

Low reproductive success in territorial male Antarctic fur seals (*Arctocephalus gazella*) suggests the existence of alternative mating strategies

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Abstract

Microsatellites were used to conduct an analysis of paternity of Antarctic fur seals (*Arctocephalus gazella*) from Bird Island, South Georgia. At most, only 28% of pups at our study site could be assigned a father, even though the majority (~90%) of candidate males within this colony were sampled. The behavioural and genetic evidence from this study suggests that a number of alternative mating strategies may exist within this fur seal population. Holding a land-based territory conferred an advantage to male reproductive success. However, this advantage was much smaller than expected from behavioural observations. At least 70% of fur seal pups born at our study site in a given year are not fathered by males who held a territory or were observed copulating with females in the previous year, implying that there exists a pool of males that seldom venture ashore at this site. To explain this discrepancy we suggest that female choice is an integral component of the Antarctic fur seal mating system and that aquatic mating may play a much larger role in the Antarctic fur seal than previously thought.

Keywords: fur seal, mating system, microsatellites, paternity analysis, pinniped, reproductive strategies

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Introduction

In polygynous mammals, males compete for mates either by excluding other males from a resource required by females (resource-defence polygyny; Emlen & Oring 1977) or by directly preventing other males from gaining access to females (female-defence polygyny; Davies 1991). In both of these mating systems, dominance among males is asserted through physical conflict. The strongest males may monopolize such a large number of females that variance in male breeding success can be considerable (Clutton-Brock 1989). For example, dominant northern elephant seal bulls defend large harems of females and as few as 3% of males may be responsible for up to 92% of observed matings (Le Boeuf & Reiter 1988).

Otariids (eared seals) are considered to be highly polygynous. They breed at high densities at traditional sites

where females come ashore to give birth and mate. Mating systems vary across species and populations, but males commonly defend territories at rookeries where females give birth (King 1983; Gentry 1997). The Antarctic fur seal (*Arctocephalus gazella*) is a typical otariid (Croxall & Gentry 1987), being highly sexually dimorphic (males are typically three to six times heavier than females) and exhibiting resource-defence polygyny. Dominant bulls vigorously defend discrete territories in breeding rookeries within which harems of up to 10 female seals give birth to and rear their pups (Bonner 1968; McCann 1980; Arnould & Duck 1997). Fighting between territorial males is common and holding territory is a costly behaviour. For example, a male can lose up to 50% of bodyweight during 60 days of territory tenure (McCann 1980).

Breeding is seasonal and highly synchronous, occurring during the southern summer on islands south of the Antarctic Convergence. At Bird Island, South Georgia, adult male Antarctic fur seals begin arriving on the breeding beaches in mid-October to compete for, establish and

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defend territories (McCann 1980; Arnould & Duck 1997). Pregnant females begin to arrive 3–4 weeks later. They give birth ~2 days after arrival and mate 6–7 days postpartum (Duck 1990; Boyd 1991). Soon after mating, females leave the colony on the first of many regular foraging trips to sea (Bonner 1968). The number of males holding territories increases steadily, peaking in early December which coincides with the greatest number of females present on the beach (Duck 1990). Thereafter, the number of territorial males decreases until the end of the breeding season in early January, by which time females with pups have largely moved off the beaches into surrounding tussock areas (Bonner 1968).

In species like the Antarctic fur seal, male reproductive success is expected to correlate strongly with male competitive ability. This in turn is often correlated with body mass (e.g. Clutton-Brock 1989; Godsell 1991), as larger, more dominant males are able to maximize the duration of tenure on territories, or among female aggregations, and hence have more opportunities to mate. Behavioural studies of male breeding behaviour (McCann 1980) and mating success (Arnould & Duck 1997) have shown that these expectations are met in the Antarctic fur seal. In a 4-year study of male mating behaviour, Arnould & Duck (1997) found that apparent mating success in the Bird Island population was biased towards a few individuals, and was positively correlated to both duration of tenure and the previous number of years in which tenure was achieved.

In some species, observed mating success can provide an accurate estimate of male reproductive success (e.g. Burke *et al.* 1989; Pemberton *et al.* 1992; Wainstein *et al.* 1998; Hoelzel *et al.* 1999). However, the relationship between observed mating success and reproductive success is not always so clear. There are a growing number of species in which the agreement between observed mating success and the number of genetically assigned paternities is poor (e.g. Birkhead *et al.* 1990; Harris *et al.* 1991; Amos *et al.* 1993; Worthington Wilmer *et al.* 1999). The objectives of this study were: (1) to determine the reproductive success of male Antarctic fur seals using molecular genetics; and (2) to relate this to the duration of territory tenure.

Materials and methods

The study site

The study was conducted at a beach on Bird Island, South Georgia (54° S, 38° W). Antarctic fur seals have been studied intensively at this site since the 1960s (e.g. Bonner 1968; McCann 1980; Lunn & Boyd 1993; Arnould & Duck 1997). The study beach is ~440 m² at high tide and ~700 pups are born there each year (Lunn & Boyd 1993). It forms part of a larger colony on Bird Island with a pup production

Table 1 Summary table showing the number of Antarctic fur seals sampled and genotyped from the study site on Bird Island, South Georgia

	1994	1995
Adult males	111	132
Adult females	159	25*
Pups with known mothers	103	81

*Does not include 74 females caught previously in 1994, recaptured with pups in 1995.

of ~60 000 (Boyd 1993). A catwalk of steel scaffolding provided the observers with access to all parts of the beach without disturbing the colony. Twice daily observations were made of marked animals on the beach each year from 1 November until the birth of the last pup, usually during the first week of January. These observations included the identity and position of territorial males, obtained from distinctive natural marks and by placing small patches of coloured gloss paint on the pelage. The paint marks remained obvious within seasons and, in many cases, remained identifiable across years. In addition, between 150 and 250 of the adult females that gave birth on the beach had been marked in previous years using cattle ear tags (Dalton Supplies) placed in the trailing edge of the foreflipper (Boyd *et al.* 1995).

Sampling strategy and sample collection

Samples for molecular genetic analyses were collected during the austral summers of 1994/95 and 1995/96. Each pup born to a marked mother was captured on the day of birth and a skin sample was taken from the interdigital margin of the foreflipper using piglet ear notch pliers (Majluf & Goebel 1992). A similar method was used to sample skin from tagged adult females, which were captured opportunistically during lactation (December to March). Territorial males were sampled using a biopsy dart system (Gemmell & Majluf 1997) or using a biopsy head attached to a pole. To reduce the risk of wound infection and to avoid sample contamination, all sampling equipment was cleaned with ethanol between uses. The skin samples were stored in vials containing 20% dimethylsulphoxide (DMSO) in a saturated salt solution (Amos & Hoelzel 1991) and stored at –20 °C. Details of the total sample set are presented in Table 1.

DNA extraction and microsatellite typing

Total genomic DNA was extracted from the skin biopsy samples either by the method described in Gemmell & Akiyama (1996) or with an adapted Chelex 100 protocol (Walsh *et al.* 1991). All DNA samples were genotyped with

Locus	No. of alleles	Size range	H_E	Null alleles	Genotypic identity	Exclusion probability
Aa4	7	204–218	0.77	0.000	0.088	0.71
Hg1.3	16	234–276	0.87	0.008	0.027	0.87
Hg4.2	28	126–190	0.92	0.270	0.013	0.93
Hg8.10	5	162–184	0.48	0.000	0.356	0.60
PvcA	9	137–153	0.78	0.012	0.075	0.77
PvcC*	9	103–121	0.82	0.005	0.057	0.77
PvcE	15	94–148	0.88	0.000	0.026	0.86
M11a	20	146–184	0.92	0.017	0.011	0.90
Overall	13.6		0.81		1.5×10^{-11}	0.99†

Table 2 Polymorphism characteristics, expected heterozygosities (H_E), estimated frequency of null alleles (Pemberton *et al.* 1995), genotypic identity and estimates of paternity exclusion (Weir 1996) probabilities for the microsatellite loci used in this study

*PvcC is a sex-linked locus, consequently the heterozygosity and genotype identity data presented here are only valid for female seals.

†Exact paternity exclusion probability is 0.9999992.

a panel of eight highly polymorphic dinucleotide repeat microsatellite loci (average number of alleles = 13.6; range = 5–28). These loci consisted of three isolated from grey seals (Hg1.3, Hg4.2, Hg8.10; Allen *et al.* 1995), three from the harbour seal (PvcA, PvcC, PvcE; Coltman *et al.* 1996), and one each from the South American fur seal and southern elephant seal (Aa4 and M11a, respectively; Gemmell *et al.* 1997; Hoelzel *et al.* 1999). The amplification and screening of microsatellite loci was performed as described in Gemmell *et al.* (1997). Table 2 describes the loci used in this study.

Identity checking

All files were checked for duplicate genotype entries using the program *IDENTITY* (Allen 1995), in order to identify individuals that may have been sampled more than once (within and/or between years). The probability of a match by chance is negligible when using eight highly polymorphic microsatellites (genotype identity 1.5×10^{-11}), therefore identical genotypes are probably the result of resampling the same individual. Any duplicates were subsequently excluded from the genotype files prior to the paternity analyses.

Mismatches in the mother–pup data sets were located manually and double-checked with reference to the original gels. All scoring errors were corrected and all genuine nonfilial mismatches (21 mother–pup pairs over 2 years) were excluded from the paternity analyses.

Paternity analyses

Paternity analyses were performed using *NEWPAT* as described in detail in Worthington Wilmer *et al.* (1999). *NEWPAT* is a general paternity analysis program, which searches for parent–offspring relationships according to user-defined criteria and then uses a randomization

approach to assess the significance of any matches found. *NEWPAT* is freely available for distribution: copies of the PC executable program and a full description of the program can be obtained from <http://www.zoo.cam.ac.uk/zoostaff/amos/newpat.htm>.

Paternity matching was conducted after setting four parameters: (i) the maximum number of unscored loci allowed in any one male–offspring comparison; (ii) the maximum number of mismatching loci allowed, usually set at zero (stringent) or one (relaxed); (iii) the status of any sex-linked loci; and (iv) the minimum acceptable probability for a match requiring null alleles (all instances where a match could exist by invoking a null allele are considered).

For our analyses, we allowed zero and one mismatches, the latter being used to examine the number of single locus exclusions enabling the estimation of error rates. We used a low acceptable probability of null matches ($P = 0.03$), permitted the inclusion of one sex-linked locus (PvcC) to be used for paternity analysis of female pups only, and allowed one unscored locus. Despite these relatively relaxed criteria, the high exclusion probabilities for the loci employed meant that the level of false assignments was low (Table 2). A paternity was assigned to a given male if (i) it was the only male found to match a pup, or (ii) it was the male with the highest relatedness value (Queller & Goodnight 1989) and lowest randomization number (highest significance) among multiple candidates. In one instance, two males had relatedness values differing by 0.01, each with equivalent randomization numbers, so in this instance each male was assigned half a paternity.

Analysis of paternal gametes from offspring of ambiguous paternity

When a pup could not be assigned to any of our sampled males, pairwise locus by locus comparisons between

mother and pup enabled the male contribution to the pup's genotype to be determined. Any alleles present in the pup but not in the mother, must have been derived from the father. In this manner, we developed a database of genotypes for gametes from successful males. Individuals where the paternal alleles were ambiguous were excluded from the analysis. These gametic data were then used to estimate the minimum number of additional, unsampled, male seals needed to account for the parentage of offspring for which paternity was ambiguous. To do this, the male gametic data derived from the pup were examined for relatedness using the options for haploid data in the KINSHIP package (Goodnight & Queller 1999). Our test hypothesis was that if gametes were derived from the same male then, on average, they should share half of their alleles. Gametes that were identified as possible relatives at a significance level of $P < 0.05$ were grouped together and the total number of gametic groups calculated. All gamete groups were checked by eye to ensure that each group possessed no more than two alleles at each locus.

Results

Resampling rates

Six hundred and thirty-nine fur seals sampled during the breeding seasons 1994–95 were genotyped for eight polymorphic microsatellite loci (Table 1). These data contain 184 mother–pup pairs and 243 of 264 adult males; the latter represents 90% of adult males that held territories on our study beach during the two breeding seasons.

Analyses of these data for genotypic identity revealed that the levels of resampling within this population were very low. Out of 264 samples taken, only one adult male was unknowingly resampled between years. A low rate of resampling is unsurprising for females and pups, both of which can be readily tagged. However, some resampling of adult males, especially between years, might be expected due to the large number of untagged individuals being sampled. The very low rate of resampling of males in this study is important, as it demonstrates that the combination of marking with paint and photographic identification used to identify adult males at this study site since 1984 (Arnould & Duck 1997) is precise and reliable. This finding is supported by the genotypic concordance of 13 pairs of samples taken from males intentionally resampled in both breeding seasons.

Analysis of paternity

For our analysis of paternity, all mother–pup pairs were compared with all adult males sampled. Allowing no mismatching loci paternity was determined for 42 pups (23% of total pups; Table 3) and rose to 65 (37% of pups; Table 3) allowing one mismatching locus. Extending this analysis we found no evidence that any one locus stood out as the excluding locus, except that as expected, the most polymorphic loci tended to be the excluding loci. Correcting for the background rate of paternity assignment (0.17 paternities per 1000 male/pup comparisons = 7.5 paternities), the total number of paternities allocated is reduced to 35. This represents only 19% of all pups. Whilst

Table 3 Paternity assignment among Antarctic fur seal males both within pup cohorts and over all years

Pup cohort (no. of pups)	No. of paternities/male	No mismatch			One mismatch		
		No. of males	No. of paternities (% of pups)	Percentage of males	No. of males	No. of paternities (% of pups)	Percentage of males
1994 (103)	0	226	0	93.0	215	0	88.5
	1	14	13	5.8	24	24	9.9
	2	3	6	1.2	3	6	1.2
	3	0	0	0	1	3	0.4
			19 (18.4%)		33 (32%)		
1995 (81)	0	221	0	91.0	214	0	88.1
	1	21	21	8.6	26	26	10.7
	2	1	2	0.4	3	6	1.2
			23 (28.4%)		32 (39.5%)		
All years (184)	0	204	0	83.9	190		78.1
	1	35*	34*	14.4	45	45	18.5
	2	4	8	1.7	4	8	1.7
	3	0	0		4	12	1.7
			42 (22.8%)		65 (37%)		

*Includes one pup for which two putative fathers were identified. These males had equal relatedness value and were therefore assigned half paternity each.

it is important to estimate the level of type I error in our paternity assignments, it was not possible to distinguish those that were false from those that were genuine. Furthermore, it is likely that type I errors are compensated for by type II error rates, so all further analyses were performed on actual assigned paternities.

Of the 42 pups assigned a father, 19 pups were born in 1994 (representing 18.4% of the 1994 cohort), while 23 were born in 1995 (representing 28.4% of the 1995 cohort). While the numbers of pups sampled in both years were approximately the same ($n_{94} = 103$ and $n_{95} = 81$) a reduction in assigned paternity for the 1994 cohort might be expected because no males were sampled in 1993 when this cohort was conceived. Thus only those fathers that returned to the site the year after successful mating will have been sampled. Despite this complication, we could still gain some indication of paternity in the 1994 cohort by using males present on the study beaches in 1994 and 1995. This approach can be justified by the observation that approximately 50% of adult males observed at the study beach in a given year return to the breeding beach in the subsequent year (Arnould & Duck 1997). Therefore, of the males sampled in 1994 ($n = 111$) and 1995 ($n = 132$), approximately half were territorial males in 1993. Testing these males against the 1994 mother-pups provides some indication of male reproductive success in 1993.

The numbers of paternities assigned to individual males were unexpectedly low (see Table 3). The majority of males sampled (83.5%) were not assigned any paternities. For the remaining males sampled (16.5%), most were assigned a single paternity (14.8%), with only four males (1.7%) being assigned multiple paternities. All four males were found to have sired two pups in the same breeding season. In 74 instances, pups were sampled from the same female in two different years, and in three of these, paternity was assigned to both pups. In all three cases the sibling pups had different fathers. Furthermore, in the 12 cases where one of the two pups was assigned a father, the father of one pup could be excluded as the father of the second pup. These results suggest that there is no evidence of mate fidelity in Antarctic fur seals.

The number of paternities determined for males sampled in 1994 was predicted to be higher than for males sampled in 1995, because the results of male reproductive success in 1994 could be directly examined in the pup cohort of 1995. In contrast, the reproductive success of 1995 males could only be inferred from pups sampled in 1994 and 1995. Analyses of the proportion of successful males identified in each year show that we could assign more paternities to males sampled in 1994. Thirty-nine successful males were identified in this study, 23 of which were sampled in 1994 and 16 in 1995. As a percentage of the total males sampled in those years, these represent 20.7 and 12.1% of males sampled in 1994 and 1995,

Table 4 Paternity assignment among successful Antarctic fur seal males by year

Year male sampled	Percentage assigned to pups born in		
	1994	1995	All years
1994	12	13	25
1995	7	10	17
All years	19	23	42

respectively. These data suggest that a bias in successful paternity assignment between males sampled in 1994 vs. those sampled in 1995 may be present. However, we found that the number of pups assigned to fathers sampled in the birth year, or later, did not differ greatly from the number assigned to fathers sampled in the year of conception (Table 4). For example, males sampled in 1994 were found to father 12 pups in the 1994 cohort and 13 pups in 1995.

Analysis of paternal gametes from offspring of ambiguous paternity

From a total sample of 184 mother-pup pairs, 42 pups were assigned a father. The maximum number of males necessary to father the unassigned pups is 142. To obtain a better estimate of the number of additional fathers required, we examined the relatedness of male gametes using the KINSHIP package (Goodnight & Queller 1999). Using this approach we identified 35 groups, each containing one to eight gametes (Fig. 1), from the original 142 unique male haplotypes. This suggests that up to 35 different males sired offspring on the study site, in addition to the resident males.

Comparison of behavioural and genetic estimates of reproductive success

During the austral summer of 1994 we observed 28 copulations in a population of 220 marked females. These 28 copulations involved 14 individual males and 27 individual females. Sixteen of these females pupped in the following year, but in only one instance was paternity assigned genetically to the male that was seen to copulate with that female. Interestingly, in one case a female was observed to copulate twice with different, sampled males, yet neither of these candidate fathers matched the resulting pup.

Males that were recorded with paternities were territorial or present, on average, for longer on the study beach than males that achieved no recorded paternities (Mann-Whitney *U* exact two-tailed $P < 0.001$ in all instances, see Table 5). Those individuals that achieved two paternities

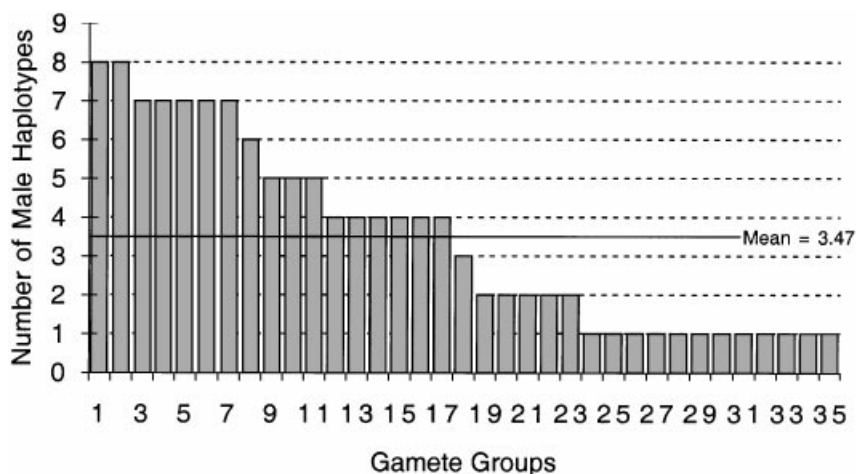


Fig. 1 Graphical representation of the numbers of male haplotypes assigned to specific gamete groups following relatedness analyses using KINSHIP (Goodnight & Queller 1999). Gametes that were identified as possible relatives at a $P < 0.05$ significance level are grouped together.

Table 5 Time spent on the breeding grounds by males that were recorded to achieve at least one paternity and those that were not recorded to achieve any paternities. Time on the breeding grounds is given as time spent in territory (territorial), time spent present on the beach (present) and time from the first to the last observation of the animal in any year (first–last). Values are expressed as means and standard errors are given in parentheses. Data are for all males recorded during 1994 and 1995

Status of male	<i>n</i>	Territorial (days)	Present (days)	First–last (days)
No paternity	225	12.5 (0.7)	15.1 (0.7)	54.3 (0.8)
One paternity	35	15.1 (2.4)	17.7 (2.6)	58.9 (1.8)
Two paternities	4	29.2 (5.2)	35.0 (7.3)	49.0 (2.4)

were territorial or present for three times the duration of individuals that achieved no paternities and about twice the duration of those that achieved one paternity. However, there was no significant difference amongst the three groups in the time from first to last observation at the breeding grounds.

Discussion

The discrepancy between genetics and behaviour

The Antarctic fur seal exhibits resource-defence polygyny in which dominant bulls defend discrete territories in breeding rookeries within which harems of up to 10 female seals give birth and rear their pups (Bonner 1968; McCann 1980; Arnould & Duck 1997). This model has remained uncontested for many years, but our data suggest that the mating system of this species may be more complex than previously thought.

As expected, there was a link between tenure duration and male reproductive success, based on previously reported copulatory data and female attendance (Arnould & Duck 1997; Table 5). However, even the most successful males performed poorly in comparison with our expectations based on copulatory data. Most males (84%) were assigned

no paternity and the majority of those that were successful were assigned paternity for only one pup. Only on four occasions (2% of males) were male seals assigned multiple parentage, and in all cases this was for two pups sired in the same season.

The overwhelming expectation at the beginning of this study was that we should be able to determine paternity for the majority of pups (70–90%) and that most paternities would be attributable to a handful of dominant males. However, having sampled and genotyped 90% of all the males attending our study beach, including all males observed to copulate with females and all males holding territory, we found that we could assign paternity for only 42 pups (23%) over all years. Even assuming that one locus has been scored incorrectly, our assignment rate only increases to 65 pups (37%) over all years (Table 3). If resource-defence polygyny is the major reproductive strategy employed by male fur seals then why is the proportion of pups assigned parentage so low? It is clear that males who held territories for longer periods obtained more paternities than males who held territories for short periods (Table 5). Therefore, territoriality does appear to have some benefits, but is what appears to us to be a small increase in reproductive success adequate to explain the high costs associated with territoriality?

Explaining the discrepancy

The discrepancy between our results and those expected had resource defence been the predominant mating strategy, may be explained by several factors. First, a small part of the discrepancy can be attributed to errors inherent in the study design. For example, only 243 unique males of 264 males sampled were genotyped successfully. The 21 untyped samples consisted of 14 duplicates and seven samples that proved intractable for genetic analyses. Consequently, ~2.8% of pups (7/250) would have not been assigned paternities even if all fathers had been present on the study beach and all had been sampled. The total number of pups with known mothers, to which paternities could be assigned, was 184. Assuming that all paternities came from animals on the beach and that all males were sampled, this would mean that our expected total number of assigned paternities would be 179. However, only 42 paternities were assigned, meaning that the animals in territory on the study beach achieved ~24% of the paternities that they should have if, as we thought, all the key individuals involved in mating were present in our sample set.

Second, there is an annual turnover of approximately 15% (range 9–35%) of females at the study site each year. Because we see almost no movement of established females between sites, almost all of the new females at our study site will be first time breeders. The actual proportions of new recruits in 1994/95 and 1995/96 were 23 and 18%, respectively. We have no idea where these females may have been mated, but can be fairly certain that it was not at our study beach. Consequently, we could only expect to assign paternity for 77–82% of mother–pup pairs sampled.

It seems probable that a small proportion of our unassigned paternities resulted because not all males were sampled. However, this is unlikely to amount to more than a few percent, because all territorial males were sampled and all males observed to copulate were sampled. It is possible that if one or two key males were missing from our analyses then a significant error might be introduced. To examine the possibility that several key males ('hot-shots') were missing from our sample set, we examined the relatedness of male gamete haplotypes derived from pups for which paternity could not be assigned.

Thirty-five gamete groups were identified, each containing from one to eight gametes. If these gamete groups can be considered to be representative of individual males then these data suggest that there were several unsampled males that could be assigned multiple paternity. Indeed, some unsampled males were up to four times as successful as the most successful male we sampled. Of course, this is probably an unnaturally low number, representing close to the minimum number of male seals necessary to explain the haplotype data. In reality, an even greater number of

male seals probably sired the offspring with ambiguous paternity. Nevertheless, it is hard to believe that we missed at least 35 key males, implicated in 142 copulations over the 2-year period, especially if these missing males were employing resource defence to increase their mating success. The question then is where do these males reside? Are these males present on the study beach but have avoided sampling, or do they reside elsewhere, for example on an adjacent beach or in the water?

Evidence for alternative, interchangeable, mating strategies

Holding territory appears to confer a small advantage to males. For example, the fathers of all 12 pups for which we could determine a probable date when the mother was mated (within the period from the date of pupping to +6 days postpartum in the previous year), were recorded as having been present during that breeding season. Furthermore, in eight of the 12 cases the father was observed at the beach during the period when the pup was sired and in all of these he held territory. However, holding territory is not the only strategy employed by male seals that are reproductively successful at our site. In 10 of 42 (23%) assigned paternities we identified males who mated with females in 1994 but were apparently not present in 1994. Clearly, either we have not sampled as many of the males that were present as we thought or there are some alternative strategies of which we are unaware (for example, males residing offshore in aquatic territories). Moreover, the 10 males that were not seen in 1994 but gained paternities in 1994, contained nine individuals that held territories in 1995. If these can be seen as different mating strategies by males then individual males apparently employ both strategies.

Female choice

Our data suggest that most males that sire pups on our study beach reside elsewhere. Consequently, it seems likely that female choice may be an important determinant of male mating success. Female choice has been predominantly neglected in studies of pinniped mating behaviour. It has often been assumed that a female seal will most probably mate with the male occupying the territory she is in when she becomes oestrous, and that she will mate only once. However, a recent study of mate choice in three conspecific fur seal species at Macquarie Island suggests that female mate choice may be a very important component of fur seal mating systems (Goldsworthy *et al.* 1999).

Arnould & Duck (1997) observed 704 copulations at our study site over a 4-year period (1984–87). In all but seven cases (1%) the females were observed to mate only once. If this is the case we should expect to be able to

predict the father of most pups if we sample the males observed to copulate with a given female. However, our paternity data suggest that female seals do not appear to be mating, at least successfully, with males holding territory at this study site. In only one of the 28 copulations observed was paternity assigned genetically to the male that was seen to copulate with that female. Furthermore, in the one female observed to copulate twice, neither of the males was the father of the pup produced in the following year. These data suggest that many female seals must mate at least twice, if not multiple times, and that the males they mate with are not observable within the study area.

Alternative mating strategies

Our favoured interpretation is that there is some other element to the mating system that we have not observed. It appears that territory is one avenue for achieving paternities, and territorial males that were predicted to be successful based on traditional behavioural estimates were more successful than their rivals. However, in order to explain the huge number of pups for which paternity cannot be assigned we must conclude that there is at least one other way of obtaining paternity.

First, it is possible that some of the reproductively successful males in our population only come ashore to breed at night and would be missed from our predominantly daytime observations. This possibility seems unlikely, even based on our limited nocturnal observations, because we did not observe any disturbance or relocation of individuals at the study site as might be expected if new males were making their way on to the beach each night and leaving before morning.

Another possibility is that males that reside in adjacent beach sites father some pups. This possibility is harder to dismiss. However, if males on adjacent beach sites are siring pups of female seals resident at our study beach, then it must be the female seals that are visiting the other beaches, otherwise we would expect to have observed and sampled at least some visiting males. Female seals at our study beach have been observed to move between their birthing site territory to harems elsewhere on the study beach prior to copulating (Arnould & Duck 1997; this study). However, the numbers of females that move between beach sites prior to mating appear to be small and no marked females have been observed mating at adjacent beach sites during more than 20 years of observations at Bird Island (McCann 1980; Arnould & Duck 1997).

The third alternative is that the traditional model of pinniped breeding behaviour has placed too much emphasis on terrestrial mating, and that aquatic mating plays a much more significant role than previously presumed.

Aquatic territories are not uncommon in pinnipeds. Many phocid ('true') seals, especially those that use ice as breeding habitat, are thought to mate aquatically (Cline *et al.* 1971; Stirling 1983; Boness 1991; Le Boeuf 1991). Aquatic mating has been implicated in the mating system of Juan Fernandez fur seals (Francis & Boness 1991), but the existence of aquatic territoriality as a successful mating strategy has not yet been documented for any other otariid. Nevertheless, the possibility of aquatic mating in fur seals should be taken seriously, and we believe it is the most probable explanation for the shortfall in assigned paternity. This contention is supported by genetic studies of harbour seals (*Phoca vitulina*; Coltman *et al.* 1998) that confirmed the difficulty in assigning paternity in an aquatically mating pinniped, being able to allocate fathers for no more than 30% of pups even at a low level of statistical confidence ($P < 0.5$). Further support for a significant role for aquatic mating in pinnipeds comes from recent genetic analyses of grey seals (*Halichoerus grypus*). Worthington Wilmer *et al.* (1999) report a large discrepancy between expected and assigned paternity and conclude that aquatic mating may play a much larger role in the grey seal mating system than has previously been thought.

Conclusions

Our results suggest that terrestrial territoriality is not the major strategy employed by Antarctic fur seals. These data imply that being on land confers an advantage to male reproductive success, but this advantage is much smaller than we had previously thought. The advantages to males of being land based are twofold. First, females come to a predictable site to breed, so that males occupying these sites may have a slightly elevated chance of obtaining a mating than they would have should they elect to stay at sea. Second, if the male encounters a female on land he stands some chance of controlling the encounter by physically overpowering the female, whereas in the water females probably manage the encounter and determine if mating occurs. Despite the apparent advantages of holding territory, we found that only 24% of paternities could be assigned to males holding beach territories.

We think it probable that our observations in this study and those of previous investigators (McCann 1980; Arnould & Duck 1997) do accurately reflect the copulations that occur on the beach. However, the timing and exact duration of female oestrus is unknown, so it is possible that most successful copulations occur after females have left the beach on their first foraging trip approximately 6–8 days postpartum (Boyd 1991). If this is the case, mating at adjacent beach sites or with males at sea is more likely to occur. Under these conditions, male success may be subject to greater female mate choice.

If female choice is important in Antarctic fur seal mating then most matings should take place away from sites where males have an advantage. The obvious location, therefore, is in the water. In the water, females probably have control over encounters and can choose with which males they mate. It is possible that aquatic mating may only be suitable for the very best (or at least preferred) males. The data from our analysis of male gamete groups (Fig. 1) suggest that some unsampled males may perform significantly better than males holding beach territories. Ironically, we may find that the use of beach territories might be a secondary strategy used by large males that can no longer compete effectively for mates in the primary mating arena at sea.

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