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MALE REPRODUCTIVE STRATEGY AND THE IMPORTANCE OF MATERNAL STATUS IN THE ANTARCTIC FUR SEAL *ARCTOCEPHALUS GAZELLA*

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Abstract.—Although mammalian mating systems are classically characterized in terms of male competition and polygyny, it is becoming increasingly apparent that alternative male strategies and female choice may play important roles. For example, females who mate with males from a dominant dynasty risk producing inbred offspring. Many pinnipeds are highly polygynous, but in some species alternative male strategies such as aquatic mating appear to be important, even when behavioral observations suggest strong polygyny. Here, we analyze male reproductive success in the Antarctic fur seal *Arctocephalus gazella*, an otariid described behaviorally as being highly polygynous, by combining a microsatellite paternity analysis spanning seven consecutive breeding seasons with detailed behavioral data on both sexes. Territorial males fathered 59% of 660 pups analyzed from our study colony. Male reproductive skew was considerable, with a quarter of all paternities assigned to just 12 top individuals on a beach where mean annual pup production was 635. Most males were successful for only a single season, but those able to return over successive years enjoyed rapidly increasing success with each additional season of tenure. We found no evidence of alternative male reproductive tactics such as aquatic or sneaky terrestrial mating. However, paternity was strongly influenced by maternal status. Females observed on the beach without a pup were significantly less likely to conceive to a sampled territorial male than equivalent females that did pup. In addition, their pups carried combinations of paternal alleles that were less likely to be found on the study beach and exhibited lower levels of shared paternity. Thus, from a territorial male's perspective, not all females offer equal opportunities for fertilization.

Key words.—Female behavior, inbreeding, microsatellite, paternity analysis, pinniped, polygyny.

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Most mammalian mating systems are characterized by sexual inequality in reproductive investment, with females bearing the majority of the reproductive costs and males often contributing little more than sperm (Trivers 1972). Consequently, males generally maximize their fitness by copulating with as many females as possible, whereas females should choose high-quality partners. Classical polygynous mating systems (Clutton-Brock 1989) result from female sexual selection for indicators of male fitness such as size, dominance, control of resources (Reiter et al. 1981; Pemberton et al. 1992), or ornamentation (Hamilton and Zuk 1982). However, especially for long-lived and philopatric species, selection against inbreeding depression may undermine polygyny by promoting female preference for subordinate males (Qvarnstrom and Forsgren 1998).

Variance in male reproductive success may have profound implications for the evolution of sexually selected traits, reproductive strategies, population genetic structure, and processes of natural selection. Behavioral studies have shown that females of many species mate with dominant males (LeBoeuf and Peterson 1969; Boness and James 1979; Appleby 1982; Cowlishaw and Dunbar 1991) and may even incite competition among males to ensure fertilization by the most dominant (Cox and LeBoeuf 1977). However, the tendency of studies to focus on dominant individuals may have led to the importance of alternative mating strategies being underestimated. The recent widespread use of genetic paternity testing is now allowing a more accurate assessment of polygyny, revealing some agreement with prior expectations (e.g. Pemberton et al. 1992; Wainstein et al. 1997) but elsewhere finding lower than expected reproductive skew (e.g. Amos et al. 1993; Coltman et al. 1999a; Pemberton et al. 1999). Alternative male mating strategies may sometimes prove highly successful (Hogg and Forbes 1997).

Many pinnipeds breed in dense colonies (Bartholomew 1970) in which males may either control access to females (female defense polygyny; Davies 1991) or defend territories where females aggregate (resource-defense polygyny; Emlen and Oring 1977). Such species usually show strong sexual dimorphism for body size and adopt an apparently classical polygynous mating system (Clutton-Brock 1989). However, the degree of male reproductive skew appears to depend upon specific features of pinniped breeding ecology (Stirling 1983; Boness 1991). For example, although all pinnipeds give birth and nurse their pups on land, approximately half of the extant species mate in the water (Coltman et al. 1998). Aquatic mating is thought to reduce polygyny because females are more mobile in water and territories more difficult for males to defend (Bartholomew 1970).

Genetic analyses have provided empirical support for behavioral estimates of polygyny in southern elephant seals *Mirounga leonina* (Wainstein et al. 1997; Hoelzel et al. 1999) and harbor seals *Phoca vitulina* (Coltman et al. 1998). However, pinniped mating success may sometimes provide a poor indicator of paternity (Harris et al. 1991; Perry and Amos 1998) and behaviorally dominant males frequently prove less successful than expected (Amos et al. 1993; McRae and Kovacs 1994; Ambs et al. 1999; Coltman et al. 1999b; Hoelzel

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et al. 1999). For example, in colonially breeding gray seals (*Halichoerus grypus*), previously described as polygynous, the majority of conceptions probably occur aquatically (Worthington Wilmer et al. 1999, 2000) and female behavior may be strongly influenced by the need to avoid inbreeding (Amos et al. 2001).

The Otariidae include fur seals and sea lions, are strongly sexually dimorphic, and have long been considered the most terrestrial of pinnipeds (Boness 1991; Arnould and Duck 1997). However, a microsatellite study of almost 200 Antarctic fur seal (*Arctocephalus gazella*) pups by Gemmell et al. (2001) could only assign paternity to 23% of pups, and concluded that alternative strategies including aquatic mating may be important. Such a finding is strongly at odds with expectations based on the known biology of the species, and suggests that one or more key factors influencing male breeding behavior may have been overlooked. Candidate factors include the ability of males to control access to females, the ability of females to control paternity, and inbreeding avoidance (Emlen and Oring 1977; Clutton-Brock 1989; Birkhead and Moller 1993; Tregenza and Wedell 2000).

Unfortunately, the brevity of this first study (two seasons) meant that little could be learned about how territorial males accumulate paternities over multiple seasons, nor about whether they could pursue strategies such as sneaky or aquatic mating conditionally (e.g. depending upon age; Gross 1996). Similarly, although female pinnipeds may show choice, at least for the correct species of partner in a mixed-species colony (Goldsworthy et al. 1999), the importance of female behavior remains unknown under more normal circumstances. To address these questions we analyzed an enlarged Antarctic fur seal dataset.

Antarctic fur seals are typical otariids, being highly sexually dimorphic (males are two to nine times heavier than females) and exhibiting resource-defense polygyny and highly synchronous seasonal breeding (Bonner 1968; McCann and Doidge 1987). Adult males begin to establish territories on breeding beaches at sub-Antarctic islands during mid-October, about one month before the arrival of females, which carry fetuses conceived the previous season (McCann 1980). Females give birth two days after coming ashore, come into estrus six to seven days later (Duck 1990), and mate before going to sea on a feeding trip. At high-density breeding rookeries, dominant males monopolize harems of up to 27 females (McCann 1980). However, holding a territory can be costly since males fast throughout their tenure, losing weight at a rate of 1.5kg/day (Boyd and Duck 1991) and injuries incurred during territorial disputes constitute a major cause of death (Baker and McCann 1989). Thus, males do not usually begin to hold tenure until reaching at least eight years of age, despite becoming sexually mature at three to four years old (Payne 1979).

Here, we present a study based on daily behavioral observations and almost 1800 Antarctic fur seal tissue samples collected at Bird Island, South Georgia, over a seven-year period. We used microsatellite polymorphism at nine hypervariable loci to conduct a detailed genetic analysis of breeding behavior in both sexes.

MATERIALS AND METHODS

Study Site, Data Collection, and Tissue Sampling

This study was conducted at Bird Island, South Georgia (54°00′S, 38°02′W) during the austral summers of 1994/1995 through 2000/2001 (hereafter, breeding seasons are referred to by the year in which they began). The study population was located at a small cobblestone breeding beach, separated from adjacent breeding sites by a cliff on the east side, open sea on the west, and rocky ridges to the north and south. The beach covered an area of 440 m^2 at high tide (Lunn and Boyd 1993) and, on average, 635 pups were born there annually. An elevated scaffold walkway (Doidge et al. 1984) provided access to all parts of the beach and minimized disturbance to animals.

Approximately 550 adult females were randomly selected and tagged using cattle ear tags (Dalton Supplies, Henley-on-Thames, U.K.) placed in the trailing edge of the foreflipper (Lunn et al. 1994). Adult males were too large and aggressive to be tagged. Hence, the majority of males occupying territories on the beach and on the surrounding rocks ($n = 705$) were individually marked using small patches of gloss paint (Arnould and Duck 1997). Paint marks were used for within-season identification and, in many cases, remained identifiable across years. Twice-daily surveys were made of all territorial males, females, and pups on the beach from 1 November until the birth of the last pup (early January). Mating events involving identifiable animals were also recorded. Age data were available for 427 females, aged using canine tooth sections (Boyd et al. 1995) and 30 adult males that were born on the study beach and retained flipper tags fitted when they were pups.

Pups born to tagged females were captured on the day of birth and a skin sample taken from the interdigital margin of the foreflipper using piglet ear notching pliers (Majluf and Goebel 1992). The majority of tagged adult females were sampled in the same way later in the season (January–March). Territorial males were sampled using a biopsy dart system (Gemmell and Majluf 1997). All sampling equipment was sterilized using ethanol between uses. Skin samples were stored individually in the preservative buffer 20% dimethyl sulphoxide (DMSO) saturated with salt (Amos and Hoelzel 1991) and stored at −20°C. Samples were already available from 184 mother-pup pairs (163 pairs matching) and 250 males (211 after removal of identical genotypes) sampled during 1994 and 1995 (Gemmell et al. 2001). Tables 1 and 2 detail the numbers of animals present on the study beach and samples genotyped for the current study.

DNA Extraction and Microsatellite Typing

Total genomic DNA was extracted from the skin biopsy samples using an adapted Chelex 100 protocol (Walsh et al. 1991). All DNA samples were then genotyped using a panel of nine dinucleotide-repeat microsatellite loci, previously characterized from a variety of seal species (see Table 3). The amplification and screening of microsatellite loci was performed as described by Gemmell et al. (1997). Samples that failed to amplify at two or more loci (n = four pups, one adult male) were excluded from the dataset. In the case

TABLE 1. Numbers of adult male Antarctic fur seals present on the study beach, determined by daily census, and samples genotyped for paternity analysis. Parentheses indicate numbers of individuals following removal of duplicate genotypes. Numbers of males of known genotype include individuals that were recognized and sampled during other years and exclude duplicate genotypes ($n = 255$). Of the 415 unique genotyped males, a small number ($n = 22$) held tenure exclusively on the rocks surrounding the colony.

Year	Number of males present	Number of samples genotyped	Number of individuals of known genotype present	Percentage of males present with genotype known
1994	188 (183)	115	122	66.7
1995	154 (153)	143	140	91.5
1996	160 (157)	73	112	71.3
1997	134 (134)	28	75	56.0
1998	143 (143)	0	88	61.5
1999	151 (148)	138	139	93.9
2000	223 (207)	173	162	78.3
1994–2000	834 (705)	670	415	58.9

of microsatellite data already available for 1994 and 1995 samples (Gemmell et al. 2001), we incorporated existing data for six loci (Aa4, Hg1.3, Hg8.10, M11a, PvcA and PvcE) into the final dataset. To compensate for differences between observers, autoradiographs for all previously genotyped samples were re-scored. Whenever an uncertain score was encountered, the sample was regenotyped at that locus. Finally, the overall genotyping and scoring error rate was assessed by independently regenotyping approximately ten percent of all samples ($n = 190$) for all nine loci.

Identity Checking

To identify individuals that may have been sampled more than once (within and/or between years) microsatellite data were checked for duplicate entries using the program IDENTITY (Allen et al. 1995). We calculated the probability of identity (Paetkau and Strobeck 1994) for each locus and across all loci to determine the probability that two randomly selected genotypes match by chance. Since adults of both sexes frequently return to the same colony in successive years and females are known to exhibit fine-scale natal site philopatry (Lunn and Boyd 1991) we also calculated, as a conservative measure, the probability of identity assuming that all individuals are siblings (Evett and Weir 1998). Both values were very low (1.354×10^{-12} and 1.204×10^{-4} respectively; see Table 3), indicating that identical genotypes probably represent individuals that were resampled. Duplicate genotypes were thus excluded from the genotype files prior to paternity analysis. Whenever genotypes matched at all but one locus, autoradiographs were checked and any scoring errors found to account for the mismatches were corrected. Finally, resulting records of genetic identity were compared with field data and, whenever genetic analysis revealed mistaken identity, field records were modified accordingly.

Paternity Analysis

Prior to paternity analysis, tests for deviation from Hardy-Weinberg equilibrium and linkage disequilibrium were implemented using Genepop version 3.1d (Raymond and Rousset 1995). Bonferroni adjustments (Hochberg 1988) with an α level of $P < 0.05$ were carried out on all tabulated results. Genepop was also used to determine expected heterozygosity (H_E), null allele frequency and the probability of paternal exclusion (Weir 1996) for each locus and across all loci.

Mother-pup pairs were checked for mismatches using the program NEWPAT XL (Worthington Wilmer et al. 1999). Mismatching genotypes were double-checked and any scoring errors were corrected. Paternity analysis was conducted using the programs NEWPAT XL (Worthington Wilmer et al. 1999) and CERVUS version 1.0 (Marshall et al. 1998; Slate et al. 2000). NEWPAT searches for matches between candidate males and each offspring's deduced paternal alleles. For our analysis, we set stringent match criteria allow-

TABLE 2. Numbers of pupping Antarctic fur seal females present on the study beach and sampled for paternity analysis. Annual numbers of females of known genotype include individuals that were recognized and sampled during other years and exclude duplicate genotypes ($n = 40$). The numbers of pups with known mothers from 1994 and 1995 are greater than reported by Gemmell et al. (2001) because we retrospectively tissue-sampled a number of females that pupped but were not sampled during those years. Since 58 mother-pup pairs mismatched at multiple loci, we present the numbers of matching pairs that were used for paternity analysis.

Year	Number of pupping females present	Number of female samples genotyped	Number of individual females of known genotype present	Number of sampled mother-pup pairs	Number of matching mother-pup pairs
1994	584	116	176	126	109
1995	797	18	128	110	102
1996	732	51	155	133	126
1997	501	26	113	86	82
1998	693	0	111	79	72
1999	444	58	89	60	56
2000	696	106	193	124	113
1994–2000		375	335	718	660

TABLE 3. Summary of microsatellite loci used in this study, including literature sources and polymorphism characteristics for the Antarctic fur seals genotyped.

Locus	Isolated from species	Reference	Number of alleles	Size range (bp)	H_E	Null allele frequency	Hardy-Weinberg equilibrium probability	Probability of identity	Probability of identity (siblings)	Exclusion probability
Aa4	South American fur seal *Arctocephalus australis*	Gemmell et al. (1997)	7	204–220	0.747	+0.0006	0.07	0.105	0.403	0.523
Hg1.3	Gray seal *Halichoerus grypus*	Gemmell et al. (1997)	13	234–276	0.868	−0.0068	0.55	0.031	0.352	0.744
Hg6.3	Gray seal *Halichoerus grypus*	Allen et al. (1995)	16	213–245	0.858	+0.0075	0.20	0.034	0.330	0.724
Hg8.10	Gray seal *Halichoerus grypus*	Allen et al. (1995)	5	162–184	0.450	−0.0064	0.71	0.389	0.622	0.191
Lw10	Weddell seal *Leptonychotes weddellii*	Davis et al. (2002)	18	100–140	0.906	+0.0079	0.12	0.017	0.301	0.806
M11a	Southern elephant seal *Mirounga leonina*	Hoelzel et al. (1999)	18	148–184	0.921	−0.0006	0.19	0.012	0.292	0.841
Pv9	Gray seal *Halichoerus grypus*	Allen et al. (1995)	11	162–186	0.771	−0.0044	0.79	0.069	0.382	0.615
PvcA	Harbor seal *Phoca vitulina*	Coltman et al. (1996)	9	137–153	0.774	+0.0098	0.74	0.079	0.383	0.587
PvcE	Harbor seal *Phoca vitulina*	Coltman et al. (1996)	15	94–148	0.872	−0.0003	0.39	0.029	0.321	0.744
Overall			12.4	94–276	0.796	+0.0008	0.26	1.354×10^{-12}	1.204×10^{-4}	0.999*

* Exact paternity exclusion probability is 0.999964.

ing a maximum of one unscored locus and no mismatches. Null mismatches, those explicable by invoking nonamplifying alleles, were effectively precluded by setting the null match parameter to 0.03. Putative matches were tested by Monte Carlo simulation and a paternity was assigned to a male if either no other male matched the pup, or this male had the lowest randomization number among multiple candidates. As an extra guard against males being excluded through scoring errors, the analysis was then repeated allowing up to two mismatches, and all mismatches were rechecked by reference to the original autoradiograms.

CERVUS (Marshall et al. 1998) is a simulation program that generates critical log-likelihood scores to assign paternity at a given level of statistical confidence. The program again incorporates user-defined input parameters, such as the frequency of gaps and errors in the microsatellite dataset. However, it also takes into account the number of candidate males and the proportion of those males that have been sampled. For our analysis, we defined ''candidate males'' as adult males who were observed at any point during daylight hours at the beach during the breeding seasons of 1994 through 2000. The number of candidates was 705 (total number of males observed excluding individuals with identical genotypes; Table 1) of which 59% had been sampled. Other parameters set for CERVUS were 99.8% for the proportion of samples typed for all loci and 0.5% for the error rate, defined as the proportion of loci typed incorrectly, averaged over all loci and individuals. Paternities were assigned at 95% and 80% confidence levels.

Skew in Territorial Male Reproductive Success

We tested the hypothesis that all males had random reproductive success over the entire study period by comparing the observed numbers assigned 0–10 paternities and the numbers expected under a Poisson distribution with the observed mean (0.93 paternities/male analyzed). To avoid artifactual inflation of the zero success class, the analysis was restricted to cases in which males were observed at some time during or before the year of pup conception.

Patterns of Territorial Male Reproductive Success

Observations of male behavior were limited to those males that came ashore at some time during the study. Consequently, the possibility of aquatic mating or alternative nonterritorial strategies was examined by elimination. Males do not abandon their territories until they terminate their period of tenure (McCann 1980), except for rare trips to sea on very hot days (Arnould and Duck 1997). Thus, when both mother and father are simultaneously present on the breeding beach at the time of pup conception, mating is likely to occur terrestrially. We determined the extent to which males were present on the beach at times when they conceived pups, both among and within breeding seasons. To investigate among-season patterns, paternity data were classified relative to the years in which males were first observed holding tenure. Since pups are born the year after conception, we defined zero displacement as when a male observed for the first time in year *x* was compared with a pup born in year $x + 1$. Thus, a pup born in year $x + 2$ was classified as displacement +1 and a pup born in year *x* was classified as displacement −1. Because males first seen in 1994 may have included some that also held tenure before the study began in 1993, we excluded paternities assigned to 1994 males at displacement −1 from the analysis. Within seasons, we determined whether males were holding territorial tenure on the estimated dates that they conceived pups. Conception dates were estimated as female pupping date plus seven days, the average postpartum delay before estrus (Arnould and Duck 1997).

Paternity Assignment and Maternal Status

Pups were classified by the ''maternal status'' of their mothers during the year of conception, namely: (1) absent from colony; (2) present but nonpregnant; (3) unknown; (4) present with pup. Maternal status was determined for all tagged females using census data and pupping records. Females of unknown maternal status were newly tagged during the year of pup birth and thus could not be identified during the conception year. Pups born during 1994 were excluded from the analysis, since no males were sampled during the year that they were conceived. To ascertain whether female age could be a determinant of paternity outcome, we checked for differences in the ages of females at pup conception among the four maternal status categories.

Paternal Haplotype Assignment Test

Although some females sometimes mate away from the beach, it is not known whether mating occurs in the shallows in the vicinity of the study area or elsewhere. While allele frequency data are not available for other populations, we do expect frequencies to differ because of high site fidelity, documented for females (Lunn and Boyd 1991). To test for differences among the paternal haplotypes of pups with known versus unknown fathers, we calculated for each pup the probability that the paternally deduced alleles were drawn from the genotype pool of sampled territorial males. Assignment probabilities were calculated simply as the probability of drawing the pup's paternal allele at each locus, multiplied over all loci.

Shared Paternity Analysis

When significant numbers of candidate fathers are unsampled, some information about the distribution of male success can be gleaned by examining the degree of relatedness between pups based on their inferred paternal alleles. The most sophisticated way to achieve this is to use a likelihood-based Markov chain Monte Carlo approach to estimate each sibship (e.g. Thomas and Hill 2000; Smith et al. 2001). Unfortunately, these methods are least effective when, as here, levels of shared paternity are low and the distribution of paternal sibship sizes is not known. Given the uncertainties associated with estimating individual sibships, we used a simple Monte Carlo randomization program, DADSHARE (written by W. Amos), which aims instead to estimate the total level of shared paternity, expressed as the average sibship size that best accounts for the data.

DADSHARE accepts data comprising mother-pup pairs and deduces paternally inherited alleles for each pup. From these alleles, an all-against-all paternal relatedness matrix is calculated, based on the methods of Queller and Goodnight (1989). With such a large number of pairwise comparisons, Type I errors tend to mask any high relatedness values due to genuine consanguinity. Consequently, DADSHARE condenses the two-dimensional all-against-all matrix to a single dimension using a simple unweighted pair-group mathematic averaging clustering algorithm. The assumption is that most of the information about close relatives will be contained in the nodes of the resulting dendrogram. As a test statistic for the level of shared paternity, we use the average relatedness between pairs of terminal branches. Higher levels of shared paternity will lead to higher mean relatedness in these terminal branches. To assist in interpretation of the results, the program then uses Monte Carlo simulation to generate randomized datasets for 10 scenarios showing different levels of shared paternity, namely with 1, 2, 3, 4, 5, $n/5$, $n/4$, $n/3$, $n/2$, and n males each fathering n, $n/2$, $n/3$, $n/4$, $n/5$, 5, 4, 3, 2, and 1 offspring each respectively, where n is the number of pups considered. Each scenario is repeated 10 times, yielding mean and standard deviation for the average branch-tip relatedness value. Relating the observed value to these preset scenarios then allows us to estimate the best-fit number of males with equal success that would best account for our data.

RESULTS

A total of 1763 fur seal tissue samples were genotyped for nine microsatellite loci. The frequency of missing single-locus genotypes in the dataset was 0.0021. After removal of identical multilocus genotypes, no locus showed significant deviation from Hardy-Weinberg equilibrium (see Table 3), nor was there evidence of linkage disequilibrium between any pairs of loci.

Typing Error Rates

Typing error rates, defined as the percentage of reactions incorrectly typed, are considered unlikely to be less than 1% for large-scale microsatellite screening projects (Slate et al. 2000), and may represent a major cause of mismatches between offspring and their true parents (Marshall et al. 1998). By independently repeat-genotyping 190 randomly selected samples at nine loci, we showed that the typing error rate for our dataset was low, at 0.0038 per reaction or 0.0022 per allele (13 reactions mistyped, accounting for 15 out of 6848 alleles incorrect). Given this observed allele-mistyping rate, we expect one in every 25.4 complete genotypes to contain a mistyped allele. Thus, on average, $1 - (1 - 1/25.4)^2 = 7.7\%$ of theoretically identical genotypes will mismatch. Mistyping was largely due to scoring and data-inputting errors, although four cases were consistent with the dropout of a single allele during PCR amplification (Gagneux et al. 1997; Goossens et al. 1998).

Animal Resampling Rates

Among 375 adult female samples, 40 duplicate genotypes were found, all corresponding to animals deliberately resampled because of illegible, broken, or lost tags. Among these

TABLE 4. Paternities assigned to Antarctic fur seal territorial males using NEWPAT. The proportions of males assigned paternities in each year are given as the numbers of fathers divided by the numbers of males of known genotype observed during the previous year. These could not be calculated for 1994, since no males were sampled in 1993. Since small numbers of pups were conceived by males that were not observed during years of conception, some percentages will differ slightly when only considering males seen during years of conception.

Pup cohort (no. of pups)	No. of paternities/male	No. of males (% of males)	No. of paternities (% of pups)
1994	0		
(109)	1	5	5 (4.6%)
	2+	9	20 (18.3%)
	1+	14	25 (22.9%)
1995	0	100 (71.4%)	
(102)	1	21 (15%)	21 (20.6%)
	2+	19 (13.6%)	53 (51.9%)
	1+	40 (28.6%)	74 (72.5%)
1996	0	66 (58.9%)	
(126)	1	24 (21.4%)	24 (19.0%)
	2+	22 (19.6%)	71 (56.4%)
	1+	46 (41.1%)	95 (75.4%)
1997	0	35 (46.7%)	
(82)	1	26 (34.7%)	26 (31.7%)
	2+	14 (18.7%)	31 (37.8%)
	1+	40 (53.3%)	57 (69.5%)
1998	0	68 (77.3%)	
(72)	1	15 (17.0%)	15 (20.8%)
	2+	5 (5.7%)	12 (16.7%)
	1+	20 (22.7%)	27 (37.5%)
1999	0	112 (80.6%)	
(56)	1	23 (16.5%)	23 (41.0%)
	2+	4 (2.9%)	15 (26.9%)
	1+	27 (19.4%)	38 (67.9%)
2000	0	119 (73.5%)	
(113)	1	30 (18.5%)	30 (26.5%)
	2+	13 (8.0%)	42 (37.2%)
	1+	43 (26.5%)	72 (63.7%)
All years	0	259 (62.4%)	
(660)	1	78 (18.8%)	78 (11.8%)
	2+	78 (18.8%)	310 (47.0%)
	1+	156 (37.6%)	388 (58.8%)

comparisons, we found two mistyped alleles of 1440, providing a second estimate of the allele-mistyping rate of 0.0014. Of 670 adult male samples, 255 duplicate genotypes were found (38.1% resampling rate), 57 of which were deliberately resampled to verify identity. The remaining 198 duplicates were not intentional and comprised 173 between-years and 25 within-years, suggesting that paint marks may have faded or been lost, mostly between seasons but occasionally within. Among male genotypes we found 27 mistyped alleles of 8784 (allele mistyping rate = 0.0030). No duplicate genotypes were found in among- or between-year comparisons of 718 pups. Thus, in total we identified unique genotypes for 415 males, 335 females, and 718 pups.

Mother-Pup Pairs

A total of 8% of mother-pup pairs genuinely mismatched ($n = 58$), comparable to fostering rates of 3–28% observed in gray seals (Perry et al. 1998) and 10% in harbor seals (Schaeff et al. 1999). Mismatching pairs were excluded from subsequent analyses, leaving 258 mothers with 113, 34, 35, 35, 19, 15, and 7 having 1, 2, 3, 4, 5, 6, and 7 matching pups respectively (total = 660 pups; Table 2).

Paternity Analysis

Using NEWPAT, paternity was assigned to 388 pups (58.8%, rising to a maximum of 75.4% in years of near-complete male sampling; see Table 4). Of these paternities, 19 (4.9%) were assigned following correction of single-locus scoring errors that would otherwise have led to paternal exclusion. Compensating for the background rate of paternity assignment (we would expect to assign 15.9 paternities by chance alone), on average 372 of the paternities allocated should be genuine. Simulations show that the majority of paternities were assigned with high confidence; the chance that an identical dataset not including the true father would yield a match by chance was less than 1% for 85.8% of paternities and less than 5% for 97.7%. Average relatedness between the pup and assigned father (Queller and Goodnight 1989) was 0.494 ± 0.092 SD.

CERVUS assigned paternity to 335 pups (50.8%) at the 95% confidence level and 471 pups (71.4%) at the 80% level (Table 5). However, a number of these assignments contained mismatches at up to four loci between the pup and candidate male genotypes and/or were incompatible mother-pup-father triads. As described previously, 19 mismatches at single loci were explained by genuine scoring errors (accounting for 18 mismatching assignments at the 95% confidence level and one at the 80% level). Following correction of these errors, considering only those paternities that did not invoke mismatches, CERVUS assigned paternity to 316 (47.9%) and 372 (56.4%) pups at 95% and 80% confidence levels respectively and assigned a ''most likely'' father for a further 16 (2.4%) pups. Using this approach, paternities assigned by CERVUS were identical to those assigned by NEWPAT, with the exception of only two cases in which there was conflict as to which male of a group of candidates was the father. Since the primary difference between the two programs was CERVUS's acceptance of paternities invoking multilocus mismatches or incompatible mother-pup-father triads we

TABLE 5. Critical log-likelihood (ΔLOD) scores and predicted and observed numbers of paternities assigned by CERVUS using 10,000 simulations.

Confidence level	Critical ΔLOD score	Predicted paternities	Paternities assigned (including mismatches)	Paternities assigned (excluding all mismatches)	Paternities assigned (excluding genuine mismatches)
95%	2.58	350 (53.0%)	335 (50.8%)	298 (45.2%)	316 (47.9%)
80%	1.01	475 (72.0%)	471 (71.4%)	353 (53.5%)	372 (56.4%)
Most likely		660 (100.0%)	660 (100.0%)	369 (55.9%)	388 (58.8%)

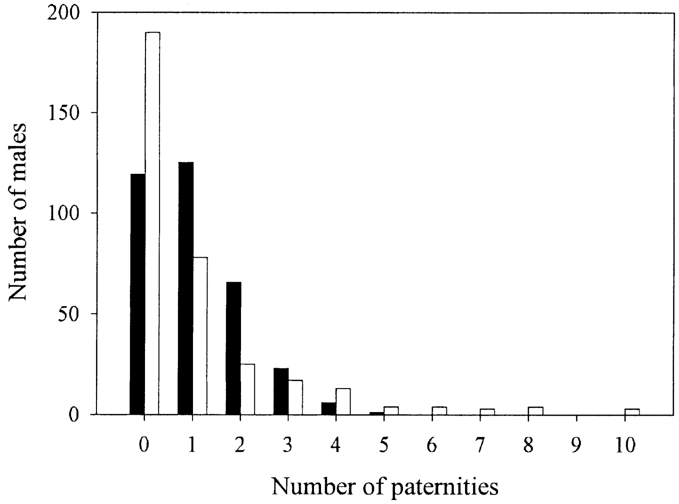

FIG. 1. Numbers of Antarctic fur seal males assigned 0–10 paternities (open columns) and numbers expected under a Poisson model of random mating (closed columns). Data are limited to those males that could be compared against pups born in years subsequent to male first sighting.

chose, as a conservative measure, to use the output from NEWPAT for further analyses.

During the study 23 copulations were observed between sampled males and tagged females that gave birth to a pup that was sampled the following year. In 16 instances (69.6%) the male observed mating was independently assigned paternity of the pup. In four other cases, the observed male was excluded and a different territorial male assigned paternity. For three pups we were unable to assign paternity to a sampled male.

Skew in Territorial Male Reproductive Success

Of the 415 territorial males genotyped, 156 (37.6%) were assigned paternity of at least one of our sample of pups from the study beach. The mean number of pups assigned per male and per father was 0.93 and 2.49 respectively. The maximum number of paternities allocated to any one male was eight in a single year. Over the entire study, the four most successful males were assigned 10 paternities each, equivalent to 67 paternities each if one extrapolates directly from our sample of 660 pups to the 4447 pups born on the beach throughout the entire study. The null hypothesis of no male reproductive skew was strongly rejected (Fig. 1; $\chi^2 = 172310.48$, df = 10, $P < 0.0001$).

Territorial Male Mating Strategy

To address the possibility of conditional aquatic mating, we determined the extent to which males were present on the study beach when they conceived pups, both among and within breeding seasons. Among seasons, for the great majority of paternities (89.8%), fathers were observed on the study beach during the years that their assigned pups were conceived. Only 16 pups were conceived before the father was first sighted and 21 pups after the father was last sighted. However, the sampling of territorial males was never complete, dropping as low as 56% in 1997. Consequently, the true proportion of terrestrially conceived pups should be higher, and may well approach 100%.

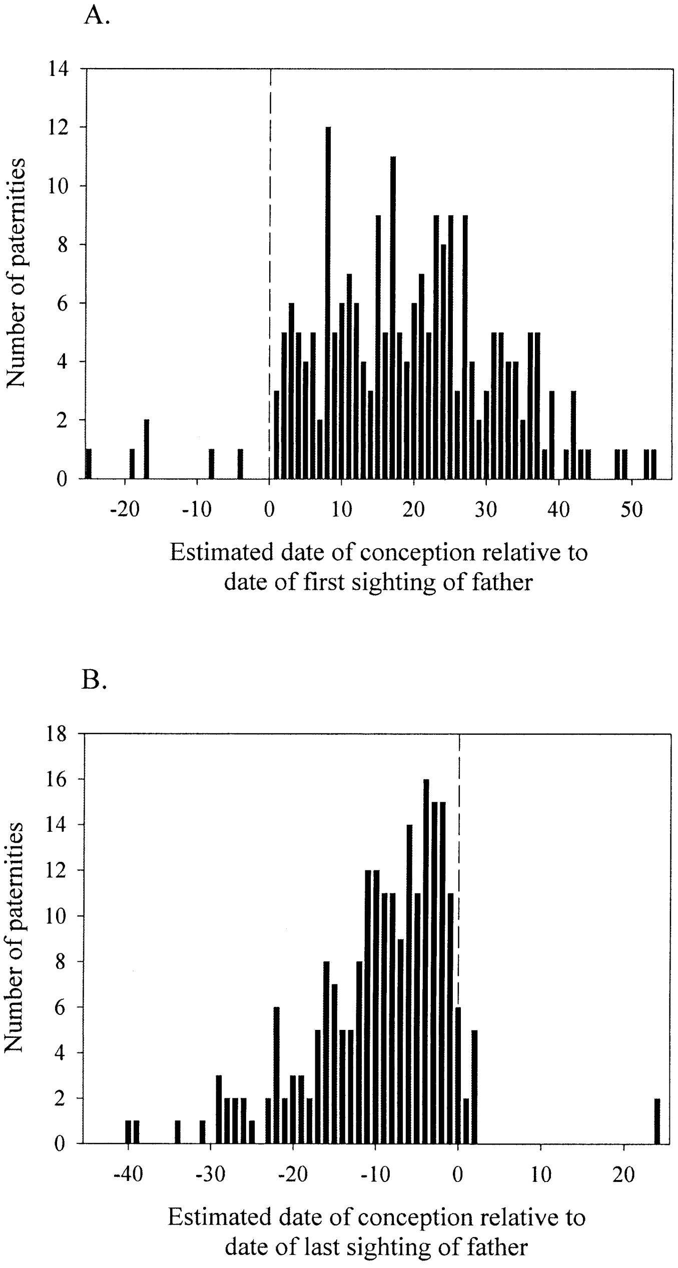

FIG. 2. Estimated dates of conception relative to (A) date of first sighting of father; (B) date of last sighting of father. Data are shown for 222 paternities, pooled across all years, for which conception date could be estimated and the father was observed at some time during the season of conception.

Within seasons, we determined whether males identified as fathers were seen on the estimated dates of conception. Pooled across all years, data were available for 222 pups. In the great majority of cases (93.2%) the estimated conception date fell within the time frame in which the father was known to be present on the beach. Estimated conception dates were prior to first sighting of the father in six cases (Fig. 2A) and after last sighting in nine cases (Fig. 2B). These small discrepancies can be attributable to both imperfect sighting records and uncertainty as to the exact dates of conception. Thus, again these data suggest strongly that aquatic mating is unimportant or even absent. If it does occur, it would have to involve males who consistently mate with females who are unlikely to be included in our sample set. To our knowledge such females do not exist.

The majority of males that held tenure exclusively on the rocks peripheral to the colony were genotyped ($n = 22$). None were awarded any paternities of pups born on the beach itself. By implication, peripheral males do not appear to increase their reproductive success by sneakily mating with females pupping on the beach.

Changes in Male Reproductive Success over Time

Paternity data were partitioned according to the time difference between the first sighting of each male and the year of conception of each of his assigned offspring (displacement). Displacement values ranged from -7 to $+5$ (Fig. 3). Male reproductive success, expressed as paternities per pup analyzed, was greatest for males at displacements 0 (i.e. male first sighted in the year of conception) and $+1$ but was lower thereafter (Fig. 3A), suggesting that the majority of pups were conceived by males during their first or second years of territorial tenure. When the same data were adjusted to allow for the number of male genotypes available for comparison, success remained high at displacement 1, but peaked at 5, the maximum level (Fig. 3B).

With a relatively small study beach and easy access to all animals, we were able to determine with reasonable accuracy which males were present during each year of the study. Consequently, we were also able to express our data in terms of success per male known to be present during the year of conception per pup (Fig. 4A), revealing a pattern in which average success increases with every extra year a male manages to hold tenure. Success might increase through extended tenure length and/or greater success per time spent on the beach. Experienced males do indeed arrive earlier during the season (Fig. 4B) and hold longer tenure (Fig. 4C). However, if success is now expressed in terms of a paternities per male per day present per pup comparison, there is still a pattern of increasing success with every extra year on the beach (Fig. 4D). Hence, experienced males increase their success both by staying longer and by being more competitive.

Age data were available for 30 tissue-sampled males that were born on the study beach and retained tags through to adulthood when they held tenure on the beach. Of these, 17 males were assigned paternities ($n = 47$ pups). To examine how reproductive success varied with age among these animals, we constructed an age-specific reproductive profile (Fig. 5). The resulting pattern was similar to the profiles in Figures 4A and 4D. The youngest males to conceive pups were eight years old, the mean age at first conception was 10.2 and success rose steadily with increasing age.

Paternity Shortfall, Male Sampling Intensity, and Maternal Status

Overall, 58.8% of all pups were assigned paternity and 58.9% of all males observed on the beach and surrounding rocks were genotyped (Table 1). Among years, the percentage of pups fathered by known males correlated positively with the percentage of males sampled during the year of conception (Fig. 6; $r_s = 0.786$, $n = 7$, $P = 0.036$ for the beach, not including the surrounding rocks). Paternity assignment was lowest for the 1994 pup cohort (22.9%) since no males were sampled during 1993 when these pups were conceived. However, whenever 60% or more of territorial males were sampled during years of pup conception, the proportion of pups assigned paternity was consistently high, varying between 63.7% and 75.4%. Despite this, the percentage of pups assigned paternity in any year still often fell short of male sampling effort, as noted by Gemmell et al. (2001).

To examine the origin of this shortfall, pups were classified by the maternal status of their mothers during the year of

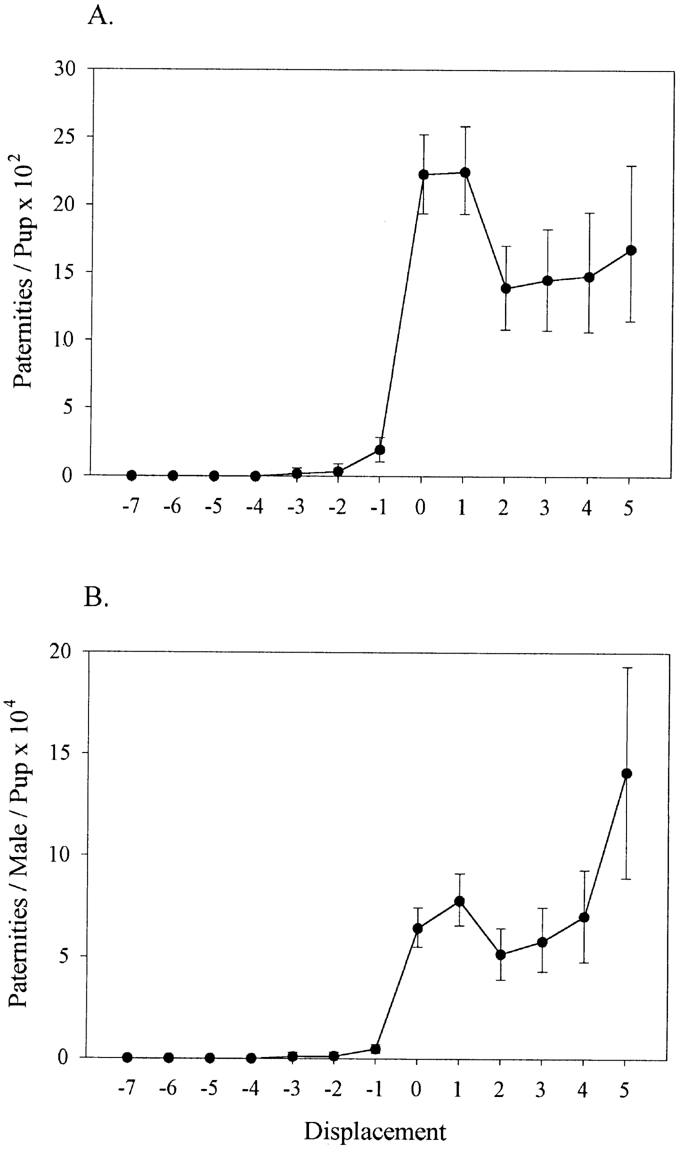

FIG. 3. Summary of the reproductive success of territorial males averaged for each level of displacement between the years in which males were first sighted and pups were conceived. (A) Paternities/pup; (B) paternities/male/pup. Error bars show 95% binomial confidence intervals.

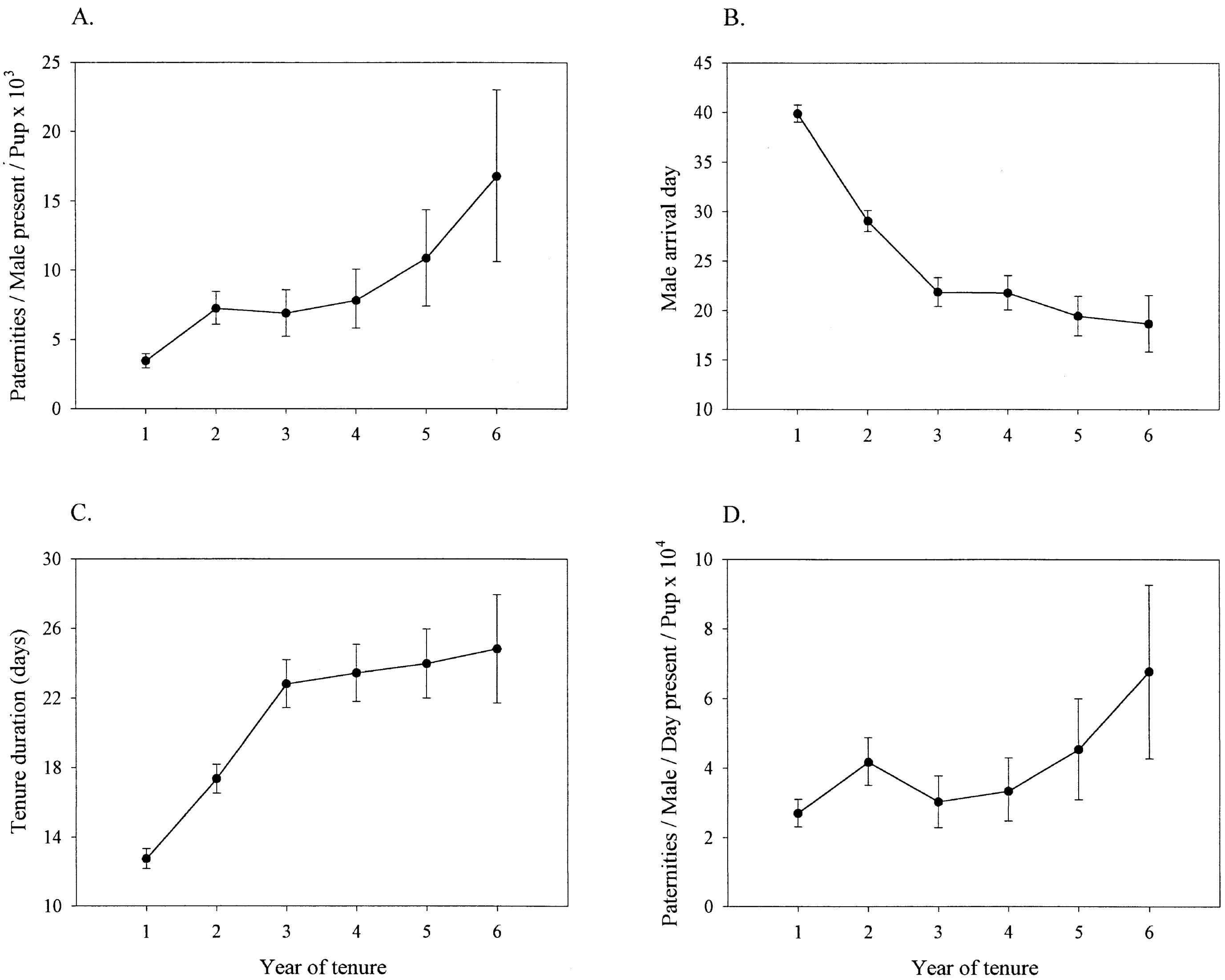

FIG. 4. Reproductive success and tenure characteristics for males observed during their first through sixth successive years of territorial tenure. (A) Paternities/male present during year of conception/pup; (B) male arrival day; (C) duration of territorial tenure; (D) paternities/male present/day present/pup. Error bars indicate 95% binomial confidence intervals for reproductive success profiles and SE for arrival day and tenure duration profiles.

conception, namely: (1) absent from colony; (2) present but nonpregnant; (3) unknown (newly tagged females); (4) present with pup. Figure 7 shows the overall percentages of pups assigned paternity for each maternal status category. The proportion of pups with known fathers varied significantly with maternal status ($\chi^2 = 74.165$, df $= 3$, $P < 0.0001$). When data were restricted to those pups whose mothers were known to have pupped in the year of conception, the full temporal pattern (Fig. 6) shows a highly significant correlation between male sampling effort in the year of conception and proportion of pups with assigned paternity ($r_s = 0.964$, $n = 6$, $P = 0.002$ for the beach, not including the surrounding rocks). Paternity assignment for females who pupped rose to a peak of almost 90% in 1996, despite incomplete male sampling when the pup cohort was conceived, suggesting that for this class of female, aquatic and other mating strategies are of little importance. When females were absent from the beach during the year of conception, the probability of paternity assignment was very low, implying that most of these females did not mate on the beach. The intermediate class, comprising females that were present but did not pup on the beach, had a fairly constant rate of paternity assignment at approximately 40% across years. This rate was significantly lower than for equivalent females who did pup ($\chi^2 = 35.963$, df $= 1$, $P < 0.0001$) indicating a behavioral difference. Patterns of paternity assignment among the maternal status classes could not be accounted for by age heterogeneity (age at conception, one-way ANOVA, $F_{(2,406)} = 0.215$, $P = 0.807$ after removing females of unknown status that were newly tagged and thus younger). Furthermore, comparing the observed frequencies of females assigned to each of the four status categories with binomial expectations showed no evidence that the observed

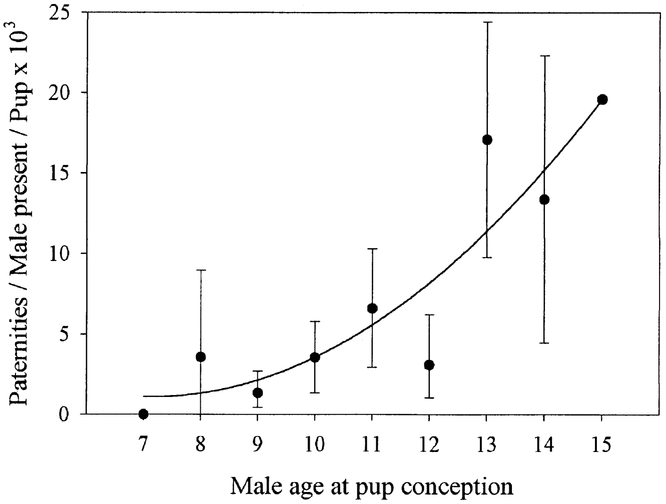

FIG. 5. Age-specific reproductive profile of 30 adult males that were born on the study beach and retained flipper tags fitted when they were pups. For convenience of viewing only, a simple second order polynomial line has been fitted to the means. Error bars show 95% binomial confidence intervals.

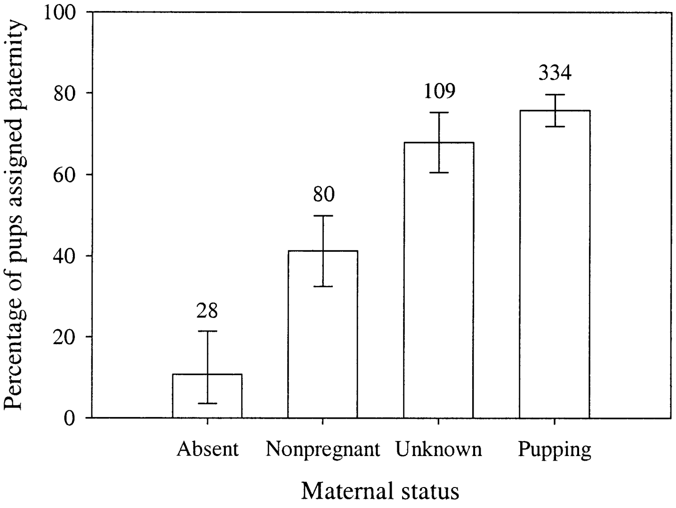

FIG. 7. Paternity assignment for four categories of maternal status in years of pup conception: (1) female absent from study colony; (2) present but nonpregnant; (3) unknown; (4) female present with pup. Maternal status was determined for all tagged females using census data and pupping records. Females of unknown maternal status could not be identified during the conception year because they were newly tagged during the year of pup birth. Error bars denote 95% binomial confidence intervals.

pattern was driven by a small number of females (data not shown).

Analyses of Paternal Haplotypes

Although not all pups could be assigned fathers, by comparing the genotypes of each mother-offspring pair, paternal haplotypes could be deduced for every pup, allowing us to find out something of the nature of the missing fathers. For each pup, we calculated the probability of observing the deduced paternal haplotype based on the frequencies of alleles among sampled territorial males. Log assignment probabilities were approximately normally distributed and pups with known fathers had significantly higher assignment probabilities compared with pups without an assigned father (two-tailed *t*-test, $t_{658} = 2.26$, $P = 0.024$). This suggests that females who did not pup on the beach tended to mate either at different populations or, less plausibly, with a genetically distinct subset of males who seldom ventured ashore.

To learn more about the nature of paternities of pups with unknown fathers, we used the program DADSHARE, which clusters deduced paternal haplotypes by relatedness and then uses a Monte Carlo simulation approach to find the best-fit level of shared paternity assuming all fathers are equally successful (Fig. 8). For each pup cohort, estimates of the level of shared paternity among pups with known fathers did not differ significantly from the level estimated through direct

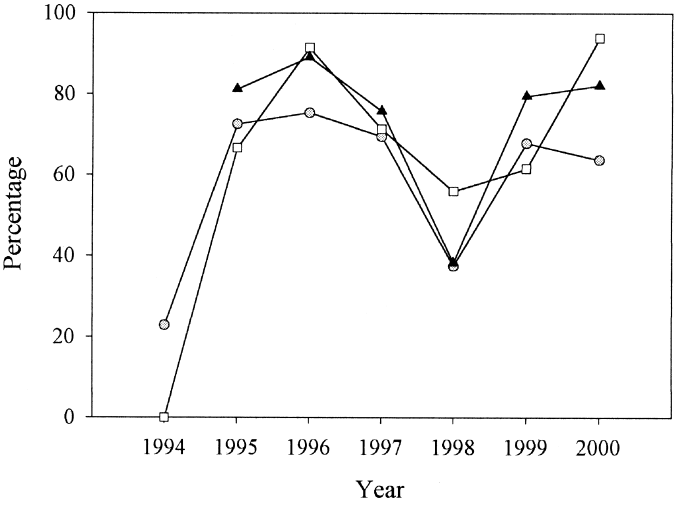

FIG. 6. Male sampling effort and paternity assignment rates throughout the study period. Percentage of males sampled in year of pup cohort conception (open squares); percentage of pups assigned paternity (gray circles); paternity assignment for the subset of pups whose mothers pupped during the year of conception (black triangles).

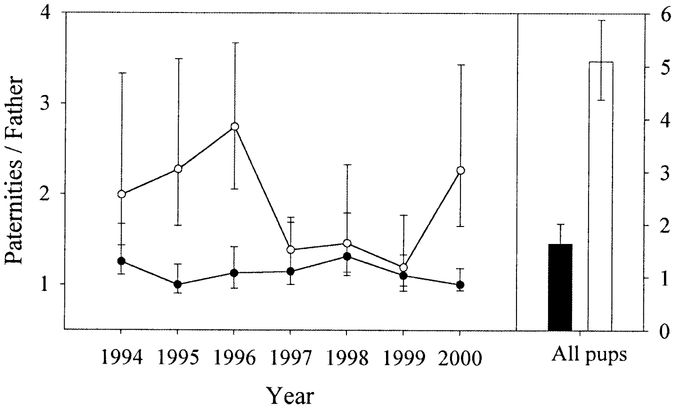

FIG. 8. DADSHARE estimates of shared paternity among pups with known fathers (open symbols) versus pups with unknown fathers (filled symbols). Circles denote individual pup cohorts and bars represent estimates derived for all pups. Error bars show 95% confidence intervals.

paternity assignment (Wilcoxon signed ranks test, $Z = -1.521$, $n = 7$, $P = 0.128$). In comparison, levels of shared paternity for pups of unknown paternity were consistently lower, both within each pup cohort and among all pups. This analysis is conservative because, as shown above, pups with unknown fathers tended to carry rarer alleles, and this would inflate their apparent relatedness. At face value, these results suggest that most females who mated with an unknown male did so with different males.

DISCUSSION

Our results reveal a mating system dominated by terrestrial polygyny, in which males did not appear either to copulate sneakily from peripheral positions or to mate aquatically when they were not holding territories on the breeding beach. Male reproductive success was strongly skewed, with those individuals able to return to the beach over multiple successive seasons enjoying the highest reproductive success. Probability of paternity assignment was strongly influenced by maternal status at conception.

Paternity Assignment

Paternities were assigned at high confidence and there was excellent agreement between the programs NEWPAT and CERVUS, which employ very different approaches for assignment. Despite a conservative approach we were able to assign paternity to 59% of pups, considerably higher than a previous study at the same colony (Gemmell et al. 2001). This difference may be explained by several factors. First, most males father pups during a single breeding season only, implying high rates of male turnover. Because the previous study spanned only two seasons, many fathers of pups born in the first year would not have been sampled, and many males sampled in year two would have fathered pups born after the end of the study. Second, we show that females who pupped on the study beach in the year of conception almost certainly conceived to territorial males on the same beach. Thus, the shortfall in assigned paternities has more to do with female behavior than with alternative male mating strategies. Finally, without exceptional effort, genotyping errors of around 1% per allele are easy to accrue. Unfortunately, this rate equates to an error affecting about one in five 10-locus genotypes, and hence only some 64% of pairwise genotype comparisons will be error free. We were particularly careful to drive error rates as low as possible through a combination of multiple gel rescoring, regenotyping and by replacing markers that were sex-linked, carried null alleles, and/or were difficult to score reproducibly. In addition, all paternity assignments requiring a single mismatch were re-examined, and this alone increased the number of fathers allocated by 5%. Our analyses illustrate how a small increase in data quality may lead to a rather large increase in the overall paternity assignment rate.

Skew in Male Reproductive Success

Our data reveal highly significant reproductive skew among territorial males, with a quarter of all paternities assigned to just twelve top individuals. At the other end of the spectrum, the majority of males (62.4%) were not assigned any paternities. The level of polygyny observed appears consistent with behavioral expectations (Arnould and Duck 1997) and is unlikely to result from sampling heterogeneity because females were selected randomly. However, our analysis may overestimate the numbers of males without success, since only some 14.8% of pups on the beach were analyzed. Despite this, a study by McCann (1980) observed fewer than 50% of territorial males actually achieving copulations during daylight hours and Arnould and Duck (1997) found that 14–29% of males did not even gain access to estrus females, since many of them held territories for short periods at times when few females were accessible. This pattern is consistent with observations of the New Zealand fur seal (*Arctocephalus forsteri*), where young nonbreeding males are known to visit breeding beaches before they return in subsequent years to hold full tenures (Carey 1991).

Using individual records of territorial tenure and paternity, we were able to construct profiles of reproductive success relative to the first years in which males held territories. Most pups were conceived by any of a large number of males during their first or second years of tenure, each of whom generally fathered a single pup. Male turnover was considerable, with only nine of 115 males sampled during 1994 holding tenure for the full seven years of the study. However, males who did manage to return over successive years enjoyed rapidly increasing success with each additional season they held tenure. With each extra year, tenure length increased, as did behavioral success per time spent on the beach. Although we cannot yet say what makes some males able to return in successive years whereas others fail, it is likely that individual quality, age, and size could all be important factors.

Do Territorial Males Ever Employ Aquatic or Sneaky Mating Strategies?

Recent studies of the gray seal have revealed that aquatic mating may play an unexpectedly important role in the overall pattern of breeding behavior, and the previous analysis of *A. gazella* suggested that the same may be true for this species (Worthington Wilmer et al. 1999; Gemmell et al. 2001). In gray seals it has also been suggested that age could be a factor contributing to mating tactics exhibited by individual males (Lidgard et al. 2001). Given that young Antarctic fur seal males may be particularly numerous in the rapidly expanding South Georgia population, and that males reach sexual maturity long before they are old enough to hold territories on breeding beaches, we considered the possibility that age-conditional alternative strategies could operate in this species.

The importance of aquatic mating was investigated by estimating the proportion of total success that could be accounted for by times when males were known to be ashore. We found that very few pups were assigned to males before they were first recorded either among or within seasons, nor after they had left the beach. The exceptions were at a level expected, given that males may have occasionally been present on the beach but not identified. Our data also suggest that individuals peripheral to the colony do not employ sneaky matings, since such individuals were never assigned paternities of pups born on the study beach. Thus, to a close approximation, territorial males appear to spend their entire reproductive careers copulating within terrestrial breeding colonies. This was consistent with the finding that male age at pup conception varied between eight and 15 years old, in line with behavioral observations that few males hold tenure before reaching eight years of age but that animals up to 14 years old have been seen ashore (Payne 1979; McCann and Doidge 1987; Boyd and Roberts 1993). However, at this stage we cannot entirely preclude the possibility that a few males may either mate elsewhere or mate aquatically as an exclusive alternative to holding terrestrial territories.

Paternity Shortfall and Female Mating Behavior

Given the dominance of terrestrial mating, it is not surprising that paternity assignment rates among years varied with the sampling intensity of territorial males when pups were conceived. However, more dramatically, we found that maternal status strongly influenced paternity outcome ($P < 0.0001$). Understandably, most pups born to females who were not recorded in the year of conception could not be assigned fathers. More interestingly though, females observed on the beach without a pup had only about a 40% chance of conceiving to a territorial male, significantly less than equivalent females who did pup. In addition, their pups carried combinations of paternal alleles that were less likely to be found on the study beach and exhibited lower levels of shared paternity. Together these observations suggest that females who visit a beach but do not pup have a tendency to leave the beach and to mate elsewhere. Although we do not rule out females mating aquatically or at localities where subadult males come ashore, results from our study colony suggest that females probably mate at other breeding beaches. However, since no marked females have been observed mating at adjacent beach sites during more than 20 years of observations at Bird Island (McCann 1980; Arnould and Duck 1997), the locations where females copulate could lie farther afield. Low levels of shared paternity among pups with unknown fathers point toward their mothers mating either at numerous different localities or at a single locality but with subordinate males (mating with dominant males would tend to lead to more evidence of shared paternity).

The reasons why females that do not pup tend to mate elsewhere remain obscure, although they do hint at the possibility that females could sometimes seek to increase offspring diversity by mating away from their natal colony. One possibility is that the pup's needs tie a female to a single beach during her critical estrus period, thereby constraining her ability to choose a mate, or even forcing her to accept a dominant male (Clutton-Brock and Parker 1995). However, this fails to explain why a nonpregnant female should visit a beach where she has no intention of mating. A second possibility is that pregnancy is acting as a measure of quality. For example, some females could miscarry due to inbreeding depression or genetic incompatibility (Zeh and Zeh 1996) and a female could use this as a cue to seek a partner elsewhere. Similarly, a nonpupping female might be less desirable to males, being of low quality or too closely related to one or more of the top males. However, even if this were the case, rejecting a receptive female could entail a direct cost to a male's fitness (Reynolds 1996). Finally, a more mechanistic explanation would be that, on a beach where there is intense competition for space, females without the strongest incentive to fight for space (i.e. a pup) become marginalized and eventually evicted from the pupping area. None of these possibilities seems entirely convincing, and the answer must await further behavioral observations.

In conclusion, our study uses a much-extended dataset to show that Antarctic fur seals do adopt a polygynous breeding system after all, much as predicted by evolutionary theory. The discrepancy between this current study and previous work emphasizes the potential pitfalls that may arise when male turnover is high relative to the length of the study. In addition, our ability to link female behavior to paternity probability has uncovered a previously undetected behavior in which females who come to the beach but do not pup appear less likely to conceive with males from that beach. This observation requires further work, but has important implications for the influence of female behavior on male success and provides a clear indication that not all females offer equal opportunities for fertilization.

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