ORIGINAL ARTICLE

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Alpha-male paternity in elephant seals

Abstract The aim of this study was to assess paternity of males that dominated mating in harems at northern (*Mirounga angustirostris*) and southern (*M. leonina*) elephant seal rookeries using DNA fingerprinting and microsatellite DNA analysis. Southern alpha males had greater reproductive success than most northern alphas at similar-sized harems. Comparison of the relatedness between pups within harems also suggested that fewer males achieved matings in the southern elephant seal population. This was consistent with behavioral observations that suggest greater competition for mates in northern elephant seal harems. Reproductive success was consistent with estimates of mating success in some cases, but lower than expected for some northern elephant seal alpha males. A lower reproductive success than predicted from mating behavior may arise from a variety of factors including sperm competition, male sperm depletion from frequent mating, or reduced fertility. The alternatives are discussed in the context of environmental and historical factors.

Key words Mating system · Paternity testing · Elephant seals · Molecular ecology

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Introduction

Mammalian females are tied to parental care through parturition and lactation, and in many species males provide little more than gametes. Thus males can maximize their reproductive fitness by mating polygynously, while females attempt to maximize access to resources associated with foraging and breeding (e.g., Trivers 1972). Factors associated with resource distribution and life history strategy can determine the distribution of females, which in turn can determine the potential for polygyny (Emlen and Oring 1977; Reynolds 1996). When females are clumped and their reproduction is neither too synchronous nor too asynchronous, males can monopolize matings and both variance in male reproductive success and the intensity of sexual selection are expected to increase (Emlen and Oring 1977). We have investigated male reproductive success in two closely related, highly polygynous species (northern and southern elephant seals), and tested the utility of observational proxies to reproductive success, by paternity testing using DNA markers.

Le Boeuf (1991) reviews the literature on the evolution of mating systems in seals, which can be divided between those species that mate on ice or in the water, and those that mate on land. Among the latter, most are highly polygynous, and the degree of polygyny among these species varies with the degree of female clumping and estrous synchrony (see Boness 1991). The pattern of clumping might be expected to be influenced by the availability of suitable beaches, away from predation risk and relatively close to food resources (see Stirling 1983). However, elephant seal females appear to cluster tightly even when suitable space is abundant (Le Boeuf 1972). One additional factor is the influence of males on female distribution. Male elephant seals accost females that remain apart from female groups, who may clump closer together as a result (Mesnick and Le Boeuf 1991).

Northern (*Mirounga angustirostris*; NESs) and southern (*M. leonina*; SESs) elephant seals are closely

related species that inhabit the northern and southern hemispheres, respectively (Le Boeuf and Laws 1994). The NES was hunted extensively in the 19th century and reduced to an estimated population of 10–30 seals in 1884 (Bartholomew and Hubbs 1960; Hoelzel et al. 1993). By 1991, the population had recovered to an estimated 127,000 seals (Stewart et al. 1994). Although SESs were hunted extensively in the last century, the population never fell below several thousand individuals, and was estimated at 664,000 in 1990 (Laws 1994). Genetic diversity in SESs is at levels observed in other large mammals; genetic diversity in NESs is very low (Bonnell and Selander 1974; Gales et al. 1989; Hoelzel et al. 1993; Hoelzel, in press).

Pregnant females returning to annual breeding sites give birth within 6 (NES) or 5 (SES) days and then fast for 3–4 weeks while nursing. During the last 3–5 days of nursing, the female comes into estrous, copulates, and then weans the pup by returning to the sea (see Laws 1956; Le Boeuf et al. 1972; Le Boeuf and Laws 1994). Most females give birth to one pup each year of their reproductive lives (Le Boeuf and Reiter 1988). Within the season, variation in the timing of female estrous among individuals is enough to allow a dominant male to mate with multiple females. Estrous synchrony in seals is facilitated by delayed implantation and an annual breeding cycle (see Riedman 1990). Based on the criteria of Emlen and Oring (1977), these various factors indicate a high potential for polygyny in elephant seals.

Males of both species fight for status in a dominance hierarchy that gives access to estrous females clumped together in harems (Le Boeuf 1974; McCann 1981). An alpha male dominates all males associated with a particular harem, attempting to deny competitors access to females while he mates with them. The large discrepancy in size between the sexes, males being three to ten times larger than females (Deutsch et al. 1994), is thought to have evolved in part because large size is associated with winning fights and achieving high social rank, which is positively correlated with access to estrous females (Haley 1994; Haley et al. 1994), while other factors such as increased fasting endurance (see Bartholomew 1970) may also play a role.

In this study we compare observational measures of mating success with that determined by paternity testing using genetic markers, and compare two colonies, one of NESs and the other of SESs. A number of paternity studies of monogamous and polygynous birds and mammals have shown less paternity than expected from mating success (Gibbs et al. 1990; Birkhead and Møller 1992; Amos et al. 1993; Kempenaers et al. 1995; Travis et al. 1996; Freeman-Gallant 1997), while some studies find more extreme polygyny than predicted (e.g., Pemberton et al. 1992). We test two primary hypotheses. First, that for both species, alpha males will achieve the largest proportion of paternities in their harems, consistent with measures of alpha-male mating success (see Le Boeuf and Reiter 1988), and consistent with predictions from mating system theory as outlined above.

Second, that the greater sexual dimorphism in SES will be reflected in a higher degree of polygyny in that species. Adult females of each species weigh about 900 kg, while adult males are much larger. The NES male weighs up to 2.5 tonnes, but the SES male can weigh over 3.5 tonnes (see King 1983).

The reproductive success of alpha males will depend indirectly on factors affecting the clumping of females, and directly on the size of harems and the level of competition from other males. In the largest harems, alpha males achieve only a fraction of all matings, and their tenure can be brief, while in smaller harems, alpha males can achieve a much higher proportion of matings (Le Boeuf 1974). Even in small harems, a proportion of matings are typically achieved by lower-ranking and peripheral males. Further, although peripheral males can be excluded from females while the females remain within the harem, males also gain access as females leave the harem and enter the water at the end of the breeding season, though, in many cases, these females will have already been mated by the alpha or other males within the harem. Young males that have achieved sexual maturity but are still similar in size to females will sometimes attempt to sneak copulations by behaving like females, though their efforts are often cut short when the female calls attention to the deception with loud vocal protestations (Cox and Le Boeuf 1977). The success of these alternative strategists will determine in part the correlation between the apparent and actual reproductive success of the alpha bulls. We compare these various factors at the two colonies and discuss the possible impact of environmental and behavioral differences on the relative success of alpha males.

Methods

Study sites

We used behavioral observation to assess the mating success of individually marked alpha males from ten NES harems at Año Nuevo, California, and six SES harems at Punta Delgada on Peninsula Valdes, Argentina. At least two environmental differences between the SES and NES colonies may be important. First, the density of harems on Peninsula Valdes is relatively low at one to five harems per kilometer along the beach (Baldi et al. 1996). At Año Nuevo, and at some SES island colonies, both the density and the size of harems can be much greater (see Le Boeuf and Laws 1994; McCann 1980). Second, the topology of the beaches differed: that at Peninsula Valdes was flat and deep, while the beach at Año Nuevo included gullies and dunes within and around the harem sites.

Field observations and sample collection

Daily observations lasted 6–7 h at all northern harems and two harems in the south (LH and GH); the other four SES harems were monitored for approximately 2 h daily. Observations were made during daylight hours. Students of one of us (B.J.L.) have made observations at night and found similar levels and patterns of activity (unpublished data). The copulations of all alphas and other males that occurred during the observation periods were recorded

at each harem throughout the breeding season (defined as the period from the initial formation of harems as males and females return to the beach to when the last females leave the beach). The mating success of a male was estimated as the proportion of copulations achieved by that male out of all observed copulations at a given harem over the course of the breeding season (Le Boeuf 1974). While it was not possible to observe every copulation, and there is some overlap due to multiple copulations by a male with the same female and by females with multiple males, this measure gives a relative indication of the mating success of each male. Either a Fisher exact (for small-sample-size comparisons at a given harem) or a Mantel-Haenszel test of independence (for the combined harem samples) was used to compare mating success as estimated by copulation frequency with reproductive success as estimated by DNA analysis. The Mantel-Haenszel test protects against type I errors. A Dunn-Sidak correction for type I error would indicate an alpha significance of $P < 0.005$ for the multiple Fisher exact tests, and the one higher value presented is therefore only suggestive. Note that throughout the manuscript, all means are shown with standard deviations.

For the purpose of this study we operationally define an alpha male as the highest-ranking male in a hierarchy established by contests between males. These interactions are dynamic and the alpha position can change over the course of the breeding season. We define a harem as a group of females in close proximity on the beach (typically within 0–2 m), all defended by the same alpha male, and separated by some physical distance (at least 5 m) from other similar groups of females. The mating of females in each group is dominated by that harem's alpha male. Males attending a harem tend to be separated from each other by about 5 m (Le Boeuf and Mesnick 1990).

Tissue samples were collected from alpha males and the principal contenders (high-ranking sub-alpha males) at each harem. Using rongeurs, tissue samples (approximately 5 g) were obtained from the trailing edge of the hind flippers. Samples were preserved in saturated salt and DMSO (Hoelzel and Dover 1989). DNA was extracted by standard methods (see Hoelzel 1992). The following breeding season, samples were obtained from returning females (40–60% of tagged females), identified by tags in their hind flippers (Le Boeuf 1974; Le Boeuf and Reiter 1988), and the pups they produced. All of these females had mated in one of the study harems the previous season. Maternity could be confirmed through observation of the birth, the close association between female and pup soon after birth, and comparison of genetic profiles. The sample size of female-pup pairs consisted of 90 NES and 50 SES.

Paternity testing

The paternity of offspring at each harem was tested against a sample of putative sires composed of alpha males, high-ranking male competitors, and neighboring males (34 NES and 29 SES males). The number of males sampled from each harem is shown in Tables 1 and 2. Comparisons between harems included all sampled males. For our sample, 13 NES and 3 SES males were present (and counted in the Tables) at more than one harem over the course of the breeding season. The total number of males attending each harem varied from day to day and ranged from 1 to 22 males at NES harems and from 1 ten 10 at SES harems. The higher a male's rank, the more predictable was his presence at a given harem from day to day (see Le Boeuf and Mesnick 1990). The composition and hierarchy of males at each harem at the time of departure for each female in the sample (and therefore at the time of her estrous) was determined, and at least the alpha and beta males relevant to each female in the sample were included in the genetic sample of males.

Paternity was estimated using two minisatellite probes, $(CAC)_n$ (Ali et al. 1986) and 33.15 (Jeffreys et al. 1985). SES males were also screened for initial paternity exclusions using a microsatellite locus (see below) and a 33.15 minisatellite single-locus probe, locus 15A5 (cloned for grey seals by I. van Pijlen; see Amos et al. 1993). No attempt was made to compare 15A5 alleles between gels or to run all pairwise comparisons on the same gels. A microsatellite or single-locus minisatellite marker of sufficient variability was not available for NESs (there were only two NES alleles for the locus used to screen SES paternities and NESs were monomorphic at other microsatellite loci; data not shown).

Minisatellite probes were labeled with ^{32}P-dCTP by random hexamer priming and hybridized to Southern blots at 60 °C in a phosphate/SDS buffer (Westneat et al. 1988). Blots were washed in $2 \times SSC$ at room temperature and at 60 °C, and probed with $(CAC)_n$ as described in Hoelzel (1994). Blots were stripped and reprobed for 15A5 with the hybridization conditions used for 33.15. For microsatellite locus M2b, primers: 5′-CCGACTG-CTGGGGTAAAG and 5′-TCAGTCTCACCCACCTAC were used to amplify from SESs only. This locus was derived from clones from a NES library in the phagemid Bluescript. The library was probed with the ^{32}P-dATP end-labeled oligonucleotide 5′-ACACACACACACACACA. Clones were sequenced by a modified chain termination method using Sequenase. Genomic DNA was amplified by PCR in 10-μl reaction volumes containing 1 ng template DNA, 1.5 mM $MgCl_2$, 10 mM Tris-HCl, 50 mM KCl, 200 pM of each primer, 100 pM dCTP, dGTP, and dTTP, 5 pM dATP and 0.5 μCi ^{33}P-dATP. The cycle profile was 58 °C for 1 min, 72 °C for 1 min and 94 °C for 45 s, repeated 35 times. PCR product was run on a 6% denaturing polyacrylamide gel (not shown, but see Hoelzel 1996). A G-test was used to compare the frequency of paternal alleles in pups with allele frequency in alpha males at this locus.

Paternity tests were conducted as follows. A pairwise comparison of the mother and her pup revealed paternally derived bands (or alleles in the case of the single-locus probes). Potential fathers were screened for a match that included all identified paternal bands/alleles, and excluded as a potential father if there was less than a 100% match. Although there were relatively few males attending each harem, all of the adult males in our sample were screened for each paternity test. The probability of misidentification could be estimated by multiplying the band frequencies (derived for the sample of males) at each paternal band (e.g., a match based on three paternal bands, each with a frequency of 0.2 among the sample of males for that species, would have a misidentification probability of $0.2 \times 0.2 \times 0.2 = 0.008$). However, all NES paternities were conservatively based on exclusions, while the SES paternities could be based on matches, given the high level of minisatellite DNA variation, the relatively small number of potential fathers, and the uniformly low level of band-sharing among all males in the sample (implying that they were not closely related).

Comparisons of band-sharing among individuals (using the multi-locus minisatellite profiles) included only unique pairwise comparisons (each profile included in a comparison only once) so that all comparisons were independent. These comparisons were used as a simple relative measure of kinship and were based on the following formulation: $s = 2n_{xy}/(n_x + n_y)$ (see Wetton et al. 1987). If only one male achieved all matings in a harem and all females in the harem were unrelated, then all pups would be half-siblings, and the expected band-sharing between half-siblings can be estimated as $x = (1 + 5q - 5q^2 + q^3)/2(2 - q)$ (see Bruford et al. 1998), where q is the estimated allele frequency (see Jeffreys et al. 1985).

Results

Size and distribution of harems

The NES and SES harems investigated ranged in size from 9 to 224 females (measured as the peak number of females) for the NES study and from 30 to 119 for the SES study (Tables 1, 2). A Mann-Whitney U-test showed no significant difference between NES and SES harem sizes ($z = 0.43$, $P = 0.66$). Three NES harems (BMS1, BMS2, and BMN) were separated on the beach

Table 1 Indices of mating success and paternity for alpha-male northern elephant seals in relation to size of harems. Sample sizes are given in parentheses (*Percent alpha paternities* high estimates based on non-exclusions, *Males tested* the number of males within a harem included in the paternity tests)

	Harem										
	TS	BMS1	BBS	MBB	BBN	BMS2	BMN	NP1	NP3	NP2	Average
Peak female number	224	99	82	51	44	39	10	32	9	38	62.8
Percent alpha copulations	25.9 (58)	42.7 (82)	31.5 (54)	90.5** (21)	80.4* (51)	70.4 (44)	54.5(11)	47.4 (19)	66.7 (6)	64.7 (17)	51.7* (352)
Percent alpha paternities	35.7 (14)	27.8 (18)	41.7 (12)	26.7 (15)	42.9 (7)	80.0 (10)	0.0 (1)	33.3 (9)	66.7 (3)	100 (1)	38.9 (90)
Males tested	7	15	12	4	3	15	13	5	5	5	9

$*P < 0.05$; $**P = 0.0002$

Table 2 Indices of mating success and paternity for alpha-male southern elephant seals in relation to harem size. Sample size is given in parentheses (*Percent alpha paternities* based on paternal matches, *Males tested* the number of males within a harem included in the paternity tests)

	Harem						
	FH	LH	GH	KH	MH	TH	Average
Peak female number	119	75	57	30	30	81	65.3
Percent alpha copulations	77.7 (9)	56.8 (81)	50.9 (57)	50.0 (4)	66.6 (3)	– (0)	55.4 (154)
Percent alpha paternities	50.0 (6)	70.0 (10)	52.6 (19)	60.0 (5)	62.5 (8)	50.0 (2)	58.0 (50)
Males tested	8	7	6	2	4	2	4.8

by a distance of less than 10 m. All other NES and SES harems were separated by at least 50 m. No attempt was made to quantify topographic differences, but all of the SES harems were situated on open beach, while only three of the NES harems (TS, BBS, and BBN) were similarly situated, with the remainder being partially or fully up among dunes or within gullies.

Alpha-male paternity tests using minisatellite markers

There was substantially more variation among fingerprint profiles in SESs than in NESs. Mean band-sharing for $(CAC)_n$ above 2 kb among unrelated SES adults was 0.333 ± 0.068 ($n = 27$) compared to 0.811 ± 0.065 ($n = 34$) in NESs. Mean band-sharing for probe 33.15 was 0.320 ± 0.056 ($n = 29$) in SESs compared to 0.792 ± 0.079 ($n = 27$) in NESs. Data from the $(CAC)_n$ and 33.15 probes were combined, except for those bands in the NES profiles that hybridized to both probes (Fig. 1).

Table 1 (NES) and Table 2 (SES) show measures of paternity and mating success of alpha males in each harem. The tables show the proportion of all copulations observed that were achieved by the alpha male at each harem (percent alpha copulations), and the proportion of female/pup pairs tested where the father was the alpha male (percent alpha paternities). Among harems where the sample size was five or greater for both the number of copulations observed and the number of female/pup pairs included in the paternity tests, paternity of alpha males at three of three SES harems was similar to that expected from observed mating success (Table 2). In the northern species, the relationship between the estimated proportion of pups sired in harems and mating success was more variable. In five of seven NES harems (where the sample size was greater than five for estimates of both mating and reproductive success), paternity estimated from non-exclusions was in the range expected from mating success; however, the alpha males at MBB and BBN harems (and the mean for all harems) indicated less reproductive success than expected (Table 1). Due to reduced polymorphism in NES, there was insufficient resolution for paternity identification in most cases, but sufficient resolution for paternal exclusions. This means that paternity estimates are over-estimates, and therefore that differences between mating and paternity success are even greater than indicated in this analysis. The probability of misidentification was determined for each non-exclusion (a potential match) for all NES paternity tests. This value ranged from 0.875 to 1×10^{-5} with a mean of 0.218 (SD = 0.210, $n = 54$).

Variation for SESs was sufficient for paternity matches. Based on mean band-sharing (0.333 for CAC and 0.320 for 33.15) and the mean number of paternal bands (6.9 and 6.6, respectively), paternities in the SES population can be determined with a roughly estimated probability of misidentification of $(0.333)^{6.9}(0.320)^{6.6} = 2.7 \times 10^{-7}$. Since fewer than 100 males are potential fathers (reproductive-age males) for the harems included in the study, this is sufficient for paternal identification with an acceptably low chance of error. Each probe alone also gives an acceptable probability of

Fig. 1 a *Hae*III digests of 4 μg
DNA from 11 northern ele-
phant seals probed with (CAC)$_n$
or 33.15. Fragment size is indi-
cated in kilobases and examples
of fragments that hybridize to
both probes (*s*), that are unique
to one probe (*u*), and distinct
fragments that co-migrate
(**c**) are shown. **b** NES paternity
test for four potential fathers
and eight mother/offspring
pairs probed with (CAC)$_n$.
Fragments useful in the exclu-
sion of potential fathers are
indicated by *arrows*
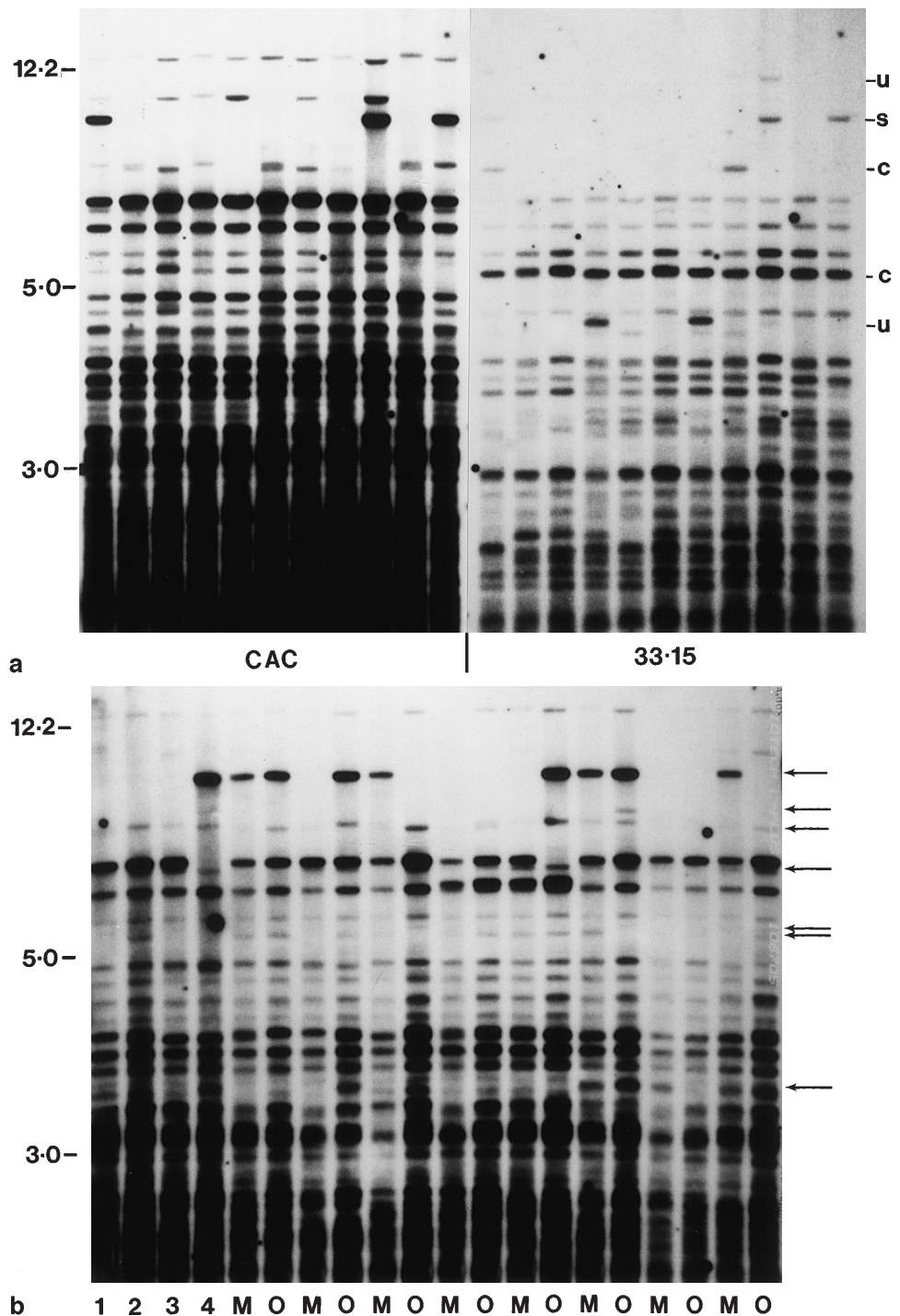
misidentification for the purposes of this study (CAC:
5.1×10^{-4}; 33.15: 5.4×10^{-4}). A simple comparison of
the number of non-exclusions scored for all NES alpha
males with the number of paternities achieved by all
SES alpha males shows significantly greater success for
SES alphas ($G = 4.74$, $P = 0.029$), while no significant
difference is seen for NES versus SES alpha mating
success ($G = 0.524$, $P = 0.5$). However, it is probably
more appropriate to compare success by individual
harem. A non-parametric comparison (Mann-Whitney

U-test) of proportional alpha success (percent alpha
paternities) in harems between NES alpha-male non-
exclusions and SES alpha-male matches indicates sig-
nificantly greater reproductive success for SES alpha
males (including only harems where the number of fe-
males tested was five or more; $z = 2.03$, $P = 0.042$). The
same comparison, but for estimates of mating success
(percent alpha copulations), showed no significant dif-
ference between SES and NES harems ($z = 0.34$,
$P = 0.74$).

The percent mating success of alpha males has been shown to be inversely related to the number of females in their harems (Le Boeuf 1974). However, in this study there was no significant regression between NES peak harem size and either mating success ($R^2 = 0.39$, $F = 5.2$, $p > 0.05$) or reproductive success ($R^2 = 0.07$, $F = 0.36$, $P > 0.5$). Reproductive success varied over a fairly narrow range in NES harems with the exception of BMS2 (Table 1).

SES alpha-male paternity using the microsatellite DNA locus

An independent test of variance of reproductive success in SESs, allele frequency comparison at a single microsatellite locus, revealed that a high proportion of paternities were achieved by alpha bulls, consistent with the minisatellite DNA data. Allele frequencies among adult males (all males in the SES sample) and among the paternal alleles in all pups from all harems combined were compared with an estimated contribution (assuming independent assortment in the distribution of alleles) from the population of all alpha bulls combined (Table 3). There was a significant difference in allele frequencies revealed by a G-test (comparing the number of alleles in each class) with the Williams correction for small sample size (Sokal and Rohlf 1995) comparing non-zero alleles (A, D, E, G, and H in Table 3) in all males to paternal alleles in pups ($G = 9.55$, $df = 4$, $P = 0.048$). A similar comparison between the estimated alpha-male-only contribution and paternal alleles in pups showed no significant difference ($G = 0.70$, $df = 4$, $P = 0.95$). Pups, however, showed some paternal alleles that were not present in any of the alpha bulls, indicating matings by other males, although the precise number cannot be quantified from this method.

Table 3 Allele frequencies at the microsatellite locus M2b in the southern elephant seal sample. Frequences included all individuals from all harems combined (i.e., all females, all males, all pups) (*Estimated contribution from alpha bulls* includes only alpha bulls and assumes independent assortment, *Paternal alleles in pups* determined by subtraction of the maternal allele from the pup genotype)

Allele	Female allele frequency	Male allele frequency	Pup alleles frequency	Estimated contribution from alpha bulls	Paternal alleles in pups
A	0.265	0.278	0.327	0.422	0.378
B	0.049	0.037	0.038	0.0	0.022
C	0.078	0.0	0.038	0.0	0.0
D	0.098	0.037	0.077	0.067	0.089
E	0.304	0.278	0.221	0.111	0.089
F	0.049	0.074	0.029	0.0	0.0
G	0.098	0.185	0.096	0.111	0.156
H	0.049	0.111	0.154	0.289	0.267
I	0.01	0.0	0.019	0.0	0.022

Reproductive success of non-alpha males

The hierarchy at most harems was dynamic, with the alpha position sometimes shifting over the course of the breeding season. Of the 21 paternities at the SES rookery that were not achieved by alpha bulls, three were achieved by previous alpha bulls that had been displaced at the same harem. In addition, one was by an alpha at another harem, and another by a male that had previously been an alpha at another harem. Two were by non-alpha males that had also been at one of the other harems in the sample (including one male that achieved paternities at two harems), four by non-alpha males that were primarily seen at one harem, and the remainder could not be matched to any of the males in the sample. Although it was not possible to be as precise about matches for the NES paternities, there was a higher proportion of paternities that excluded all the males in the sample (35% for NES vs 20% for SES, $G = 3.86$, $df = 1$, $P = 0.05$), despite a similar effort to include the most active males at each harem for both SES and NES. Observed copulations were not a strong indicator of reproductive success in either population (30.8% resulted in paternities for SES and 27.5% could not be excluded as paternities in NES). One NES female was observed copulating with one male on 3 consecutive days and with a second male on the 3rd day; both males were excluded as possible fathers of her pup.

Level of polygyny as indicated by kinship among pups within harems

Band-sharing analyses, which reflect the degree of relatedness among individuals and, hence, the level of polygyny, support the results of paternity tests by indicating a smaller proportion of males siring pups in SES harems than NES harems. For NES, we compared DNA fingerprint band-sharing coefficients for the $(CAC)_n$ probe between pups within harems and among adult males and adult females as a standard. We compared only the most variable bands, 6 kb or larger (Fig. 1). Mean within-harem band-sharing ($\pm SD$) among 43 independent pairs of adult females was not statistically different from that of 15 independent male pairs (0.624 ± 0.135 vs 0.571 ± 0.153, respectively) so these data were combined to yield a mean of 0.610 ± 0.141. This combined mean was not significantly different from the mean band-sharing among 38 independent pup pairs compared within harems (0.612 ± 0.139). The average for adults can be used to estimate the expected level of band-sharing for half-sibs, based on the assumption that adults on the beach are for the most part not closely related. This gives an estimate of 0.685. A one-sample t-test comparison of band-sharing among pups against a hypothetical mean of 0.685 shows a significant difference ($t = 3.26$, $df = 37$, $P = 0.002$). Our paternity matches identify a total of eight unique pup pairs that are likely half-siblings. Their mean band-sharing was 0.726 ± 0.121, which is also significantly greater than the overall pup mean ($t = 2.33$, $df = 44$, $P = 0.012$).

We found no difference in mean band-sharing among pups within (0.612) and between (0.624) harems.

As with NESs, we compared band-sharing between independent SES pup pairs within harems with that expected for half-siblings. The mean band-sharing between 25 independent adult pairs was 0.333 ± 0.068, with no significant difference between males and females. The mean band-sharing among 18 independent pup pairs within harems was 0.429 ± 0.100, significantly greater than the mean for adult males and females ($t = 3.8$, $df = 41$, $p = 0.0002$). The expected level of band-sharing for half-sibs (calculated using the adult average as an estimate for unrelated pairs) was 0.483. If 58% of the pups (the mean proportion of SES alpha paternities) were half-siblings and the remainder were unrelated, the expected mean band-sharing for independent comparisons among all pups would be 0.42, close to the value observed.

Discussion

Comparisons between mating success and paternity

The proportion of pups sired by alpha males was consistent with that expected from observed mating success in our small sample of SES alpha males. SES alpha males were actually more successful than the within-harem paternity tests indicate, because at least 24% of the 'non-alpha' paternities were achieved by alpha males at other harems, or males that had been alpha at another time during that breeding season. Reproductive success comparable to mating success was also seen for some NES alpha males we studied (though based on non-exclusions, which over-estimates paternal success), but others had very low reproductive success despite dominating mating. Relative to our measure of mating success based on observed copulations, the alpha males at two harems (MBB and BBN) were less successful than expected. Studies of reproductive success in various other mammal species have shown lower success for dominant males than expected, due to the success of peripheral or neighboring males (e.g., Travis et al. 1996). For NES, this will reflect the success of sub-dominant males competing for access to females, although among NES harems in this study, there was no clear association between the size of the harem (which will be related to the ability of the alpha to exclude competitors when the harem is very large) and the relative success of alpha males. There was also no clear relationship between the number of peripheral males at a given harem and the success of the alpha male, though this was hard to quantify as the composition of males at each harem was dynamic over the course of the breeding season. Another possibility is that some alpha males were less fertile than others. Frequent mating may decrease the number of mature sperm available for insemination. Alpha males at MBB and BBN did not, however, mate more frequently than alpha males at other harems (e.g., 25.9% of copulations with

224 females at TS amounts to more mating than 90.5% of copulations with 51 females at MBB; see Table 1). However, reduced fertility of some NES males relative to SES and other NES males cannot be excluded by, and is consistent with the available data. If true, this could be due to sperm anomalies associated with a reduction in genetic variation caused by an extreme population bottleneck in the last century (Bartholomew and Hubbs 1960; Bonnell and Selander 1974; Hoelzel et al. 1993), although sperm quality has not yet been investigated in NES males. Reduced male fertility and sperm abnormalities are evident in lions and cheetahs as an apparent result of population bottlenecks (Wildt et al. 1983, 1987).

Comparisons between the NES and SES harems

SES alpha males were more successful than NES alpha males for a similar range of harem sizes. Although the average level of mating success was similar between the two species, the level of reproductive success was greater for SESs, suggesting greater success than expected from peripheral males in NES harems. In support of this, kinship among pups within harems (as estimated by band-sharing coefficients) was greater among SES than among NES pups. Although the power of the NES analysis was relatively low due to the low level of variation in that species, the result was quite striking in that the mean band-sharing for NES pups was almost identical to that for NES adults, while the difference between SES pups and adults was pronounced (and consistent with that predicted by the paternity-testing data).

Differences in the behavior of female and peripheral male elephant seals at the two locations may explain, in part, the higher success of SES alpha males. Preliminary, ongoing research at the same two breeding sites indicates that females at the NES harems mate significantly ($P < 0.001$) more frequently (a mean of 5.1 vs 4.1 times) and with more males (a mean of 2.7 vs 1.9 males) than females in the SES population (M. Wainstein, A. Yamzon, B.J. Le Boeuf, C.L. Ortiz, unpublished data). Furthermore, the relative number of peripheral males encountered by departing females may be greater for the NES than the SES harems. For the NES population, a 95% confidence interval of five to nine males are present as females depart (Mesnick and Le Boeuf 1991). In the SES population zero to ten males were present, but differences in the tidal range, distribution of harems and behavior of the females meant that departing without encountering peripheral males was more common for the SES than the NES population. This apparent greater access by non-alpha males and consequent higher proportion of non-alpha matings in the NES population may contribute to the lower average reproductive success of alpha males at NES compared to SES harems. If this difference is representative of the breeding biology of the two species over their evolutionary history, then it may have contributed to the evolution of more extreme sexual dimorphism in the southern species. Haley et al. (1994)

investigated the relationship between alpha male size and copulatory success in NESs and concluded that selection for large size was partially a consequence of advantages in male dominance interactions. However, they also point out that while alpha male size was correlated to copulatory success, the correlation accounted for only 29–44% of the variance, and was non-significant when the effects of dominance were statistically removed. Differences in sexual dimorphism could also be due to differences in life history strategy or possibly to exploitation by male SESs of a more abundant resource.

Some of the differences in behavior may be due to environmental differences between the two breeding sites. The NES site has greater topographic structure providing gullies and dunes that could locally concentrate females, but also provide cover for peripheral males trying to obtain copulations. Some SES colonies appear to be more similar in this respect to the NES colony at Año Nuevo, though detailed studies are not available for direct comparison. The greatest distance between harems is also less at the NES site, and there is a very large harem on an island just offshore from the beach, providing more opportunity for the movement of males between harems. The SES site at Punta Delgada is a relatively unstructured, open beach.

In conclusion, a proxy measure of reproductive success (mating success defined as proportional copulatory success) was a good indicator of reproductive success in SES harems, but over-estimated the success of some alpha males at the NES colony. The relatively lower variance in reproductive success of NES males is probably due in part to the behavior of females and the greater success of NES non-alpha males, though the very low success of two NES alphas may suggest reduced fertility for those specific males. Future research should investigate further the possible relationship between environmental conditions at the colony and variance in male reproductive success.

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