femelles, ce qui contredit l'hypothèse de la « rareté des mâles ».

[Traduit par la Rédaction]

Introduction

The southern elephant seal (*Mirounga leonina*) population at Marion Island has been studied extensively since 1973 (Condy 1977; Skinner and van Aarde 1983; Wilkinson 1992; Bester and Wilkinson 1994). Declines in this and several other populations in the southern Indian Ocean have been evident since the 1970s (Condy 1978; van Aarde 1980*a*; Skinner and van Aarde 1983; Burton 1986). Condy (1978) suggested that killer whales, *Orcinus orca*, may have contributed to the decline at Marion Island, as orca are abundant there and have regular annual visitation patterns coinciding with elephant seal breeding (Condy et al. 1978). Given the near absence of these predators at other islands (îles Kerguelen, Heard Island, and Macquarie Islands) that also experienced declines during the period considered in this study, other factors may well be acting at Marion Island.

Skinner and van Aarde (1983) noted the general lack of subordinate bulls surrounding harems at Marion Island compared with the harems at îles Kerguelen. At this latter location, van Aarde (1980*b*) observed that all cows leaving their harem were mated by a lower-ranking bull outside the harem. Skinner and van Aarde (1983) suggested that such matings provide a mechanism to ensure that all cows are inseminated before leaving land. The general lack of lower-ranking bulls peripheral to harems at Marion Island might have resulted in the negation of this insurance mechanism. If so, all cows would not have been being inseminated, because either the dominant bull (controlling the harem) had failed to mate with all cows or, although mating with them, the matings had been unsuccessful. Both scenarios would have the same result: cows failing to haul out to pup in the following

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season. Data available for Marion Island indicate a significant correlation between the number of cows ashore to pup (and hence the number of pups produced) and the number of bulls present ashore in the preceding year, that is, the year of fertilisation. The "paucity-of-males" hypothesis advanced by Skinner and van Aarde (1983) therefore predicts that, despite the polygynous nature of *M. leonina* breeding, harem holding (dominant) bulls are unable to mate with and (or) successfully inseminate all cows in the harem, and that peripheral subordinate males (sexually mature) are an important insurance mechanism to ensure that most or all females are inseminated.

To test the paucity-of-males hypothesis, this study aimed to: (*i*) determine the number of bulls in the population; evaluate how widespread the phenomenon of single bull harems is on Marion Island; and determine the adult sex ratio over the entire island for comparison with other breeding sites; (*ii*) examine the reproductive behaviour of bull elephant seals at this site, in particular, how they interact with the cows present during the breeding season; and (*iii*) determine the relationship, if any, between the sexual activity of bulls and the probability of cows producing a pup in the following year.

Methods

Census

Weekly counts of adult bulls, cows, unweaned pups, weaned pups, and dead pups were conducted on foot in the main study area (MSA) on the northeast coast of Marion Island (46°54′S, 37°45′E) between September and mid-November in the years 1974–1989.

During 1986, 1987, and 1988, total-island counts of bulls and cows were made on 15 October, the date of maximum haul out of cows and the time, therefore, at which most bulls are assumed to be ashore (Hindell and Burton 1987). This assumption is made as, in contrast with cows, bulls do not necessarily stay at one beach during the season (Laws 1956; Jones 1981), and so sequential counts of bulls on beaches will not produce the total number hauling out during the season. Harem size, the number of bulls associated with harems, and the number of cows with or without a bull in attendance were recorded. At Marion Island, elephant seal social organisation is different from other larger breeding sites, as harems do not contain assistant beachmasters (ABMs). An ABM is a subordinate bull that controls part of a large harem that is controlled by a dominant bull (beachmaster) (Carrick et al. 1962). Bulls censused in the present study were divided into those controlling harems (dominant) and those peripheral to (occurring within 50 m of a harem), but associated with, harems (subordinate bulls). No harems had more than a single dominant bull.

Trends in adult sex ratio (calculated using the maximum numbers of bulls and cows) were analysed using data from the MSA for the years 1974–1989 (cf. Skinner and van Aarde 1983). Adult sex ratios for the entire island were calculated from the 15 October census data for 1986–1988 and compared with those of the MSA.

Observations

Observational data were collected during three complete breeding seasons at Trypot Beach, Marion Island. The beach has a flat, even profile composed predominantly of pebbles and small boulders. Observations were made between dawn and dusk from the day the first cow arrived (early September) until the last cow departed from the rookery in mid-November. All bulls and cows were bleach marked (Lady Clairol "Ultra Blue," Clairol Inc., Johannesburg, South Africa) (after Le Boeuf and Peterson 1969), to facilitate individual identification. Bulls and cows were photographed and double-tagged with Allflex "medium duplex" tags (Allflex New Zealand Ltd., Palmerston North, New Zealand) in their hind flippers, to enable identification in subsequent years.

All attempted and successful copulations were recorded during continuous observations, noting the identification of the bull and cow involved. The following parameters were derived for each cow: (*i*) the total number of copulations involving the dominant bull occurring in the harem during the cow's mating period (first to last observed copulation); (*ii*) the mean number of cows (including the cow in question) mated per day of the cow's mating period; (*iii*) the number of copulations by a cow with the dominant bull, expressed as a percentage of the total number of copulations that bull had with all cows during the cow's mating period; (*iv*) as an indication of the level of sexual activity and fertility of the bulls, the number of copulations by the dominant bull (total for all cows) for each day of a cow's mating period was calculated. A bull was only recorded as "attempting" a copulation when he was observed to mount the cow. Copulations were regarded as successful if intromission was achieved.

Agonistic activity

All interactions in which one bull retreated from another in and around the study harem between 2 October and the end of each breeding season were recorded. Frequencies of interactions per hour were determined for the dominant bull for this period each year.

Level of sexual activity and its influence on pup production

The sexual parameters detailed above were compared for cows known to have produced pups in 1987 and 1988 and those known to have failed to pup. The production of pups was determined from actual observation of the cows in the subsequent breeding season. Given the fidelity to breeding sites shown by females at Marion Island (I.S. Wilkinson, unpublished data), those not seen breeding in consecutive breeding seasons at Trypot Beach or at other breeding beaches on Marion Island were assumed to have failed to pup, if seen during subsequent moult or breeding periods, or to have died, if never seen again.

Statistical procedures

All procedures follow Zar (1984). Comparisons of means were made using one-way ANOVA when variances were comparable. When two means with noncomparable variances were compared, Mann–Whitney *U* tests were used. Ratios and proportions were compared using χ^2 values. Relationships between variables were compared using least-squares regression analysis, and levels of significance show the probability of departure of the slope from zero. All mean values are followed by 1 standard error (±SE) of the mean.

Results

Sex ratio

Adult sex ratio (bull:cow) on 15 October each year in the MSA ranged between 1:9.8 and 1:38.8, but there was no significant ($\chi^2_{13} = 19.26$, $P > 0.05$) trend during the period from 1974 to 1989 (Table 1). The number of bulls did not correlate with the peak number of cows present in the MSA each year ($r_{12} = 0.50$; $P > 0.05$). There was also no significant correlation between the number of bulls ashore in one season and the number of cows seen in the next year ($r_{10} = 0.52$; $P > 0.05$). Adult sex ratio was not correlated with the

Table 1. Adult sex ratios and the maximum number of bulls (dominant and subordinate), cows, and pups ashore at beaches in the MSA (see Methods) at Marion Island during breeding seasons from 1974 to 1989; no comparable data are available for 1978 and 1979.

		Maximum no. ashore		
Year	Adult sex ratio (males:females)	Bulls	Cows	Pups
1974	1:21.7	18	391	406
1975	1:22.8	14	319	317
1976	1:11.3	25	283	301
1977	1:14.9	17	253	260
1978	—	—	—	—
1979	—	—	—	—
1980	1:20.7	11	228	239
1981	1:12.9	17	219	243
1982	1:38.8	5	194	205
1983	1:12.9	14	180	199
1984	1:18.4	9	166	192
1985	1:22.2	9	200	200
1986	1:18.9	9	170	183
1987	1:9.8	16	157	177
1988	1:14.1	12	169	177
1989	1:11.3	15	170	184

proportional change in pup numbers from the year the sex ratio was observed and the following year.

The cow component of the MSA population declined exponentially at 5.6% per annum, while the bull component followed no distinct trend over the same period. The adult sex ratio in the MSA did not differ significantly from that of the whole island in 1986, 1987, or 1988, during which period the ratio ranged from 1:9 to 1:12. (Table 2).

Social structure

Whole-island counts from 1986 to 1988 showed that at least 95% of the cows were in the presence of at least one bull, either in a harem or alone with an attendant bull (Table 2). The number of bulls in and peripheral to harems ranged from one to seven. In both 1987 and 1988, around 35% of cows were found in harems with a single bull in attendance, compared with 46.6% in 1986. In all 3 years, most harems were attended by a single bull. There was a significant positive relationship between harem size (x) and the number of bulls (y) in attendance ($y = 1 + 0.04x$; $F_{[1,87]} = 31.8$, $P < 0.001$, $r^2 = 0.26$). Harem size ranged from 2 to 59 cows, with a mean over the 3 years of 20.1 ± 0.4 ($n = 89$).

Sexual activity of bulls at Trypot Beach

Details of sexual activity for each season are given in Table 3, and the results of interyear comparisons of sexual activity parameters are summarised in Table 4.

The number of copulations achieved by a cow (Fig. 1) was positively and significantly related to the length of the cow's mating period, but was not related to the date on which the cow mated for the first time. For cows, intervals between first and last copulations ranged from 1 to 9 days.

Table 2. Summary of details of breeding associations around the entire Marion Island coast, recorded during censuses carried out on the day of peak cow haul out (15 October) in 1986, 1987, and 1988.

		Number of bulls					Number of cows					
	Number of Harems	Dominant	Subordinate/ peripheral	Associated with harems	Other	Total ashore	In harems	Single with bulls	Total with attending bulls	Unattended	Total ashore	Total bulls ashore : total cows ashore
1986	27	27	16	43	11	54	624	1	625	16	641	1:11.9
1987	30	30	21	51	16	67	569	4	573	29	602	1:8.9
1988	32	32	27	59	8	67	597	2	599	6	605	1:9.0

The level of sexual activity, that is, copulations per hour, of the dominant bull (z) increased as the season progressed (day = y) in each year (x) (multiple regression: $z = 0.03 + 0.12y - 0.10x$; $F_{[2,118]} = 27.05$, $P < 0.001$, $r^2 = 0.30$). The number of copulations per hour divided by the number of females mated by the dominant bull did not change within a season. When copulations per hour per female (z) were regressed against the numbers of females involved in the matings (y), there was a significant negative relationship each year (x) of the study (multiple regression: $z = 0.17 - 0.004y - 0.02x$; $F_{[2,100]} = 7.68$, $P < 0.001$, $r^2 = 0.13$).

Agonistic activity of bulls at Trypot Beach

Agonistic activity was significantly ($F_{[2,118]} = 9.84$; $P < 0.001$) less frequent in 1986 and 1987 than in 1988 (Table 5), whereas bulls were less common in 1987 and 1988 ($F_{[2,118]} = 15.67$; $P < 0.001$; Table 5). Copulation frequency was higher in 1986 than in 1987 or 1988 ($F_{[2,118]} = 9.26$; $P < 0.001$; Table 5).

Level of sexual activity and its influence on pup production

Data on future pup production were collected on 54 of the females pupping in 1986 and 1987. Forty-eight produced pups in the following season, while 6 failed to pup. No parameter pertaining to sexual activity that was measured had any influence on whether or not the cow pupped in the following season (Table 6).

Table 3. Summary of sexual activity at Trypot Beach in 1986, 1987, and 1988.

	Year		
Activity	1986	1987	1988
Bulls			
No. observed copulating at least once	6[a]	2	2
No. of attempted copulations	383	218	203
Dominant bull	365	215	200
Subordinate bull	18[b]	3	3
No. of successful copulations	303	156	170
Dominant bull	296[b]	153	168
Subordinate bull	7	3	2
Success rate (%)	79.1	71.6	83.7
Dominant	81.1	71.2	84.0
Subordinate	38.9[b]	100.0	66.7
No. of copulations by dominant bull	296	153	168
Cows			
No. copulating with single bull	49	33	41
Copulating only with dominant bull	49	32	41
Copulating only with subordinate bull	0	1	0
Copulating with dominant and subordinate bulls	7	2	2
First copulation with dominant bull	6	2	2
First copulation with subordinate bull	1	0	0
No. of cows not seen to copulate	1	0	3
Total no. of cows in harem	57	35	46

[a]No more than three bulls were at the beach at any one time.
[b]Sexual activity of five subordinate bulls was combined for display in the table (individual success rates ranged from 25 to 100%).

Discussion

Our data suggest that most, if not all, females that visit Marion Island each year during the breeding season are mated. Notwithstanding the lack of genetic paternity tests in this study, if all, apparently successful, copulations result in insemination, then the paucity-of-males hypothesis advanced by Skinner and van Aarde (1983) would not account for the decline in this population. At Marion Island, the adult sex ratio does not differ from those for sites at which populations are stable or increasing, dominant bulls monopolise mating opportunities and exclude subordinates almost entirely from the breeding aggregations, and evidence suggests that single bulls are capable of inseminating all cows in the harem.

Numbers of bulls

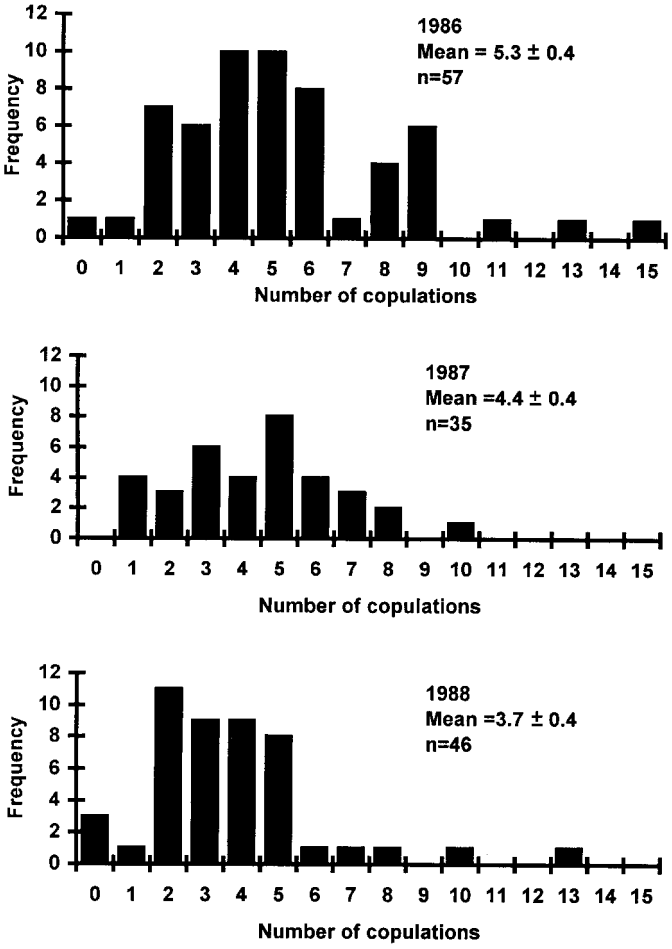
The lack of any significant trend in the adult sex ratio over the period from 1974 to 1989 suggests that, despite the lack of a trend in bull numbers during this period, the patterns of population change for bulls and cows do not differ greatly. This agrees with data for Macquarie Island for 1949–1985 (Hindell and Burton 1987), while contrasting with previous findings for the Marion Island population (Skinner and van Aarde 1983).

The ratio of bulls to cows ashore was as low as that reported for South Georgia (1:9; McCann 1980) and lower than those reported for Iles Kerguelen (1:12.8; Bester and Lenglart 1982), Macquarie Island (1:12; Hindell and Burton 1987), and Peninsula Valdes (1:13.6; Campagna et al. 1993). The observation that sex ratios at Marion Island are equal to or lower than those at locations with lower observed rates of decline (Macquarie Island, Hindell and Burton 1987; îles Kerguelen, Guinet et al. 1992; South Georgia, Boyd et al. 1996) or where populations are increasing (Peninsula Valdes, Campagna and Lewis 1992) suggest that bull numbers are not limiting. This is further supported by observations made at the MSA between 1974 and 1989 that the adult sex ratio did not correlate with the proportional change in pup numbers from the year in which the sex ratio was observed and the subsequent season. Years with bull:cow ratios of 1:38.8 and 1:12.6 both produced a proportional change in pup numbers of 0.97.

Censuses conducted at peak cow haul out (15 October) in each year of this study showed that over 95% of all cows were in the presence of at least one bull, either within a harem or singly with an attendant bull. Comparable figures for Peninsula Valdes show that at least 99% of cows had an attendant bull, with between 91 and 93% in harems depending on the year (Campagna et al. 1993). The small number of cows not seen with bulls at Marion Island would likely be mated by subordinate bulls that move between beaches during the breeding season (Laws 1956; Jones 1981; I.S. Wilkinson, unpublished data).

The majority (58%) of harems observed in the study had only one associated bull, but the mean size (13.9 ± 0.5) of these single bull harems was small enough that bulls would likely be able to inseminate the entire harem. By way of comparison, at the one location where the population of southern elephant seals is known to be increasing, Peninsula

Fig. 1. Frequency of copulation of cows at Trypot Beach during the breeding seasons of 1986, 1987, and 1988. Mean numbers (mean ± SE shown for each year) of copulations per cow differed significantly between years ($F_{[2,135]} = 5.1$; $P < 0.01$).



Valdes, 43% of 123 harems contained a single bull (Baldi et al. 1996).

Sexual activity of bulls

The social structure at Marion Island, when compared with other sites, suggests that there is a sufficient number of bulls ashore during the breeding season to ensure that all females are inseminated prior to their departure from the rookeries. However, this assumes that this number is translated into sexual activity on the beaches, and it is necessary to document the sexual activity of these bulls in relation to the cows ashore.

Dominant bulls at Trypot Beach monopolised sexual activity, with only 12 of 629 successful copulations being achieved by subordinates. This relationship between social status and breeding success is consistent with several other studies of southern elephant seals (McCann 1981*a*; Campagna et al. 1993; Baldi et al. 1996; Modig 1996) and with studies of the congeneric northern elephant seal, *Mirounga angustirostris*, (Le Boeuf 1972, 1974; Haley et al. 1994). However, the extent to which dominant bulls monopolised mating is not as evident at other sites. At Peninsula Valdes, where harems are similar in size to those at Marion Island,

Table 4. Interyear comparisons of parameters relating to sexual activity among southern elephant seal cows at Trypot Beach, Marion Island, between 1986 and 1988.

	Mean no. of copulations received per cow*	Length of mating period (days)	Proportion of copulations received*	Mean no. of cows mated during a cow's mating period*	No. of copulations received by a cow per day of the mating period*	Total no. of copulations by dominant bull for all cows/duration of mating period of a single cow*	(Total no. of copulations/duration of mating period)/number of cows mated*
1986	5.3±0.2 (57)	3.4±0.2 (56)	0.19±0.06 (50)	6.4±0.2 (56)	1.7±0.1 (56)	10.3±0.2 (50)	1.67±0.08 (50)
1987	4.3±0.3 (35)	3.3±0.2 (35)	0.32±0.09 (32)	4.2±0.2 (35)	1.3±0.1 (35)	5.5±0.3 (32)	1.35±0.09 (32)
1988	3.7±0.2 (46)	3.5±0.2 (43)	0.23±0.08 (41)	5.8±0.2 (43)	1.2±0.1 (43)	7.5±0.3 (41)	1.31±0.07 (41)

Note: Differences between years were identified using one-way analysis of variance (ANOVA) and significant differences at $P < 0.05$ that were identified using Tukey's multiple range test (Zar 1984). Values are given as the mean ± SE, with sample size in parentheses. Parameters follow the definitions in the Methods.
*Significant difference between years.

Table 5. Number of agonistic encounters and copulations per hour involving the dominant bull, and the number of bulls present each day during the period 2 October to the end of the breeding season at Trypot Beach, Marion Island, in 1986, 1987, and 1988.

Year	No. of observation days	No. of agonistic encounters per hour	No. of copulations per hour	No. of bulls present at the beach per day
1986	42	0.12±0.06	0.51±0.09	3.21±0.18
1987	41	0.25±0.07	0.27±0.11	2.28±0.11
1988	38	0.55±0.14	0.29±0.07	2.28±0.11

Note: Values are given as the mean ± SE.

Table 6. Comparison of values pertaining to sexual activity of southern elephant seals at Trypot Beach, Marion Island, between cows pupping and those not pupping in the following season.

	n	No. of copulations	Day of first copulation (Julian day)	Length of mating period (days)	Mean no. of cows mated during cow's mating period	Total copulations per day of cow's mating period	Proportion of copulations received (%)
Cows:							
producing pups	48	5.3±0.2	25 Oct.±0.5	3.5±0.2	5.4±0.3	7.8±0.3	24.8±6.6
failing to produce pups	6	4.8±0.6	25 Oct.±1.4	2.8±0.4	5.4±0.7	8.8±0.8	32.3±24.0

Note: Values are given as the mean ± SE. Parameters are as defined in the text. Mann–Whitney *U* tests (Zar 1984) revealed no significant differences for any of the parameters.

Campagna et al. (1993) found that dominant bulls were involved in just 65% of 361 observed copulations, while Baldi et al. (1996) reported that 13 of 51 bulls observed achieved 67% of 698 copulations.

The exclusion of subordinate bulls from breeding activity may be a consequence of harem size and topography at Marion Island, where most beaches are small discrete areas only accessible from the seaward side. This contrasts with other breeding sites, where harems (frequently more than one per beach) are often situated at intervals along long open stretches of sand or pebble beaches (Carrick et al. 1962; van Aarde 1980*b*; Modig 1996). Such harems are more difficult to defend from other bulls. Indeed, Stewart (1989, 1992) reasoned similarly for the effects of beach topography on the social status of northern elephant seals in California waters.

Subordinate bulls attempted few copulations, but these had a relatively high success rate. Subordinates adopted "sneaking" strategies: both attempted and successful copulations were limited to occasions when the dominant bull was mating or had recently mated with one of the cows successfully. On several occasions, subordinate bulls attempted copulations with cows not in oestrus, which may indicate, along with their occasional attempts to mate weaned pups (I.S. Wilkinson, unpublished data), a reduced ability to recognise receptive cows (see Modig 1996; for northern elephant seals see Le Boeuf 1974; Rose et al. 1991).

The exclusion of other bulls from breeding activity had a negligible effect on coverage of cows in the harem: only 1 of the 134 cows seen to copulate did not copulate at least once with a dominant bull, and each cow was mated on several (4.6 ± 0.1) occasions. One cow not seen to copulate in the present study was observed in the following year with a pup. It is possible that this cow was mated either at night or after she left the beach. Data collected during several nights of observation indicate that bulls defend their harems as vigorously at night as they do by day (I.S. Wilkinson, unpublished data), thus, if she was mated while ashore, it would likely be by the dominant bull.

Interseason differences

Differences in the level of sexual activity between seasons may result from individual differences in the reproductive effort of bulls (see Anderson and Fedak 1985; Deutsch et al. 1990; Bartsch et al. 1992). This would explain the difference between 1986 and 1987 when the dominant bulls were different individuals but, in 1987 and 1988, the bulls were the same. The difference in the level of sexual activity between 1987 and 1988 was probably the result of the dominant male injuring his left front flipper (on 2 November of an unknown cause). This bull appeared to favour his left flipper when mounting cows and was not as successful when using his right one after the injury occurred. In addition, his locomotory capabilities were greatly reduced, and many cows were able to evade his mating attempts.

Intraseason differences

In addition to interseason differences in sexual activity, it is also important to note the change in levels of sexual activity within seasons. Dominant bulls increased their level of sexual activity as the season progressed in all 3 years of the study and this corresponded to an increasing number of cows being mated. However, the negative correlation between the frequency of copulations per cow and the number of cows involved in the matings suggests that the bull's sexual activity with any one cow becomes limited with increasing numbers of receptive cows on the beach. It appears that, as the breeding season progresses, the bull spreads mating events across all available cows. It is unclear if bulls can detect previously mated cows (see Modig 1996), which may explain the random matings. Consequently, the likelihood of

a cow not being mated increases as the number of cows available for mating increases, which may occur in some of the larger single-bull harems seen at other breeding sites. In such cases, subordinate bulls surrounding the harems may be an important "insurance" mechanism, as suggested by Skinner and van Aarde (1983).

The frequency of copulation per cow recorded in the present study (3.7–5.3) was higher than that recorded (when data were standardised for comparable observation effort) at either South Georgia (2.6; McCann 1981*b*) or Peninsula Valdes (2.5; Campagna et al. 1993), or at Año Nuevo Island for northern elephant seals (1.9–3.6; Le Boeuf 1972). The higher frequencies at Marion Island may be a result of the combined effect of small harem size and low numbers of attending bulls. The small isolated harems are easily defended from peripheral bulls that form a social hierarchy early in the season. Consequently, the dominant bull can repel these bulls by ritualised postures rather than by actual conflict, which leaves more time for sexual activity.

At South Georgia (McCann 1981*b*) and Año Nuevo (Le Boeuf 1972), harems are large, ranging in size from 100 to 300 cows, and are attended by many bulls. Higher levels of activity by dominant bulls have been reported at both South Georgia (McCann 1983; Modig 1996) and Año Nuevo (Deutsch et al. 1990), reducing time for copulation. Interseason comparisons at Marion Island show that higher levels of sexual activity (0.51 copulations per hour) in 1986 corresponded to the lowest levels of agonistic activity (0.12 incidents per hour). Levels of agonistic activity for dominant bulls in the present study are considerably lower than comparable figures for the larger South Georgia harems (1.6 incidents per hour; Modig 1996). Given the lower levels of agonistic activity at Marion Island, it might be expected that the number of copulations per hour (0.51 ± 0.09 in 1986) would be greater than at South Georgia (0.5 ± 0.1; Modig 1996), but this was not the case. Modig (1996) showed that the number of copulations for each bull per hour was related to harem size, with copulations per hour reaching a peak in harems of 100–150 cows. The present study showed that, within a given harem, copulations per hour increased during the season. However, activity levels (copulations per hour) at Marion Island may be limited by harem size and the number of receptive cows.

Level of sexual activity and its influence on pup production

The finding that the level of the bull's sexual activity had no effect on the chances of conception indicates that he is capable of inseminating the cows that are present at this site. The observation that the first and last cows mated by the dominant bull in both 1986 and 1987 produced offspring in the following season suggests that the bull was fertile at the beginning and at the end of the season. It does not, however, preclude that, during the peak of sexual activity within the season, frequent ejaculation may result in lowered fertilisation capability. However, sexual activity, measured in total copulations by the dominant bull per day of a given cow's mating period, had no effect on whether the cow produced a pup in the next year or not. It is not possible to say up to what harem size a single bull can successfully inseminate all cows but, in the present study, a harem of 57 cows was successfully "managed." In larger harems, where dominant bulls exclude all other bulls, there may be a relationship between the time a cow is first mated and her success in pupping the following season, given the lower probability of individual cows being mated described previously.

In conclusion, the study has provided data showing that (*i*) the adult sex ratio is not significantly different from ratios for other sites at which populations are increasing or stable; (*ii*) dominant bulls are capable of mating with all cows in the harem on several occasions; and (*iii*) from consideration of sexual activity and subsequent reproductive success, these bulls do not exhibit reduced fertility during the course of the season that would result in the failure to inseminate all cows on the beach. These three findings provide justification for refuting the paucity-of-males hypothesis proposed by Skinner and van Aarde (1983), and other mechanisms should be considered to explain the observed population decline at Marion Island.

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