

Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands

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Elephant seals are known from long-term behavioral studies to be highly polygynous and to show high variance in reproductive success among males. However, genetic studies have determined that the level of polygyny varies between the closely related northern and southern elephant seals. In the present study, we investigate paternal success at the Sea Lion Island southern elephant seal colony in the Falkland Islands by using both behavioral measures and genetic markers. We find that the average success of harem holding males at Sea Lion Island is significantly higher than both the northern species and the nearby southern elephant seal population at Punta Delgada. We compare genetic paternity with various behavioral indices of male mating success, and we find that the behavioral measures provide a good estimate of the variance in male reproductive success. Only 28.2% of males achieved paternities, and among these, harem holders accounted for 89.6%. We discuss the implications of our results in the context of the demographic and physical environment. Specifically, a comparatively high variance in resource holding potential among males, differences in male social behavior, and a small tidal cycle limiting peripheral male access during female departure from the harem at this colony may be important factors leading to the comparatively high variance in male reproductive success at Sea Lion Island. *Key words:* elephant seal, Falklands, mating success, microsatellites, *Mirounga*, paternity, polygyny. [*Behav Ecol* 15:961–969 (2004)]

Elephant seals are among the most sexually dimorphic and polygynous species of all mammals (Le Boeuf and Reiter, 1988; McCann, 1981). During the breeding seasons, males arrive on land first and compete with each other to set up a dominance hierarchy that determines the breeding role of each male (Galimberti et al., 2003; McCann, 1981). Typically, one male (the harem holder, HH) has almost complete control of each female group (harem), and other males remain peripheral to the harem. Females arrive onshore and aggregate into harems of up to hundreds of individuals (McCann 1980). They give birth within a few days after their arrival and nurse their pup for approximately 23 days, before weaning it and returning to the sea (Galimberti and Boitani, 1999). They are in estrus for the last 2 or 3 days of the nursing period (Campagna et al., 1993; Galimberti and Boitani, 1999; Laws, 1956), and males attempt to copulate with them when they are either in the harem or departing from the colony. In polygynous species in which only female parental care is required, males should maximize fitness by competing for as many mates as possible, whereas females should maximize fitness by ensuring offspring survival and choosing “good mates” (Andersson, 1994).

The application of molecular techniques has contributed to changing perspectives on vertebrate mating systems (Westneat, 2000), and studies on paternity in polygynous mammals have shown that observational estimates are frequently inconsistent with genetic assessments. For example, behavioral data reflected parentage but slightly underestimated the variance in seasonal and life-time male reproductive success in a red deer population (*Cervus elaphus*: Pemberton et al., 1992) and in fallow deer (*Dama dama*: Say et al., 2003). In Soay

sheep (*Ovis aries*), census-based observations were inaccurate predictors of paternity, and the level of genetic polygyny was lower than expected from field data (Coltman et al., 1999). In pinnipeds, studies on grey seals (*Halichoerus grypus*: Amos et al., 1999; Worthington et al., 1999) showed that behavior-based measures overestimated male mating success and, hence, the level of polygyny in the study populations. On the contrary, a recent paternity analysis on Antarctic fur seals revealed a mating system dominated by terrestrial polygyny and no evidence of alternative male mating strategies (Hoffman et al., 2003).

Behavioral studies on *Mirounga* predict a high variance in both seasonal (Le Boeuf, 1974; McCann, 1981) and lifetime male reproductive success (Le Boeuf and Reiter, 1988). Observational estimates of reproductive success gave contrasting results in the two species, more accurately reflecting male paternity success in the southern (*Mirounga leonina*: Hoelzel et al., 1999; Wainstein, 2000) than in the northern elephant seal (*M. angustirostris*), for which the discrepancy was sometimes large (Hoelzel et al., 1999). The discrepancy in the northern species could be owing to relatively high access by peripheral males to departing females, or to reduced male fitness as a result of an extreme population bottleneck. The southern elephant seal population studied (at Punta Delgada, Peninsula Valdés, Argentina) showed greater average success for HHs, and both observational and genetic estimates agreed on an average paternity success rate of about 50% for HHs (Hoelzel et al., 1999).

In the present study, we describe the distribution of mating success and paternity among male southern elephant seals of Sea Lion Island (Falkland Islands) across two consecutive breeding seasons. We quantify the level of polygyny and male reproductive variance in seven harems, and test the hypothesis of extreme polygyny in this species. We also compare genetic results with estimates based on demographic and behavioral data, testing the hypothesis that the latter are effective indices in predicting paternity, and use these data to

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help assess the factors important in facilitating high reproductive success for HHs in this population.

METHODS

Study area and population

Fieldwork was conducted during three breeding seasons (September–November, from 1996–1998) on Sea Lion Island (SLI, hereafter), the main breeding colony of southern elephant seals in the Falkland Islands (Galimberti et al., 2001). The population is small and localized, with no other breeding sites on the remaining islands of the archipelago. The study area covered the whole coastline occupied by breeding seals (total length approximately 4.4 km). The whole study area was divided in three different zones, each comprising a continuous stretch of two to six sandy breeding beaches and clearly separated from other zones by rocky areas unsuitable for breeding (mean zone length = 1451 m). Daily censuses of the whole study area were done throughout the breeding season at low tide. Each year, 527–567 breeding females and 68–81 males were present on land. All males and almost all females (more than 95%) were tagged by using nylon cattle tags (Jumbo Rototags, Dalton Supplies Ltd) and marked by using commercial black hair dye (Galimberti and Boitani, 1999). Tags and dye marks allowed for the identification of copulating males and females 100% and 93–95% of the time, respectively (Galimberti et al., 2000a).

Definitions and behavioral observations

We defined harem as a group of two or more females with a male in attendance (Baldi et al., 1996), and daily harem size as the number of females in the harem based on daily counts. We refer to harem size as the maximum daily size reached over the season (87–90% of the total number of females that actually breed in the harem during the whole season). We classified males on a seasonal basis as HHs, if they gained control of a harem for more than 24 h (at least two consecutive censuses). If more than one male during the breeding season controlled a harem, the male that held it for the longest period was defined as the seasonal holder, and the others were defined as temporary holders (usually keeping the control of the females for short periods). All other males were classified as nonharem holders (NHH). During each breeding season, four people made social behavior observations at all harems. Male-male and male-female interactions were recorded during 2-h periods by using an all-occurrence sampling technique (Altmann, 1974) with continuous recording of events on log sheets (details in Fabiani, 2002; Galimberti et al., 2000a). We did the genetic analyses on one breeding zone (STRE), which included almost half of the whole population. The genetic results from seven harems (five for 1996 and two for 1997) were then compared with observational data. The behavioral observations were balanced both among harems and males. We carried out a total of 1088 h of observation (mean = 155.42 ± 72 h per harem), and recorded 395 copulations (mean = 56.42 ± 33.10 copulations per harem).

We estimated male reproductive success from demographic and behavioral data by using an index of fertilization success (the estimated number of females fertilized [ENFI]: Le Boeuf, 1974), which is in widespread use for elephant seals. It is calculated as the product between the proportion of copulations achieved by a male in one harem (from behavioral observations) and the number of females that bred in that harem (from individual records of marked females), summed over the harems in which the male is observed mating.

To each mother/pup pair for which a paternity was found (see below), we assigned a father from the behavioral and demographic data by using various criteria. We then compared each behavioral/demographic father with the genetic assigned father to determine which index was a good predictor of paternity. We considered four criteria: HOLDER, the father was the (seasonal) holder of the harem in which the female gave birth (data from standard observation periods and daily censuses); ASM_E, the father was the male associated with the female for the longest period during her estrus (data from female daily records combined with the estimated beginning of the estrus: see Galimberti and Boitani 1999); CO, the father was the male with the highest number of observed copulations with the female (data from standard observation periods); and FIR_CO, the father was the first male seen mating with the female (data from standard observation periods).

Sample collection and DNA extraction

We collected tissue samples from the hind flippers of unrestrained, resting seals, by using ear-notching pliers (Pembererton et al., 1992). Sampling of mothers of the zone STRE and putative fathers during one season was coupled with sampling of pups born during the next season. Newborn pups were tagged and matched with their mother on the day of birth. Complete series of samples were collected for 1996 and 1997: 115 mother-pup pairs and 78 males sampled for 1996; 77 mother-pup pairs and 62 males for 1997. Thirty females and 39 males were present both seasons, for a total of 162 females and 101 males analyzed over the 2 years. The sampling covered 95% of breeding males of the colony for both years and 54 to 90% of the females that bred in each harem and came back to give birth the next season. The skin samples were preserved in 95% EtOH (Dessauer et al., 1990), and DNA was phenol/chloroform extracted (Hoelzel and Green, 1998) from a small piece of skin 2–3 mm wide.

Microsatellite DNA characterization and paternity analysis

The extracted DNA was genotyped at nine microsatellite loci, previously isolated from various seal species (Table 1). Except for BETA, they all amplified dinucleotide repeat sequences and for one locus. BETA amplified pentanucleotide repeats (GGAAA)_n and for two loci (four alleles). Multiple alleles of BETA at a given size could be detected by the height of the peak, but single-locus genotypes could not be determined (Slade et al., 1998). These two linked loci were treated as a single locus with four alleles and used separately from the other microsatellites in the analyses. Depending on each locus, the PCR amplifications were performed in 10–20 µl reaction volumes containing the following: 0.2 mM dNTPs, 0.75–1.5 mM MgCl₂, 10 mM Tris-HCl (pH 8.4), 500 mM KCl (Hoelzel and Green, 1998), 0.02 U/µl Taq polymerase, 250 pM, 150–250 pM of each primer, and 5–50 ng/µl of DNA. PCR reactions involved 5 min of denaturing at 95°C; and 34 cycles consisting of 1 min 30 s of annealing at 51–60°C, 1 min 30 s of extension at 72°C, and 45 s at 94°C. The primer BETA was amplified following a “touchdown” procedure: 94°C for 5 min, 40 s at variable annealing temperatures, 2 min at 72°C, and 94°C for 45 sec. The annealing temperatures were 67°C for the first cycle, 66°C for the second, and 65°C for 25 cycles. Amplification products were visualized on an automated ABI PRISM 377 DNA Sequencer (Applied Biosystems) and analyzed for length variation with GeneScan Analysis 2.0 and Genotyper 2.0 software packages (Perkin-Elmer Corp.).

Tests for significant deviation from Hardy-Weinberg equilibrium (HWE) and genotyping disequilibrium were

Table 1

Genotype data for each locus, including observed (H_O) and expected (H_E) heterozygosities and the probability associated with the test for deviation from H-W expected frequencies

| Primer species | Isolated from alleles | No. of (bp) | Allele size | H_O | H_E | Null allele frequencies | HWE probabilities |
|---------------------|---------------------------|-------------|-------------|-------|-------|-------------------------|-------------------|
| BETA ^a | <i>Mirounga leonina</i> | 15 | 269–339 | — | — | — | |
| Hg4.2 ^b | <i>Halichoerus grypus</i> | 4 | 135–141 | 0.582 | 0.572 | –0.007 | 0.574 |
| Hg6.3 ^b | <i>Halichoerus grypus</i> | 6 | 215–225 | 0.574 | 0.622 | 0.042 | 0.133 |
| Hg8.10 ^b | <i>Halichoerus grypus</i> | 9 | 178–191 | 0.783 | 0.753 | –0.020 | 0.101 |
| Hg8.9 ^b | <i>Halichoerus grypus</i> | 9 | 175–195 | 0.678 | 0.701 | 0.012 | 0.712 |
| M11a ^c | <i>Mirounga leonina</i> | 6 | 141–151 | 0.779 | 0.769 | 0.007 | 0.946 |
| M2b ^c | <i>Mirounga leonina</i> | 10 | 235–255 | 0.734 | 0.726 | –0.011 | 0.564 |
| PV9 ^b | <i>Phoca vitulina</i> | 4 | 162–170 | 0.460 | 0.446 | –0.018 | 0.252 |
| Overall | | 7 | | 0.656 | 0.655 | | 0.425 |

Primer sequences are from the following: ^a Slade et al. (1998), ^b Allen et al. (1995), and ^c Hoelzel et al. (2001).

implemented in GENEPOP 3.3 (Raymond and Rousset, 1995). Genetic polymorphism at each locus was inferred by using the program GENETIX version 4.0.1 (Belkhir et al., 2001). Null allele frequencies were calculated with CERVUS 2.0 (Marshall et al., 1998).

We assigned paternity by using both exclusion and likelihood-based approaches. First, we used an exclusion approach for an initial screening on offspring and candidate males for the primer BETA, with a program developed ad hoc in Hypercard (Apple Computers). From this first comparison, we selected a list of putative fathers for each offspring. Second, we used the file containing the offspring with their individual list of candidate fathers as the “offspring file” in CERVUS 2.0 (Marshall et al., 1998). From a set of genotypes, CERVUS 2.0 calculates the likelihood of each male being the true father of each pup, relative to the likelihood of not being the true father. For a given confidence level, a simulation analysis estimates the critical difference in log-likelihood scores (Δ) between the most and the second most likely candidate male. We used the allele frequencies from males from both years ($n = 101$) as the set of genotypes and did the simulation on the two breeding seasons separately. In the case of individuals present in both years, they were included in both simulations. Each year, all males observed in the study area at some point during the breeding season were considered as candidate males. These also included some males of the juvenile class (3–5 years of age). We sampled 96.2% of the males on land in 1996 and 91% in 1997. Both years, we typed 99% of loci for all genotypes. We estimated the rate typing error with CERVUS from the frequency of mother-pup mismatches, and it was set equal to 0.004 and 0.002 in 1996 and 1997, respectively. Paternity was assigned with 95% (strict) and 80% (relaxed) levels, and 10,000 paternity simulations were generated.

Statistics

We present statistics as mean and SD, or median (med) and median absolute deviation from the median (MAD) for asymmetrically distributed variables. The MAD is a measure of spread analogous to the SD. It takes the median of differences between points and the median, and as median is less vulnerable to extreme data points than the mean, MAD is less vulnerable to outliers than standard deviation. We describe the variability of distributions with the coefficient of variation (CV). Paternity analyses were carried out on the subsample of males ($n = 46$ males) that were occasionally or regularly seen in zone STRE, where harem genetic data were available. Because of the high frequency of asymmetric

distributions, we used mostly nonparametric tests, with exact or randomization estimation of probability. Data from the 2 years were pooled together after being checked for homogeneity. Parametric tests were run in StatView 5.0 (SAS Institute). Nonparametric tests were run in StatXact Turbo 4.0 (Cytel Software Corporation). For randomization-based tests, we show the number of replicates as subscript. We used the coefficient of determination (R^2) as a measure of effectiveness of behavioral estimates in predicting paternity (Coltman et al., 1999; Pemberton et al., 1992). It measures the proportion of paternity variance that is explained by the variance of each behavioral index. Probability levels and 95% confidence limits for the coefficient of determination were calculated with the R2 software (Steiger and Fouladi, 1992; available at: <http://www.interchg.ubc.ca/steiger/r2.htm>). To correct probabilities in multiple comparisons, we applied the sequential method of Holm (1979), as implemented in Multiplicity Program 2.0 (Brown and Russell, 1996).

RESULTS

Genetic diversity

We analyzed all loci for the adult population of SLI (total $n = 263$; n males = 101, n females = 162) and found no difference in the allele frequencies between sexes. No locus showed significant deviation from HWE, nor was there evidence of linkage disequilibrium for pairs of loci. Null allele frequencies were smaller than 0.05 (Table 1).

Behavioral observations

Only 28.2% of the males in the colony were observed mating at least once in the two breeding seasons ($n = 149$ males). The copulation distribution had a mean of 5.65 ± 15.97 for all males (med = 0, MAD = 0) and of 20.05 ± 25.0 for males that copulated ($n = 42$, med = 7, MAD = 6). Among males that copulated, 54.8% achieved less than 10 copulations. The ENFI distribution was skewed, with a median value of zero (MAD = 0) and large variation among individuals (range = 0–125, CV = 2.89).

HHs accounted for 93.5% of the observed copulations in the colony ($n = 790$ copulations). In each harem, the holder always achieved the majority of matings, with a mean of 81% (± 16.5) of the copulations (range = 50–100%). Nevertheless, values of ENFI varied among HHs, with a mean of 52.2 ± 31.4 (range = 18–125, $n = 19$ HHs). Among NHHs, ENFI ranged from 0–6.0, with a mean of 0.25 ± 0.91 per male ($n = 122$ NHHs).

Table 2
Paternity influence results

| | Year 1996 | | | Year 1997 | | |
|----------------------|-------------|----------|----------|-----------|----------|----------|
| | 80% | 95% | Unsolved | 80% | 95% | Unsolved |
| Critical Δ | 0.06 | 1.30 | | 0.05 | 1.63 | |
| Expected paternities | 94% | 61% | 6% | 93% | 60% | 7% |
| Assigned paternities | 94.8% (109) | 74% (85) | 5.2% (6) | 96% (74) | 86% (66) | 4% (3) |

The criteria strict (95%) and relaxed (80%) are shown. Expected paternities: the percentage of tests (out of 10,000) in which paternity was assigned at the required criterion and in which no father was identified. Assigned paternities indicates the proportions of paternities (corresponding number in brackets) assigned at the two confidence levels and for which a father was not identified at the relaxed level.

Paternity analysis

All putative mother-pup genotype pairs were consistent with mother-offspring relatedness. In 1996, we determined paternity for 109 pups out of 115 (94.8% of pups) at 80% statistical confidence. Of these, 85 paternities (74% of all the tested paternities) were assigned at 95% confidence. In 1997, we found a father for 74 out of 77 pups (96%) at 80% confidence level, and of these, 66 (86% of pups sampled in 1997) were assigned at 95% confidence (Table 2). Out of 183 paternities, only two were assigned with a mismatch at one locus between the father and the pup. In both cases, the mismatch was at the locus Hg 8.9 and interpreted as a mutation by the CERVUS that assigned the paternities respectively at 95% and 80% confidence level. For three of the nine pups without paternity assigned, all males were incompatible at two or more loci, whereas the remaining six paternities did not show mismatches but were assigned to a single male at a lower level of confidence. We chose to discard these paternities and instead analyze only those with 80% and 95% confidence, following the method of Marshall et al. (1998).

Considering the males frequenting STRE, the mean number of paternities per male was 3.9 ± 8.0 (med = 1.0, MAD = 1.0; $n = 46$ males). Among those that achieved at least one paternity ($n = 25$ males), 11 (44%) were HHs, accounting for 89.6% of the paternities assigned over all harems combined. Among the HH males, only six had more than 10 paternities assigned, for a maximum of 32 and 25 paternities, for a different male in each year. Two to nine males accounted for all the paternities achieved in each harem (Figure 1), with a mean number of paternities per male per harem ranging from 0.86 (± 1.92) to 8.33 (± 15.58). In each harem, the holder was assigned the largest proportion of paternities, with a median value of 85.7% (range = 56.8–96.0%) (Table 3). There was no correlation between the number of paternities assigned to the HH and either the size of the harem ($\rho = -0.071$, $p_{10K} = .90$) or the total number of males associated with it ($\rho = -0.52$, $p_{10K} = .242$).

In case of more than one holder for a harem, we summed the paternities achieved by temporary holders with the paternities achieved by the seasonal holder to see if the turnovers (i.e., brief periods during which another male takes control of the females) affected the success of the seasonal HHs. The sum of paternities achieved by all HHs combined was larger than those of the seasonal holder alone in only two harems. In particular, for SI296, the seasonal holder lost the control of the harem when there were still 21 females breeding, and the percentage of HH paternities increased from 56.76% for the seasonal holder to 83.78% for the total of three holders. A smaller increase was recorded for SI297 (from 65.26% for the seasonal holder's paternities to 67.34% for two holders). This harem split into two different groups in the middle of the season: the seasonal holder kept the control of the group with the larger number of females, whereas the

temporary holder got control of the smaller group, after achieving some copulations in SI297.

Among the paternities assigned to HHs ($n = 164$ paternities), 140 (85.3%) were assigned at 95% confidence, whereas among those assigned to NHHs ($n = 19$ paternities), only eight (42%) were assigned at 95% confidence. Among NHH males frequenting the sampled harems ($n = 34$ NHHs), nine (26%) achieved one paternity and five (14.7%) achieved two. Only in one case was a NHH male seen copulating with the mother of the pup he fathered. Ten (71.4%) of the NHHs that achieved paternities were males associated with the harem in which they mated, whereas four of them were more often observed frequenting other areas of the colony. Three of these four males were young subadult seals and their paternities were all assigned at 80% confidence.

Mating performance and paternity

Genetic results confirmed the holder's success in each harem (Figure 2). The proportion of the paternity's variability explained by ENFI (calculated as R^2) was always very high, both within harems (from 83–99%, $.0006 \leq p \leq .00015$) and each season (91% and 97%, $p \leq .00004$).

We assigned a father with all four behavioral/demographic criteria to 103 (56.3%) of the 183 mother/pup pairs for which a genetic father was found. There was a median of four behavioral/demographic criteria (MAD = 0) for each mother/pup pair, and in 85% of the cases, the criteria were all congruent (i.e., same father for each behavioral/demographic criteria). Considering the criteria separately, the male assigned from behavioral/demographic data and the genetic father were the same individual a mean of 71–96% of the times in each harem. Coefficients of determination (R^2) between genetic and behavioral/demographic fathers ranged from .882, for H_ENFI and HOLDER, to of .967, for ASM_E (Table 4).

We observed copulations for 123 (67.2%) of the 183 mother/pup pairs for which a father was found, with a mean of 1.85 ± 1.02 copulations per female (med = 2, MAD = 1, range = 1–8). Sixty-nine (56%) of these females were seen copulating more than once, of which eight (11.6%) copulated with two different males. For seven of these, the father of the pup was the first male seen copulating with that female, whereas in the remaining case he was not the first or the second male (both of which copulated with the female while she was departing the harem), but the HH.

During the two seasons, we recorded male-female interactions during 140 female departures, and in 73 (52%) we observed at least one copulation. The females mated with only their holder during 33 departures (45.2%) and with other males only during 32 (43.8%) departures. Genetic data were available for eight departures. For six of them, the father was the HH: the holder was seen copulating during five departures

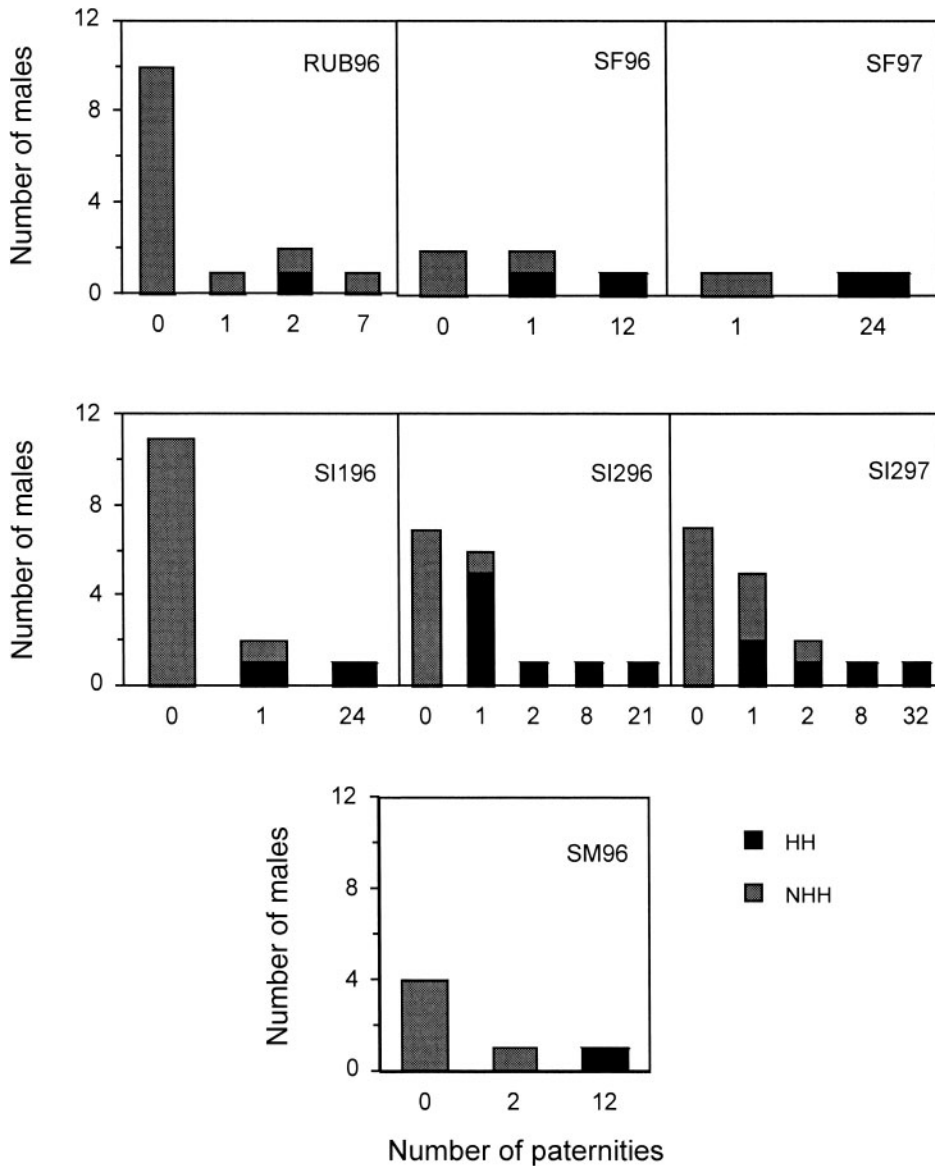


Figure 1
Number of paternities achieved by the holder and the males associated to each harem.

(the first of two males in one case). For four of these six females, the HH was the first male recorded copulating with the female during the season (index FIR_CO, see above). In the first of the two departures for which the father was a NHH, the father was seen mating during the female's departure (also as FIR_CO during the season), whereas in the second, the father of the pup was not seen copulating with the female.

DISCUSSION

Level of polygyny in the colony

At the SLI breeding colony, the average success of HHs was high (75%, range = 57–96%), greater than the averages for both southern elephant seals at Punta Delgada (58%) and northern elephant seals at Año Nuevo (38%; Hoelzel et al., 1999). Our genetic results confirm previous observational findings (estimated from various breeding inequality measures, see Galimberti et al., 2002) indicating extreme variance in male reproductive success, higher than the level observed

in lekking birds or in other mammalian species with harem-based mating systems (e.g., *Cervus elaphus*: Pemberton et al., 1992). Moreover, some SLI males are able to hold a harem for up to six consecutive breeding seasons (Fabiani, 2002), and thereby achieve an estimated lifetime fertilization success that can be up to three times larger than the maximum estimated for northern elephant seals by Le Boeuf and Reiter (1988).

Paternity inference and behavioral indices of mating success

An assumption of nongenetic studies of mating systems is the agreement between demographic/behavioral measures of mating success and true reproduction; however, nongenetic estimates can be misleading (DeYoung et al., 2002; Hasselquist and Sherman, 2001; Heckel and von Helversen, 2003; Radespiel et al., 2002). In some cases the discrepancy can be owing to the methodology used in the study, for example, the difficulty in observing individuals of different age and rank (Drickamer, 1974), factors related to attempts to increase the productivity of observation (Sharman and Dunbar, 1982),

Table 3
Paternity distribution statistics and demographic details for each harem

| Harem | % Pat holder (<i>n</i> total pat) | Harem size | Mean (\pm SD) daily NHHs | Maximum daily NHHs (tot NHHs) | Males pat > 0 | Mean pat per male (\pm SD) |
|-------|---------------------------------------|---------------|--------------------------------|----------------------------------|------------------|----------------------------------|
| RUB96 | 58.3 [12] | 18 | 0.29 (\pm 0.56) | 2 [11] | 4 | 0.86 (\pm 1.92) |
| SF96 | 90.0 [20] | 35 | 0.12 (\pm 0.39) | 2 [2] | 3 | 4.0 (\pm 7.84) |
| SI196 | 92.3 [26] | 55 | 0.66 (\pm 0.78) | 2 [13] | 3 | 1.86 (\pm 6.38) |
| SI296 | 56.8 [37] | 75 | 1.25 (\pm 1.15) | 4 [13] | 9 | 2.31 (\pm 5.35) |
| SM96 | 85.7 [14] | 20 | 0.15 (\pm 0.47) | 2 [5] | 2 | 2.33 (\pm 4.80) |
| SF97 | 96.0 [25] | 40 | 0 | 0 | 2 | 8.33 (\pm 13.58) |
| SI297 | 65.3 [49] | 91 | 0.95 (\pm 1.46) | 5 [12] | 9 | 3.06 (\pm 7.96) |

Percentage of paternities assigned to the harem holder with, in brackets, the total number of paternities analyzed in the harem; harem size; mean (\pm SD) daily number of NHHs associated with the harem; maximum daily number of NHHs and in brackets, total of different NHHs associated during the breeding season; number of males with at least one paternity assigned in the harem; mean (\pm SD) number of paternities assigned per male.

disturbance by the observer (Rasmussen, 1990), or using an inappropriate sampling protocol (Hoffman et al., 2003). However, elephant seals are comparatively easy to observe; they show little, if any, reaction to human observers, and their social behavior, including copulations, is relatively unambiguous and easy to observe. Moreover, the methodology at SLI was planned to balance the effort among the different breeding units and seasons, in order to reduce the risk of observational and sampling biases.

In our study, the distribution of observed matings was highly correlated with the distribution of paternities ($R^2 = 0.84\text{--}0.99$), and behavioral indices predicted individual paternities 56.8–100% of the time (average of 77.7–87% among harems). Only eight females were observed mating with more than one male; however, the first male to copulate was the father seven times out of eight, and this may be an indication of a first male advantage in sperm competition. The largest proportions of paternities were predicted by identifying the first male seen

copulating with the female, or the male with the highest number of copulations recorded, both data requiring the accurate recording of each female's breeding history. At the same time, knowing the HH in association during the female estrus (ASM_E) gave a good estimation of the distribution of reproductive success among males.

The quality of the genetic data is another potential source of discrepancy between behavioral and genetic measures of paternity (Marshall et al., 1998; Neff et al., 2001). In our study, the inference success was high, similar to that reported for red deer with 84 loci (Slate et al., 2000). Even so, the molecular methods used determined 32 paternities (17.4% of the total paternities assigned) at levels of confidence from which we expect one in five (80% confidence) to be incorrect (82% of the paternities were assigned at 95% confidence level). Considering the larger sample size of NHHs compared to HHs, and that NHHs had a much higher percentage of paternities at 80% confidence (58% of the total NHH

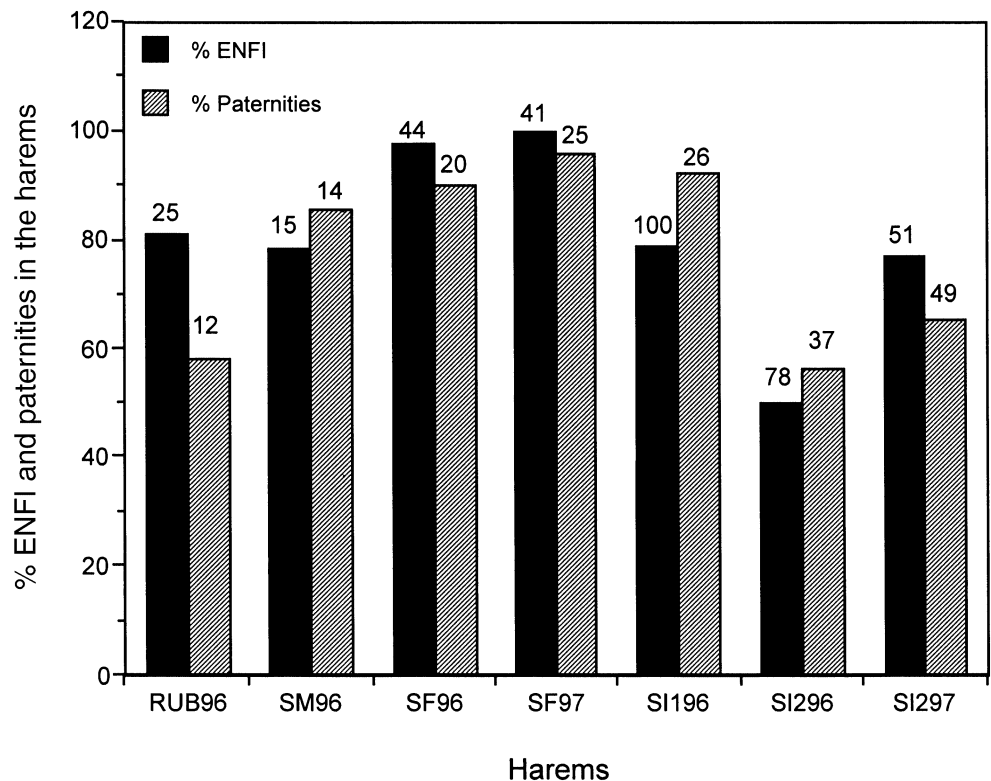


Figure 2
 Percentage of ENFI and paternities achieved by each holder in each harem. Harems are ordered from the smallest (RUB96) to the largest (SI297); numbers indicate paternity and observed copulation sample sizes for each harem.

paternities versus 14% of the total HH paternities: Fisher Exact test: $\phi = 0.336$, $df = 1$, $p < .0001$), it is possible that NHH males were more frequently assigned false paternities than HHs. This implies that the relative success of HH males in this population could be even greater than that reported here.

Alternative mating tactics and effects of the demographic and physical environment

Pinnipeds often show “unconventional” and “sneaky” mating tactics to increase their reproductive success, and these can be less easy to observe (e.g., aquatic mating: Worthington Wilmer et al., 1999). Male southern elephant seals can also sometimes control more than one harem at the same time or switch between being the holder of one harem and the peripheral of another harem (Baldi et al., 1996). The success of each tactic depends strongly on the local breeding situation (Honigman, 1988). At SLI, controlling a harem was by far the most rewarding mating strategy; nevertheless, males also pursued other strategies. They associated with harems (waiting for opportunities to sneak in and mate), they tried to copulate with solitary females, and they followed and mated with departing females.

On SLI, associating with a harem and trying to sneak into the female group appeared most successful among the alternative strategies, as the majority of NHHs that achieved paternities were associated with a harem for most of the season. This strategy is likely to be more successful in larger harems, in which the HH is less able to defend all parts of the harem (Le Boeuf, 1974). However, the range of harem sizes at both SLI and Punta Delgada is relatively small, and no significant correlation between HH success and harem size was seen at either colony (c.f. Hoelzel et al., 1999). The harem sizes are larger at South Georgia (mean = 74.2, range = 6–232: McCann, 1980), Macquarie Island (mean = 277, up to 1000: Carrick et al., 1962), and Kerguelen (mean = 102, range = 5–1350: Van Aarde 1980), and this may well be a factor there. In northern elephant seal colonies, in which individuals breed at higher density and form larger harems with several associated males, the percentage of copulations of the HH does decrease with increasing harem size (Le Boeuf, 1974; Le Boeuf and Reiter, 1988).

An important factor affecting the level of mating monopolization is variability in resource holding potential (RHP: Parker, 1974) among males (i.e., body size, dominance rank and fighting experience: Dawkins and Krebs 1979; Haley et al., 1994; Modig, 1996). Despite the similar harem sizes and density, SLI harems had significantly fewer associated males than do the harems at Punta Delgada (Galimberti et al., 2000a), and NHHs achieved significantly fewer paternities on average (Fisher Exact test: $\phi = 0.205$, $df = 1$, $p = .0059$): 22% at SLI versus 42% at Punta Delgada (cf. Hoelzel et al., 1999). The difference could be related to a smaller variance in RHP among males at Punta Delgada, estimated as variance in interaction rate, fighting success, experience, and body size (Fabiani, 1996). The degree of linearity in male dominance hierarchies was also higher on SLI than on DEL (Galimberti et al., 2003), allowing a higher level of female monopolization.

Copulating with solitary females could in theory be rewarding, but solitary females are extremely rare, both at SLI (0.38% and 1.2%, respectively, in the 2 years of this study) and in other southern elephant seal colonies (Campagna et al., 1993). With so few females available, males pursuing this strategy could not achieve high reproductive success.

Mating with departing females was not frequently observed at SLI. Female elephant seals are in estrus for the last 2–3 days of their nursing period, just before they return to the sea (Le Boeuf, 1974; Campagna et al., 1993; Galimberti and Boitani,

Table 4

Coefficients of determination (R^2) between paternity and each behavioral/demographic estimate, for each year and overall

| Index | Years | | Overall |
|--------|-------|-------|---------|
| | 1996 | 1997 | |
| HOLDER | 0.835 | 0.917 | 0.882 |
| ASM_E | 0.952 | 0.987 | 0.967 |
| CO | 0.925 | 0.953 | 0.941 |
| FIR_CO | 0.925 | 0.953 | 0.941 |

Sample size was 19 males for 1996 and 15 males for 1997; always $p < .000001$.

1999). During this period female protestations to male approaches visibly decrease (Galimberti et al., 2000b), and this behavior is therefore a good indicator of their morphophysiological estrus (Laws, 1956). On SLI, most females mated in their harem with either the HH or other males before departure. However, females still in estrus as they leave the harem provide an opportunity for matings by peripheral males.

The local topography could affect the likelihood of interception and copulation during female departures, and influence the potential for polygyny in the population. Major environmental differences are present between SLI and the colonies of northern elephant seals on Año Nuevo and southern elephant seals on Punta Delgada, the most evident being the tidal range. The mean tidal amplitude ranges from 2.93–4.28 on Peninsula Valdés, and from 0.88–1.89 in the Falklands (Servicio de hidrografía naval, 1994). This and local topographical features mean that females at Punta Delgada experience greater variation in the distance between the harem and the water than do the females of SLI. As a consequence, female departures are shorter and a smaller percentage are intercepted by secondary males on SLI (Galimberti et al., 2000a).

In summary, northern and southern elephant seals have a similar mating system, but differences are present both between the two species and between different southern elephant seal populations. This range in the pattern of monopolization among populations is apparently influenced by phenotypic, behavioral and environmental factors. The variance in male reproductive success for southern elephant seals on SLI is among the highest reported in the literature, and for a population in isolation this could significantly reduce the effective population size, and hence affect the rate of loss of genetic variation over time. However, we have recently reported evidence for gene flow among regional populations, and for a single very long-range genetic dispersal event (for a male migrating from Macquarie Island to SLI) that resulted in a significant number of paternities (Fabiani et al., 2003). This would tend to counter the effects of high variance in reproductive success and drift in regional populations, and is consistent with the high levels of genetic variation seen for this species throughout its range (see Fabiani et al. 2003).

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