



Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands

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Southern elephant seals are highly gregarious during the breeding season, and both sexes show fidelity to the colony. We used microsatellite DNA analysis to assess kinship among seals in the main colony on the Falkland Islands. Specifically, we investigated whether females tend to cluster with close kin and avoid mating with male kin. We also tested expectations for kinship patterns based on sex differences in site fidelity and philopatry. Relatedness within a harem was significantly greater than between harems for only two of seven harems and was not related to harem size. Some long-term associations of female kin were found within harems, including associations of up to 5 years, but kinship among these females was not significantly higher on average than among dyads of other returning females. There was no pattern suggesting that females tended to choose harems with harem holders that were either more or less related to them than alternative harem holders. Overall, pairwise comparisons of females showed significantly greater kinship than pairwise comparisons of males, consistent with previous studies suggesting greater male dispersal.

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In classical models of population genetic structure, individuals mix and mate randomly within populations. However, a nonrandom distribution of individuals with respect to their genotype may provide an additional hierarchical level at which genetic variation may be maintained (Suggs et al. 1996). This can affect inbreeding and outbreeding behaviours (Chesser 1991a, b), facilitate kin selection (Höglund et al. 1999) and influence population demography and dynamics (Lambin & Yoccoz 1998; Coltman et al. 2003).

The importance of the socioecological environment is most evident and widely studied in species that form permanent or semipermanent groups and long-term relationships (e.g. *Lycaon pictus*: Girman et al. 1997; *Macaca fascicularis*: De Ruiter & Geffen 1998). Nevertheless, social

context is also likely to be important for species that form short-term aggregations (Burland et al. 2001; Pomeroy et al. 2001), as breeding success can be influenced by when an individual arrives at and leaves the breeding site, by the individual's position within a breeding group and by the other individuals forming the aggregation.

Social organization can result in nonrandom matings when one sex or both shows site fidelity (i.e. returning to the same breeding colony in consecutive seasons) and philopatry (i.e. returning to the natal colony to breed). In many mammals, females are the philopatric sex and males tend to disperse to breed (Greenwood 1980). Female philopatry coupled with male dispersal can result in differing degrees of genetic relatedness within and between the sexes (Chesser 1991a). It can result in high relatedness between female members of a social group, and high relatedness may in turn lead to greater cooperation between group members. High polygyny together with site fidelity can produce consistently high gene correlations among offspring and adults within social groups (Chesser 1991b). However, to the best of our knowledge, studies on intrapopulation patterns of genetic relatedness in polygynous mammal species are rare (Schaeff et al. 1999; Surridge et al. 1999; Coltman et al. 2003). In the European wild rabbit, *Oryctolagus cuniculus*, populations were

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found to be genetically subdivided among social groups, although individuals did not necessarily group with kin (SurrIDGE et al. 1999). Among harbour seals, *Phoca vitulina*, little within-colony site fidelity was observed, and no pattern of relatedness was found either within groups of females or linked to fostering behaviours (Schaeff et al. 1999). Finally, a nongenetic study of grey seals, *Halichoerus grypus*, found evidence of site fidelity and philopatry, with mark–recapture data showing the formation of groups of females suggesting kin aggregations (Pomeroy et al. 2000).

Southern elephant seals are the most sexually dimorphic and polygynous species of all mammals, and their mating system is thought to be among the purest forms of harem defence polygyny (McCann 1981; Le Boeuf & Reiter 1988; Fabiani et al. 2004). During the breeding season they are highly gregarious and females aggregate in large groups (harems) of up to hundreds of seals. For breeding, males arrive on land first and compete with each other to set up a dominance hierarchy, so that the hierarchy rank determines the breeding role of each male (McCann 1980; Galimberti et al. 2003). The male with the highest rank (alpha) has almost complete control over each female group, while the males not able to control a harem are kept outside the female groups as peripheral males. Females typically stay on land for 27–28 days during the breeding season. Once ashore, they join a harem where they give birth, nurse their pup for approximately 23 days, wean the pup, mate and then depart to the sea. Both males and females can have a long reproductive life span. Females become sexually mature at 3–4 years of age, and live on an average 19 years, with a documented maximum of 23 years (Hindell & Little 1988). Males reach social reproductive maturity not before 9–10 years old and live on an average up to 14–16 years (Le Boeuf & Reiter 1988). Therefore, a high level of philopatry could lead to kin clustering, including the association of different generations from the same family. The extent to which this happens would depend on the degree of spatial and temporal synchronization of philopatry and site fidelity. Site fidelity of males could lead to repeated matings with either the same or related partners. Mark–recapture studies on southern elephant seals have reported site fidelity in both sexes, with males tending to disperse more than females (Hindell & Little 1988; Lewis et al. 1996). Despite significant genetic differentiation between colonies, evidence of male-mediated genetic dispersal has also been shown, revealing male dispersal over a vast geographical range (over 8000 km) with consequent gene flow between distant colonies (Fabiani et al. 2003).

On Sea Lion Island (off the Falkland Islands; SLI, hereafter), females are faithful to the breeding site, often returning to the same part of the colony during consecutive seasons (see below). Females on SLI may change harem between arrival and parturition, but this is rare. Typically, only isolated females, after giving birth in unsuitable places, have been recorded moving to nearby harems where they remain for the rest of the breeding season (Galimberti et al. 2000a). On the other hand, males may move between different harems more often. The kin-based substructure of southern elephant seal harems has not previously been addressed with molecular markers. Both the initial formation of harems and individual

movements within the colony could be affected by kinship, if seals chose to associate with either relatives or nonrelatives. If this were the case, the level of relatedness could influence the way in which the colony developed, and thereby affect individual reproductive success (i.e. through the influence of seal distribution on mating opportunities).

We assessed the level of genetic relatedness among elephant seals of the SLI colony. First, we determined the accuracy of the relatedness estimate by analysing pairs whose relationship was known. Second, we assessed the kinship among seals to investigate whether their social structure corresponds to genetic structure within the colony. Third, we investigated whether the levels of within-colony genetic relatedness reflect site fidelity and philopatry reported for this species (Lewis et al. 1996).

METHODS

Study Site and Population

We carried out fieldwork on SLI (52°26'S, 59°05'W), Falklands, during six breeding seasons (September–November, 1995–2000), under licence from the Falkland Islands Government. Genetic samples were collected from 1996 to 1998, while demographic data were recorded in each year. Because some of the females sampled were also present in 1995 and in the 1998–2000 seasons, we could track them during those years as well, and collect data on their site fidelity. The SLI population has been estimated at approximately 1820 seals and 527–567 breeding females (Galimberti & Sanvito 2001). Large and uniform sandy beaches represent the breeding habitat on the island (total length ca. 4.4 km), which are occupied by the 'harems'. A harem was defined as a stable group of 2–129 females clearly separated by more than 10 SBL (standard body length ≈ 2.6 m, Baldi et al. 1996) from other groups.

For each harem, we defined the 'harem holder' as the male within the female group (Deutsch et al. 1990; Baldi et al. 1996; Galimberti et al. 2002). We marked individuals with at least two plastic cattle tags (20-mm Jumbo Rototags, Dalton Supplies Ltd, www.dalton.co.uk) in the rear flippers. Jumbo Rototags are the standard tags for this species. Seals were unrestrained and resting when tagged; they reacted briefly but the tags had no observable lasting effects. We recorded the presence and position of each marked animal during daily censuses carried out on the whole population. The likelihood of losing both tags between two consecutive seasons was 0.21–0.31%, as estimated from tag loss rate in double-tagged individuals (Galimberti et al. 2000c). Details of marking and census protocols are reported elsewhere (Galimberti & Boitani 1999). Since detailed maps of the island were not available, we divided the whole study area into three 'zones' by using topographical landmarks. A zone was defined as a continuous stretch of two to six sandy beaches, used by breeding seals and clearly separated from other zones by rocky areas unsuitable for breeding (mean zone length = 1451 m; total length = 4354 m). The position of each landmark was identified with GPS receivers with differential postprocessing (precision <3 m root mean

square; Magellan Systems Corporation, San Dimas, CA, U.S.A.) and located on a map drawn from aerial photography (RAF Mount Pleasant Airport, Falkland Islands; Fig. 1).

We obtained tissue samples from all males present on the island in 1996 ($N = 78$) and 1997 ($N = 62$). Thirty-nine males present in 1996 were also present in 1997; tissue samples were taken only once from these males, making a total of 101 males. Females belonging to seven harems of only one zone (Fig. 1; five harems in 1996: RUB96, SF96, SI196, SI296, SM96; two in 1997: SF97, SI297; total $N = 162$) were sampled with their respective pups from the next season ($N = 192$). The females were sampled from both the core and the periphery of each harem, and there was no sampling bias towards external individuals. Thirty females were present in both years and were sampled only once, making a total of 192 mother–pup pairs in two seasons (Table 1).

Tissue samples were taken with ear-notching pliers from the hind flippers of unrestrained, resting seals, (Pember-ton et al. 1992), and preserved in the field in 90–95% EtOH (Dessauer et al. 1990). There was typically a brief ‘startle’ reaction to tissue sampling, but no observable lasting effects. The tissue sample was approximately 8 mm² and the pliers were thoroughly cleaned in between sampling. Wounds were monitored during the course of the breeding season, and healed quickly; no infection was ever detected.

Characterization of Microsatellite Loci

DNA was extracted by the phenol–chloroform method described in Hoelzel & Green (1998) and genotyped at seven autosomal microsatellite loci. The loci consisted of four loci isolated from grey seals (Hg4.2, Hg6.3, Hg8.9, Hg8.10 from Allen et al. 1995), one from the harbour seal (Pv9 from Allen et al. 1995) and three from southern elephant seals (BETA from Slade et al. 1998; M11a, M2b from Hoelzel et al. 1999). The PCR amplifications were carried out in 10–20- μ l reaction volumes with the following final concentrations: 0.2 mM dNTPs, 0.75–1.5 mM MgCl₂, 10 mM Tris–HCl pH 8.4, 500 mM KCl (Hoelzel

& Green 1998), 0.02 U/ μ l Taq polymerase, 150–250 pM of each primer, 5–50 ng/ μ l 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 s. 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 and analysed for length variation with GeneScan Analysis 2.0 and Genotyper 2.0 software packages (Perkin–Elmer Corporation, Wellesley, MA, U.S.A.). The primers Hg4.2, Hg8.9, Hg8.10, Pv9 and M11a amplified fragments of 130–200 bp; Hg6.3 and M2b fragments of 200–260 and BETA fragments of 250–350.

Tests for significant deviation from Hardy–Weinberg equilibrium and genotyping disequilibrium were implemented in GENEPOP 3.3 (Raymond & Rousset 1995). Null allele frequencies were calculated with CERVUS 2.0 (Marshall et al. 1998).

Genetic Relatedness Analysis

We estimated Hamilton’s relatedness coefficient (R) between females, between males and between females and males with the program KINSHIP 1.3.1 (Goodnight & Queller 1999). For each dyad, the program uses the allele frequencies in the population and each individual genotype to estimate the extent to which they have alleles that are identical by descent. The coefficient ranges from -1 to $+1$: a positive R value indicates that two individuals share more alleles that are identical by descent than expected by chance, while a negative R value indicates that two individuals shared fewer such alleles than expected by chance.

The allele frequencies obtained from the adult population of SLI (263 individuals) were used for the calculation of relatedness. The large sample size and the seals’ natural history (i.e. one pup per year, absence of ‘clans’ of

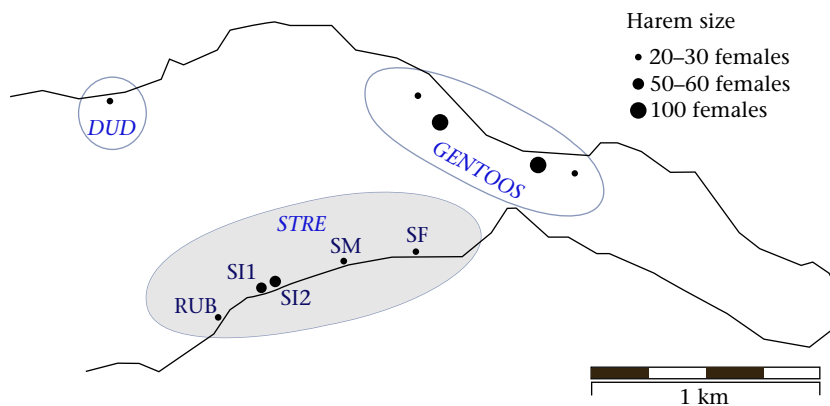


Figure 1. Distribution and dimensions of the harems (black dots) in 1996. The study area was divided into three zones (DUD, GENTOOS, STRE) and the females belonging to the harems of the zone STRE (grey circle) were tissue sampled. See text for more details. The distribution of the harems in 1997 was very similar.

Table 1. Sampling and genotyping effort for each harem

Harem	Harem size	Sampled females	Sampling effort (%)	Returning females	Genotyped females	Genotyping effort (%)
RUB96	25	21	84.0	15	13	86.7
SF96	35	31	88.6	22	20	90.9
SI196	58	53	91.4	33	27	81.8
SI296	80	69	86.3	55	40	72.7
SM96	19	18	94.7	18	15	83.3
SF97	44	38	86.4	30	26	86.7
SI297	83	78	94.0	61	51	83.6
Total	334	308	92.2	234	192	82.1

Harem size: total number of females that bred in each harem (as determined by tagging and resighting); sampled females: females tissue sampled; sampling effort: percentage ratio between sampled and total females; returning females: females that came back the next season and gave birth; genotyped females: tissue-sampled females that came back the next season, gave birth to a pup that was also sampled and genotyped (i.e. genotyped mother–pup pairs); genotyping effort: percentage ratio between genotyped and returning females.

relatives) should avoid bias resulting from the probable inclusion of relatives in the calculations (Queller & Goodnight 1989; K. Goodnight, personal communication).

To test the accuracy of estimated R values using dyads of known relatedness, we calculated the mean R value for 192 mother–offspring pairs (expected R value = 0.5) identified from behavioural and parentage analyses (Fabiani et al. 2004). We also tested 30 half-sibling pairs sharing the same mother and assumed to have different fathers (expected R value = 0.25). Finally, using 263 and 46 adult seals from SLI and Elephant Island (EI, hereafter), respectively, we compared nonrelatives (expected R value = 0). The colonies of SLI and EI are about 1000 km apart and showed weak genetic structure in previous studies (Fabiani 2002; Fabiani et al. 2003).

We tested whether females belonging to the same harem were more closely related than females belonging to a different harem. For each harem, we compared the distribution of the R estimates between females within the harem with the distribution of R values between females belonging to that harem and females belonging to other harems. To test the hypothesis that females select unrelated mates, we investigated the level of kinship between the harem holder and the females breeding in his harem.

To compare the levels of genetic relatedness between different sets of individuals, we used two different approaches. When possible, we used the individuals as observations and we analysed the data with a nonparametric two-tailed Wilcoxon signed-ranks test for paired samples with the Monte Carlo method (10 000 resamplings). When this was not feasible, dyads of individuals were used, and the data were analysed with a two-tailed Mann–Whitney or a Kruskal–Wallis test with a Monte Carlo estimation of probability (10 000 replications). The tests were run in StatXact 4 (Cytel Software Corporation, Cambridge, MA, U.S.A.) or in SPSS (SPSS Inc., Chicago, IL, U.S.A.) for Windows. This approach was taken for three reasons. First, the cells of a square matrix of relatedness coefficients between dyads of individuals are not independent and therefore not suitable for standard parametric analyses (Manly 1997; Ludbrook & Dudley 1998). Second, randomization tests are frequently used in testing square matrices where dyads of individuals are the analysis units (e.g. dominance matrices: De Vries 1995). Third,

nonparametric tests are more robust against outliers that might result from genotyping errors (Potvin & Roff 1993).

To see whether the between-harem kinship was related to geographical distance we applied a Mantel test (Monte Carlo with 10 000 duplicates), which checks the linear correlation between two matrices. We used the program MANTEL for Windows (by M. J. Cavalcanti, available at <http://life.bio.sunysb.edu/morph/>). The test was run only for the harems of 1996 ($N = 5$), because only two harems were genotyped in 1997.

We present statistics as mean \pm SD or median and median absolute deviation (MAD) for asymmetrically distributed variables. For multiple comparisons, we applied a sequential correction (Holm 1979) as implemented in Multiplicity Program 2 (Brown & Russell 1996).

RESULTS

Site Fidelity and Philopatry

From mark–recapture data collected from 1995 to 1999, 84% of 646 females that returned to the island for two to four breeding seasons gave birth within an average of 500 m from the previous year's location (72% returned to the same zone, 33% to the same harem site). Philopatry for a small sample of females ($N = 38$) marked as newborn in 1995 and that later returned to breed in 1999 was high, with 63% of these primiparous females returning to breed in their natal birth zone.

Genetic Diversity

All loci were analysed for the adult population of SLI ($N = 263$). The most variable locus was M2b with 10 alleles and the least variable were Hg4.2 and Pv9 with four alleles. Heterozygosity ranged from 0.46 for Pv9 to 0.78 for Hg8.10. No locus showed significant deviation from Hardy–Weinberg equilibrium ($0.13 < P > 0.95$ for each locus), nor was there evidence of genotyping disequilibrium for pairs of loci (test implemented in GENEPOP 3.3, Raymond & Rousset 1995). Null allele frequencies (calculated with CERVUS 2.0, Marshall et al. 1998) were always lower than 0.05. Only two mother–offspring pairs mismatched, each at one locus.

Relatedness from Known Relationships

The mean relatedness for comparisons between EI and SLI (presumed unrelated individuals; expected value: 0.0) was -0.041 ± 0.229 (95% CI = $-0.045, -0.037$, $N_{\text{dyads}} = 12\,098$). Mother–offspring pairs with a predicted relatedness of 0.5 had a mean *R* value of 0.482 ± 0.147 (95% CI = 0.461, 0.503; $N_{\text{dyads}} = 192$), while the mean *R* value for half-sibling pairs (expected value: 0.25) was 0.293 ± 0.240 (95% CI = 0.204, 0.383, $N_{\text{dyads}} = 30$). The three distributions differed from each other (Kruskal–Wallis: $H_2 = 541.8, P < 0.0001$), although they were partially overlapping (Fig. 2). However, by comparing the distributions of parent–offspring and half-siblings, we could determine the probability of misclassifying a dyad to a particular relationship. According to Blouin et al. (1996), the midpoint between the means of two distributions can be used as a cutoff value for the classification of the dyads. For half-siblings and parent–offspring, the cutoff value between the two distributions would be 0.39, hence a dyad with $R \leq 0.39$ would be included in the distribution of half-siblings, whereas a dyad with $R > 0.39$ would belong to the full-sibling distribution. The percentage of randomly generated half-siblings that fall to the right of the cutoff value would represent the type I error rate (which in this case is 43%), while the percentage of randomly generated parent–offspring that fall to the left of the cutoff value would be the type II error rate (25%). To reduce the error probabilities, we pooled the parent–offspring and the half-sibling distributions and used the data to discriminate related from unrelated dyads (cutoff point = 0.25). In this case, an expected 11% of related dyads would be misclassified as unrelated, and 11% of unrelated dyads classified as first- or second-order related seals.

Kinship Assessment in the Colony

The mean relatedness among seals from SLI ($0.002 \pm 0.239, N_{\text{dyads}} = 34\,453$) was higher than the mean

relatedness calculated for SLI–EI dyads ($-0.040 \pm 0.229, N_{\text{dyads}} = 12\,098$; Mann–Whitney *U* test: $U = 260\,256\,883, Z = 16.78, P < 0.0001$). The mean *R* value for all adult seals sampled on SLI was -0.003 ± 0.238 ($N_{\text{dyads}} = 18\,528$) in 1996 and -0.001 ± 0.241 ($N_{\text{dyads}} = 9591$) in 1997. There was no difference between the 2 years ($U = 88\,379\,056, Z = -0.74, P = 0.464$). The mean relatedness level among females ($N_{\text{dyads}} = 9481$) was higher than the mean relatedness level among males ($N_{\text{dyads}} = 4894; U = 21\,388\,146, Z = -7.69, P < 0.0001$); the difference was significant in 1996 ($P < 0.0001$) and close to significance in 1997 ($P = 0.053$; Table 2).

Kinship Patterns Among Females

The average value of relatedness within harems (1996: 0.016 ± 0.079 ; 1997: 0.013 ± 0.079) was significantly greater than the value between harems (1996: 0.013 ± 0.078 ; 1997: -0.011 ± 0.084) only in 1997 (Wilcoxon signed-ranks test: 1996: $T_+ = 3592, Z = -0.717, N = 115, P = 0.469$; 1997: $T_+ = 3592, Z = 0.258, N = 77, P = 0.0095$; Fig. 3). However, for five harems out of seven, relatedness within a harem was not significantly different from relatedness between harems (Table 3). The within-harem relatedness was highly variable between harems (Kruskal–Wallis: $H_6 = 25.36, P < 0.0001$), and the mean level of relatedness between females within a harem was not related to the size of the harem (Spearman rank correlation: $r_s = 0.42, N = 7, P = 0.355$). Similarly, when the geographical distance between harems was taken into consideration, the between-harem relatedness did not decrease as a function of distance (normalized Mantel test: $r = 0.319, N = 5, P_{10K} = 0.838$).

From 1995 to 2000, all females sampled in 1996 and 1997 ($N = 162$) returned to breed for at least 2 years, for a total of 13 041 pairs of females present for one to six seasons on the island (3.74 ± 1.25 , median = 4, MAD = 1). The females of each dyad were recorded breeding zero to five times in the same harem. When we standardized

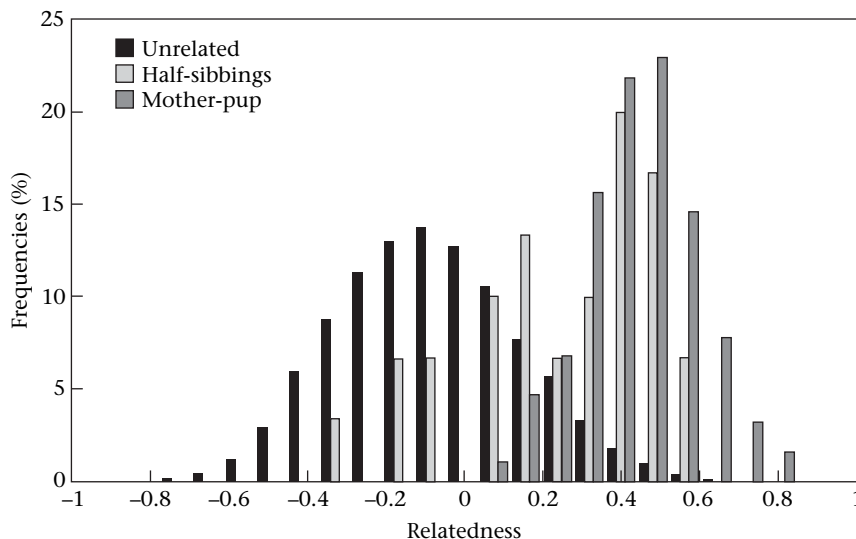


Figure 2. Distributions of relatedness values of known unrelated, mother–offspring and half-sibling pairs.

Table 2. Estimates of relatedness (R) in the population of SLI in the 2 years of study

	1996			1997		
	Mean \pm SD	N	Range	Mean \pm SD	N	Range
FF	0.014 \pm 0.238	115	-0.668-0.889	0.007 \pm 0.247	77	-0.780-0.808
MM	-0.030 \pm 0.231	78	-0.686-0.730	-0.008 \pm 0.236	62	-0.620-0.754
All	-0.003 \pm 0.238	193	-0.691-0.889	-0.001 \pm 0.241	139	-0.780-0.828

Mean R values \pm SD, number of individuals (N) and range are given between females (FF), between males (MM) and between all seals of the colony.

the years in the same harems for the total number of seasons that they were both breeding on SLI, they bred in the same harem a mean of 0.187 ± 0.230 times (median = 0, MAD = 0). In total, 6478 dyads (49.6%) bred at least once in the same harem.

We analysed the level of relatedness for the dyads of females breeding on SLI for at least 3 years ($N_{\text{dyads}} = 10383$). Of these, 440 (4.2%) came to breed in the same harem for at least three consecutive seasons, 25 (5.7%) of which had an R value higher than 0.39 (Table 4). The females breeding for three to five seasons in the same harem (0.025 ± 0.239 , $N_{\text{dyads}} = 440$) did not show significantly higher kinship than those that did not share a harem or shared a harem for less than three seasons (0.012 ± 0.242 , $N_{\text{dyads}} = 10398$; Mann-Whitney U test: $U = 2659491$, $Z = -1.124$, $P = 0.26$).

Kinship Between Females and Holders

The relatedness between the females of each harem and their harem holder varied between harems (Kruskal-Wallis: $H_6 = 28.88$, $P < 0.0001$). When the relatedness of female-harem holder pairs was compared with the relatedness between females and holders of the other harems, the results were not consistent among harems. For harem SI196, females were significantly less related to their own harem holder than to the holders of other harems, while the opposite was true for SI297 (Wilcoxon signed-ranks test: SI196: $T_+ = 87$, $Z = -2.451$, $P = 0.0118$; SI297: $T_+ = 966$, $Z = 2.840$, $P = 0.0048$; Table 3). None of the other harems showed a significant difference.

DISCUSSION

Genetic Assessment of Kinship

Data generated from the seven microsatellite loci investigated in this study were sufficient to discriminate between second-order kin and nonrelatives. However, a higher level of resolution may be needed to discriminate first- from second-order kin. Nevertheless, the data allowed the assessment of related and nonrelated individuals with small error probabilities. The mean estimated R values for pairs of known kinship were close to the expected values, although the half-sibling average of 0.29 was higher than the expected 0.25. This estimate may be inaccurate because of the relatively small sample size for half-siblings (the distribution of values as seen in Fig. 2 is consistent with sampling effects) or inflated because of mothers mating with the same male in different years and/or kinship among parents.

Site Fidelity and Philopatry

In elephant seals (Nicholls 1970; Lewis et al. 1996), as in other pinnipeds (Pomeroy et al. 1994; Twiss et al. 1994), both males and females show site fidelity to their colony. However, tag recovery data suggest that males disperse more than females, even though they tend to forage over shorter distances (McConnell & Fedak 1996; Campagna et al. 1999). In this context, all seals from the same colony would be expected to show some level of relatedness, and females should be more related to one another than males are.

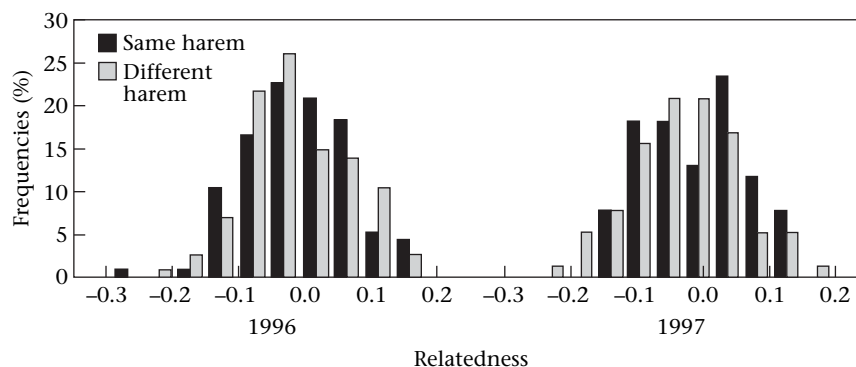
**Figure 3.** Relatedness distribution among females within and between harems each year.

Table 3. Mean relatedness (*R*) values ± SD between females within and between harems and between females and harem holders within and between harems

Harem	No. of females	Females–Females	Females–Holder
RUB96			
Within	13	−0.029±0.071	0.085±0.201
Between		−0.003±0.087	−0.016±0.070
SF96			
Within	20	0.0439±0.078	−0.062±0.149
Between		0.0211±0.092	0.001±0.084
SI196			
Within	27	0.046±0.078*	−0.086±0.181*
Between		0.014±0.069	0.014±0.080
SI296			
Within	40	0.005±0.08	0.030±0.291
Between		0.015±0.081	−0.008±0.086
SM96			
Within	15	−0.009±0.055	−0.102±0.189
Between		0.010±0.071	−0.003±0.063
SF97			
Within	26	−0.029±0.063	−0.082±0.187
Between		−0.011±0.105	−0.017±0.119
SI297			
Within	51	0.034±0.077*	0.120±0.232*
Between		−0.011±0.072	0.015±0.084
All			
Within	192	0.015±0.078	0.060±0.235
Between		0.004±0.082	0.001±0.087

For each harem and relationship, the first row shows results within the harem and the second row between harems. *Harems for which the two distributions of *R* values were significantly different (two-tailed Wilcoxon signed-ranks test: *P* < 0.03).

Consistent with the observed site fidelity, the mean relatedness between seals from SLI was significantly higher than the mean relatedness for SLI–EI dyads. Furthermore, relatedness between females was higher than relatedness between males in both years. These data are also consistent with earlier studies that compared data for mitochondrial and nuclear DNA, and showed much stronger population structure for the mitochondrial than for the nuclear DNA markers (Hoelzel et al. 1993, 2001; Slade et al. 1998; Fabiani et al. 2003). Such data

Table 4. Dyads of related females returning in more than three seasons to breed in the same harem

Time in the same harem	Relatedness		Total dyads
	<i>R</i> >0.25	<i>R</i> >0.39	
Three seasons	73 (81.1)	20 (22.2)	73
Four seasons	13 (14.4)	5 (5.5)	13
Five seasons	4 (4.4)	0	4
Total dyads	90	25	90

The number and the percentage (in parentheses) are shown for those dyads with level of kinship higher than 0.25 and 0.39 (cutoff points explained in the text).

are difficult to interpret because of the difference in effective population size for the two types of markers; however, they are in agreement with our results. Furthermore, evidence for a very long-range genetic dispersal event was recently reported for a male southern elephant seal on the basis of both mtDNA genotype and microsatellite DNA exclusion data (Fabiani et al. 2003).

Female Fidelity and Relatedness

The site fidelity of SLI females is greater than that recorded for the nearby population at Peninsula Valdés, Argentina (the 3-km criterion adopted by Lewis et al. 1996 would include almost 100% of the females if applied to the SLI population). Although, Peninsula Valdés and SLI differ in size, shape and topography, the potential breeding space is comparable, and breeding animals are concentrated into a small part of the potential breeding space in both locations (cf. Campagna & Lewis 1992). The level of philopatry at SLI is comparable to the 77% of females giving birth within 4 km of their natal site on Macquarie Island (Nicholls 1970), and the 71.4% reported for the northern species, *M. angustirostris* (Reiter et al. 1981).

Breeding habitat topography and the population’s mating system can influence female movements and patterns of individual site fidelity. On SLI, elephant seals breed on long open beaches, with no obvious topographical features that might attract females to specific areas (as has been reported for grey seals: Twiss et al. 2000; Pomeroy et al. 2001), or preclude the formation of a harem. Population density is low (Galimberti & Boitani 1999), there is virtually no limitation of breeding space (although seals do not occupy large parts of the beaches), and the distance between adjacent harems ranged from 130 to 415 m. In spite of this lack of obvious topographical features, the geographical locations of harems are constant across years, and harems only rarely appear in locations where they were not observed in previous breeding seasons. The mating system of the southern elephant seal is based on female defence, and not on territory defence as in other Pinnipedia species that show strong site fidelity (Gentry 1998). Interactions among seals can play an important role in regulating female settlement in the colony and consequently the location of the harems. Le Boeuf (1991) suggested that females join a harem at their arrival to reduce the likelihood of encountering secondary males, and thereby, avoid associated short- and long-term breeding costs. The level of harassment by secondary males and, subsequently, the capability of the harem holders in herding females can influence the precise location and the size of a harem. In this context, the ability of the holder to herd females is an important factor (Galimberti et al. 2000a). As these ‘social’ factors change between seasons, it is thus remarkable that females still show a significant tendency to give birth in the same place in different years. Note that female fidelity is measured to the location where they give birth, and therefore reflects their positions after any redistribution caused by social interactions. A common explanation for fine-scale site fidelity is the facilitation of kin associations, although there is no evidence in

this species for the altruistic interactions (such as foster parenting) that might be promoted by such affiliations.

The consistency of harem locations together with the high level of site fidelity would be expected to generate kin structure among harems. In support of this, we found average within-harem kinship values to be significantly higher than between-harem kinship values, but only for two of the seven harems. This may imply that kin structure is weak at this spatial scale on the beach (as indicated by the results of the Mantel test), and this result may therefore reflect a need for greater resolution (i.e. screening of more loci) to detect patterns at this scale.

A low level of structure at this scale is also consistent with population genetic data suggesting long-term movement of females between colonies (Slade et al. 1998; Hoelzel et al. 2001; Fabiani et al. 2003). While the colony at Peninsula Valdés appears isolated based on Wright's (1965) inbreeding coefficient (F_{ST} , where 0 implies panmixia and 1 complete isolation; mtDNA F_{ST} ranges from 0.53 to 0.92), a group of oceanic islands including Falkland, South Georgia, Elephant and Heard Islands shows less differentiation ($F_{ST} = 0.05-0.22$).

Close kin were found within the same harems for up to 5 years. However, close kin were not significantly more likely to be found in these long-term associations than in dyads with short-term associations. The mechanisms of philopatry and site fidelity may be sufficient to generate some long-term kin associations within harems by chance.

A strategy associated with interactions between males and females has been proposed as another important mechanism determining female membership in harems (Cassini 2000). A study on reproductive strategies of SLI females carried out during the same time as this study (Galimberti et al. 2000b) showed that females tend to prefer breeding in larger harems. Among females that settled in one harem on arrival and then moved to another harem for parturition ($N = 205$), 70% shifted to larger harems. This may reflect a female strategy to reduce the likelihood of encountering secondary males, and this could disrupt the tendency for kin clustering. However, although short- and long-term breeding costs caused by male harassment have been documented for females of the northern species (Le Boeuf & Mesnick 1990a, b), severe effects have only rarely been recorded on SLI (Galimberti et al. 2000a). This is likely to be caused by the low population density on SLI, compared to other colonies where female density is higher and mean harem size larger, with consequent higher pup mortality rates (Galimberti & Boitani 1999).

Our assessment of possible kinship between females and males within a harem, illustrated that females showed a significant difference in kinship with their harem holder compared to holders at other harems in only two of the seven harems tested. This does not support Amos et al.'s (2001) suggestion that females should choose to minimize kinship with mating partners (although, note that the genetic data for our study covered only 3 years, and it was not possible to compare partners of the same females in different seasons, as Amos et al. 2001 did with 48 grey seal females). It is, however, consistent with the idea that females are not joining harems on the basis of

encouraging or avoiding kin associations with harem holders. Furthermore, a harem can change its holder during the season (an event that is independent of female preferences), females almost never move after giving birth (unless they are isolated and join a harem after parturition), and there is no indication that they follow their holder to other harems (Galimberti et al. 2000a).

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