



Proximate factors associated with high levels of extraconsort fertilization in polygynous grey seals

SUZANNE M. AMBS*†, DARYL J. BONESS†, W. DON BOWEN‡, ELIZABETH A. PERRY† & ROBERT C. FLEISCHER†

*Department of Biology, George Mason University

†Department of Zoological Research, National Zoological Park, Smithsonian Institution

‡Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography

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Behavioural estimates of male mating success in polygynous grey seals, *Halichoerus grypus*, may be misleading as females are known to be promiscuous. At Sable Island, Nova Scotia, we collected behavioural observations and skin samples for paternity analysis from 56 females and their attending males. Twenty-four of these females were found in the following year and their offspring were sampled. Using seven hypervariable microsatellite loci, we excluded the consort male as the father in 43% of the cases. The probability of exclusion of these seven loci was 98.2%. Contrary to expectations, inland females had higher rates of extraconsort fertilizations (ECFs) (70%) than beach females (23%). Younger females (<9 years) had slightly more ECFs than older females, but this was not significant. The duration of male consortship did not differ between females with ECFs and females fertilized by their consort male. Two explanations may account for the inland females having more ECFs: a higher ratio of females to tenured males inland may provide a greater opportunity for nonconsort males to obtain copulations; and inland females travel greater distances to depart for the ocean and may attract more males. These results are more consistent with the hypothesis that ECFs are a by-product for females of male strategies to maximize reproductive success than with hypotheses concerned with either material or genetic benefits gained by females.

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Genetic paternity analyses are dramatically changing our understanding of animal mating systems and male and female reproductive strategies. Among birds, where many species exhibit behavioural systems that suggest monogamous relationships, genetic analyses have often shown that extrapair fertilizations (EPFs) occur (Morton et al. 1990; Westneat 1990; Gowaty & Bridges 1991; Wagner et al. 1996). Moreover, both males and females may be responsible for EPFs (Westneat et al. 1990; Birkhead & Møller 1992; Wagner 1992; Strohbach et al. 1998). The benefits to males of engaging in extrapair mating that leads to fertilizing additional females are reasonably clear. However, whether there are benefits to females for a given species and what they are is often less so.

Correspondence: D. Boness, Department of Zoological Research, National Zoological Park, Washington, D.C. 20008, U.S.A. (email: dboness@nzp.si.edu). S. M. Ambs is now at the Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02906, U.S.A. W. D. Bowen is at the Marine Fish Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, NS B2Y 4A2, Canada.

Among polygynous species, especially in mammals where courtship behaviour and formation of bonds is often not required for mating, the factors shaping male and female reproductive strategies may be even more variable and complex. In many polygynous species, males form associations with one or more females sequentially or simultaneously by defending territories within which females reside, or by defending groups of females directly (Emlen & Oring 1977; Clutton-Brock 1989; Davies 1991; Boness et al. 1993). Males are able to devote their reproductive effort directly toward acquiring multiple females because they are not required for successful rearing of young (Trivers 1972), nor do they have to invest effort in courting females prior to copulation. In some polygynous species where males defend females, females are known to behave promiscuously, that is, they mate with males other than the ones defending or guarding them (Gibbs et al. 1990; Pemberton et al. 1992; Amos et al. 1993; Westneat 1993; Morin et al. 1994; Craighead et al. 1995; Gray 1997a, b). What underlies (e.g. the benefits to females) such promiscuity and its impact on the reproductive success of individual males or particular male

strategies has received much less attention than EPFs in monogamous species.

Polygyny is the predominant, and may be even the sole, form of mating system in pinnipeds. Female promiscuity is known from behavioural observations in several phocid species (Carrick et al. 1962; Le Boeuf 1972; Boness & James 1979) and may be more common than initially thought among otariids (Boness et al. 1993). However, little effort has been directed at assessing genetic outcomes of this promiscuity or at trying to understand why it occurs. In this paper, we investigated the extent to which female promiscuity in the polygynous grey seal, *Halichoerus grypus*, results in extraconsort fertilization (ECF) to evaluate behavioural estimates of the success of alternate male strategies and to compare our findings with those of a previous study at a different colony (Amos et al. 1993). We also examined several proximate factors that might help to explain why some females are fertilized by their defending consorts and others are not. Until recently (Amos et al. 1995) the presumption has been that female promiscuity in grey seals, and other seals such as elephant seals, has simply been a consequence of male-male competition.

Grey seals show moderate levels of polygyny based on behavioural (Anderson et al. 1975; Boness & James 1979; Tinker et al. 1995) and genetic (Amos et al. 1993, 1995) data. Females aggregate on land to give birth and nurse their pups for approximately 15–17 days. Females become receptive to males about 2–3 days prior to weaning their pups (Boness & James 1979; Boness et al. 1995). Males defend loosely defined clusters of females, shifting their positions to be closer to females that are receptive and even to follow receptive females when they move (Boness & James 1979). Females have been reported to mate multiple times and with as many as four different males (Anderson et al. 1975; Boness & James 1979). Recent genetic studies of grey seals at North Rona, U.K., revealed that female promiscuity results in consort males being less successful than expected from behavioural estimates: 36% of fertilizations were by nonconsort males (Amos et al. 1993, 1995). These studies suggest that most ECFs were not by neighbouring established ('tenured') males but by transient males roaming through the colony or offshore. In contrast, behavioural data on grey seals at Sable Island, Nova Scotia, indicate that most extraconsort copulations were by neighbouring tenured males and occurred while females were departing to sea after weaning their pups (Boness & James 1979).

We examined three proximate factors that may influence the frequency of ECFs in grey seals: the location of females with respect to the shoreline, the age of females, and the length of time the consort male had been associated with the female prior to becoming receptive.

(1) The density of males along the shoreline is greater than inland gullies and dune tops occupied by seals because of a greater number of transient males in this area. In so far as female promiscuity is primarily a consequence of male-male competition, we expect more females residing along the shoreline to have ECFs than females that reside inland.

(2) We were uncertain of how maternal age might affect ECFs. On the one hand, older females are experienced breeders and may be better at resisting male advances than young females. However, data from northern elephant seals, *Mirounga angustirostris*, suggest that older females might obtain more ECFs than younger females because older females are more likely to mate with aggressive males to avoid injury (Mesnick & Le Boeuf 1991).

(3) Females might actively seek ECFs based on the quality of their male consorts. Females that are attended by a male for shorter periods before they become receptive may be less certain about the quality of their consort and more likely to seek and mate with other males. Both grey and elephant seal females respond aggressively to males making sexual advances, do so more often when it is not their consort, and this response incites male competition (Cox & Le Boeuf 1977; Boness et al. 1982).

METHODS

Field work was conducted in January 1995 and 1996 at Sable Island, Nova Scotia, Canada (45°55'N; 60°00'W). Sable Island is a vegetated sandbar approximately 42 km long and 1.5 km wide, located 288 km east of Halifax, Nova Scotia. The island consists of vegetated dunes, long, narrow beaches, large, flat, sandy areas and narrow, sandy cuts between dunes. Male and female grey seals haul out on the island in mid-December through early February. The first females become receptive in early January. For the past several decades, pup production on Sable Island has been increasing at about 13% per year, and in 1995 about 19 000 pups were born (Mohn & Bowen 1996).

Behaviour Study Site

In January 1995, we created a grid (110 × 80 m) by driving stakes into the sand at 10-m intervals. The study area was oriented perpendicular to the shoreline and was divided into thirds (each 2933 m²). The north section was adjacent to the shoreline area (between the tideline and the first dunes), where large numbers of males moved to and from the water and females and males dispersed inland. We classified this as the 'beach' area. The centre and innermost sections were beyond that area (on vegetated dunes or in sand gullies further inland), where the distribution of animals was less dense and fewer animals moved in and out of the area. These sections were considered 'inland' areas. We recorded behavioural observations from a blind overlooking the study area approximately 50 m away. We collected behavioural data during daylight hours from 13 January to 3 February, with the exception of 28 January when a storm prevented observations.

We observed the behaviour of 35 females located within the study grid. Females that had recently given birth were chosen so that we could follow them throughout lactation and mating. We paint-marked and radio-tagged 30 of these 35 females and five had unique brands that had been applied when they were pups. For easy

identification, we also paint-marked 69 males that either remained in the study area for periods longer than 1 day or were seen copulating with a focal female.

Five or six times each day we recorded the location of these females and males on maps of the study area to determine the movements of females and the status of males with respect to tenure and consort relationships. These data were subsequently digitized (Summagrid III tablet, Summagraphics, Inc.; Roots software, Harvard University), providing *X*, *Y* coordinates for 104 individuals. To determine between-day movement patterns of females, we calculated the distance between the locations of a female on the first map of each pair of consecutive days. We determined within-day movement patterns using the distance between locations on consecutive maps within each day.

We used the maps to classify males similarly to earlier studies of grey seals (Boness & James 1979; Anderson & Fedak 1985), which showed that some males take up positions and defend females while others move frequently and seek mating opportunities when females might not be defended. Using a frequency distribution of male residency in a given location, Boness (1979) showed that a large number of males stayed less than 2 days, while other males stayed from 4 to 30 days, with most remaining in an area for 16–26 days. Based on this, males that remained within the study site for less than 2 days were considered transient and males that remained in the study area for more than 2 consecutive days were considered tenured with respect to the study site. Secondly, for a given focal female, we classified males based on their association with her. For a male to be considered a female's consort, the male had to be in association with (defending) the female for at least 2 consecutive days. We used 2 days as our measure because for those females outside the behaviour study site, a spot check for male association on any single day could yield misleading results. In other words, the male closest to the female at the time of checking might not actually be in control of her. However, by requiring that a male be attending a female for a second day consecutively increases the likelihood that the observed male was not simply a temporary intruder briefly taking advantage of the actual consort being otherwise occupied with a neighbouring male or female.

We also determined the duration of consortship and the rate of turnover of consorts for females in the study area using the daily maps. Turnover rate was calculated as the number of different consort males with a female during lactation divided by the number of days she was observed.

We conducted a census of adult females and males, including tenured and transient males to estimate the density in inland and beach areas. We calculated the number of transient males by subtracting the number of known tenured males within the study site from the total number of males. From these data we calculated the female-to-tenured-male sex ratio and the percentage of males that were transient.

During the daily observations, we recorded all aggressive interactions between males three times a day for

30-min intervals. This was done to establish possible differences in the amount of male aggressive activity between the inland and beach areas of the study area. To help identify putative fathers of offspring of females within the study site, we recorded all observed copulation attempts and successful copulations for the 35 females, noting identification and status of the male (tenured or transient and consort or nonconsort), and location with respect to the shoreline.

In 1995, we collected skin samples from all 35 females and their associated males. However, in 1996, we failed to find the 30 radiotagged females, so we could not sample their pups that were sired in 1995. We did relocate the five branded females and their pups in 1996. Subsequent experimentation with placing the radiotags on several branded females revealed that the failure to relocate the radiotagged females was likely the result of radiotags being lost at sea.

Outside the Behaviour Study Site

For paternity analyses, we selected an additional 21 branded females located outside but in proximity to the study grid because our method of radiotagging had not been used prior to this study and we were uncertain as to how many of the 30 radiotagged females would be relocated in 1996. We collected minimal behavioural data and skin samples from these 21 branded females and their associated males ($N=38$). The age of branded females ranged from 6 to 25 years. The females outside the behaviour study site were classified according to their location with respect to the shoreline, as were those in the behaviour study site (see previous section). Females were visited briefly each day to determine whether their nearest male was the same as the previous day. For easy identification from day to day, we paint-marked nearest-neighbour males using a brush attached to a long pole. As noted above, males were considered a female's consort if they were in attendance of her on at least 2 consecutive days. Nineteen of the 21 branded females outside the behaviour site were relocated in 1996 and their pups sired in 1995 were sampled for paternity analyses. In total, for paternity analyses, we obtained samples from pups of the 24 branded females relocated in 1996 (five from within the behaviour site in 1995 and 19 from outside it).

We sampled males remotely by using a metal pole with a biopsy punch fastened to the end to remove a small piece of skin. This technique minimized disturbance in the colony, as capturing large males can be disruptive and cause males to abandon their positions.

Statistical analyses were performed with SYSTAT version 5.0 and SAS version 6.12. *G* tests were performed using the Yates' correction when sample sizes were small (Sokal & Rohlf 1981). Sample means are given with standard errors unless otherwise noted.

DNA Analysis

We stored skin samples in 20% DMSO, 0.25 M EDTA in a saturated NaCl solution (Seutin et al. 1991) at -20°C .

Table 1. Allele frequencies from 95 individuals calculated using Genepop version 1.2 (Raymond & Roussett 1995) for seven microsatellite loci

Allele			Allele			Allele		
Locus	Size	Frequency	Locus	Size	Frequency	Locus	Size	Frequency
Hg 8.10	185	0.010	Pv 9	162	0.170	Hg 4.2	149	0.425
	187	0.311		164	0.450		151	0.220
	189	0.423		166	0.060		153	0.165
	191	0.148		170	0.320		155	0.015
	193	0.107					157	0.135
						159	0.040	
Hg 6.3	217	0.010	Pv 11	158	0.010	Hg 8.9	199	0.105
	219	0.025		160	0.020		201	0.015
	221	0.155		162	0.046		205	0.010
	223	0.170		164	0.388		207	0.040
	225	0.045		166	0.393		209	0.430
	227	0.425		168	0.077		211	0.210
	229	0.160		170	0.036		213	0.145
231	0.010	172	0.031	215	0.045			
Hg 3.6	86	0.084						
	92	0.011						
	94	0.063						
	96	0.058						
	98	0.279						
	100	0.221						
	102	0.284						

Genomic DNA was digested with 50 µl of 10-mg/ml Proteinase K and 2 ml of lysis buffer (1 M Tris, 0.5 M EDTA, 10% SDS, 5 M NaCl) placed in a water bath overnight at 55°C. A standard phenol/chloroform extraction and salt/ethanol precipitation was used to isolate the DNA (Amos et al. 1991).

Isolated DNA was diluted to 50 ng/µl for the polymerase chain reaction (PCR) amplification of microsatellites. We amplified seven hypervariable microsatellites developed for eastern Atlantic grey seals and harbour seals, *Phoca vitulina* (Allen et al. 1995), for the paternity analysis. We conducted preliminary analysis using these six microsatellites on 50 grey seal males at the Molecular Genetics Laboratory at Cambridge University following the protocol of Allen et al. (1995). We analysed the remainder of the samples at the Molecular Genetics Laboratory at the National Zoological Park, Smithsonian Institution, adding an additional microsatellite locus to all seals. All 24 mother–pup pairs from 1995 and 1996 and 77 males were amplified using ³⁵S-dATP instead of ³²P-dCTP (modified from Strassmann et al. 1997).

For visualization of the microsatellites, we loaded 4 µl of the ³⁵S-labelled PCR product on a 6% denaturing polyacrylamide gel and then exposed it to autoradiograph film for 3–14 days (following protocols in Sambrook et al. 1989). M13mp18 size marker labelled with ³⁵S-dATP was run alongside the microsatellites for comparison.

Paternity Exclusion

We scored all 24 mother–offspring pairs and males at seven microsatellite loci. Population allele frequencies for

each locus (Table 1) and deviation from Hardy–Weinberg equilibrium were calculated using Genepop version 1.2 (Raymond & Rousset 1995). In one case, the pup did not match the mother's genotype for either allele at two loci. Because fostering is known to occur among grey seals on Sable Island (Perry et al. 1998), we assumed that the pup was not hers and the lack of compatibility between the two was not a result of a mutation. This pair was excluded from the paternity analysis. If a consort male did not have the paternal allele at any one locus, we excluded him as the potential father. The probability of excluding a randomly chosen male from the population was calculated for each pup using probability of exclusion equations from Weir (1990) and Chakravarti & Li (1983). The probability of exclusion for each locus, assuming Hardy–Weinberg equilibrium, was calculated following the equation in Selvin (1980), and the probability over all loci according to Chakravarti et al. (1988). In addition, we used Kinship version 1.2 (Goodnight et al. 1997) to test further the power to exclude putative fathers that were not excluded by the method described above. We determined the most likely father when one or more males could not be excluded using maximum likelihood ratios calculated with Kinship version 1.2.

RESULTS

Paternity Analysis and Behaviour

Of the 23 branded females that could be included in the paternity analysis, all consort males were excluded as the father in 10 cases (43%) based on matching the pups' genotypes to the putative fathers' genotypes. The mean

Table 2. The number of alleles, per cent heterozygosity and Hardy–Weinberg equilibrium probabilities for seven microsatellite loci and the probability of exclusion P_{ex} for each locus

Locus	Number of alleles	%Observed heterozygosity	Hardy–Weinberg equilibrium probabilities	Probability of exclusion P_{ex}
Hg 8.10	5	69.0	0.57	0.550
Hg 6.3	8	81.0	0.98	0.520
Hg 4.2	6	72.0	0.42	0.490
Hg 8.9	8	78.0	0.71	0.520
Pv 9	4	64.0	0.31	0.390
Pv 11	8	76.5	0.99	0.470
Hg 3.6	7	75.0	0.08	0.570
Combined P_{ex}	NA	NA	NA	0.993

Per cent heterozygosity and Hardy–Weinberg equilibrium were calculated using Genepop version 1.2 (Raymond & Roussett 1995).

\pm SE probability of exclusion calculated for each pup across all loci was 0.982 ± 0.005 . The probability of exclusion for each locus based on allele frequencies in the population are shown in Table 2. Our exclusion probability over all loci was 0.993 (Table 2).

In all 13 cases of females judged to have been fertilized by their consort males using the above method, the consort male was also not excluded as the father at $P < 0.05$ using the maximum likelihood ratios from Kinship version 1.2. In nine cases, the consort male was the most likely father with the greatest maximum likelihood ratio. In each of the other four cases, there was one other male that could not be excluded as the father, however, the locations of these males made it less likely that they were the father than the consort males. These males were not observed near the female during her receptive period.

We used a logistic regression analysis to consider the possible effects of female age, female location and the length of association of the consort male on ECFs. Female location was defined as either beach or inland based on the criteria described in the Methods. We considered females less than 9 years of age as ‘young’ and females greater than or equal to 9 years as ‘old’. We chose these classes because other pinniped studies have shown that female age effects are not linear but rather the greatest differences occur between females that have had only a few years (2–4) of breeding experience and older females. The youngest grey seal females to breed are 4-year-olds and all have bred for the first time by 8 years. Some females are still breeding at age 32 (personal observation).

The results from the logistic regression ($\text{CF} = 0.64 + 3.43(\text{location}) - 2.12(\text{age}) - 0.19(\text{consortship duration})$) suggest that female location affects the likelihood that a female will be fertilized by her consort male ($P < 0.02$). However, this result was in the opposite direction than that expected, with inland females having a higher rate of ECFs (70%, $N = 10$) than beach females (23%, $N = 13$). The results of female age ($P = 0.11$) and duration of consortship ($P = 0.36$) were not significant. Although female age was not significant, the low power, given the small sample size, and the relatively low P value suggest that further

research on female age and ECFs is needed. The non-significant tendency was for more ECFs among younger females. We performed univariate analyses on the effect of female location and age on the rate of ECFs and the results were similar to the logistic regression (Fisher's exact: $P = 0.04$ and $P = 0.34$, respectively).

Behaviour within the Defined Study Site

Census data

As we did not relocate the radiotagged females from 1995, we were unable to use the more detailed behavioural data from the study grid to examine possible correlations between behaviour and ECFs. However, we can use these data to investigate further the apparent correlation between female location and ECFs reported above. There was a steady decline over the breeding season in the density of females located both inland and on the beach. The decline in female density resulted from more females leaving the site, having finished lactation, than were arriving to give birth. Both inland and beach areas had a relatively constant density of males throughout the season (Fig. 1). The mean density of females on the beach was significantly less than inland (3.6 ± 0.58 versus 7.5 ± 1.32 females/1000 m^2 , $N_1 = 17$, $N_2 = 17$; Wilcoxon signed-ranks test: $Z = 3.575$, $P < 0.001$). The mean density of males on the beach was significantly higher than inland (4.0 ± 0.41 versus 2.9 ± 0.36 males/1000 m^2 , $N_1 = 17$, $N_2 = 17$; Wilcoxon signed-ranks test: $Z = 3.626$, $P < 0.001$). Females located in the beach area were exposed to more transient males than inland females (42.5 ± 5.97 versus 26.2 ± 4.16 males, $N_1 = 17$, $N_2 = 17$; t test: $t_{32} = 2.24$, $P = 0.03$). The mean number of females per male (both tenured and transient) was 0.9 ± 0.17 on the beach and 2.6 ± 0.42 inland (combined mean = 1.8 ± 0.3). This difference appears to be due to both the greater abundance of transient males along the beach and the higher density of females inland. The mean number of females per tenured male was significantly higher inland than on the beach (Fig. 2).

Despite the higher density of males on the beach and

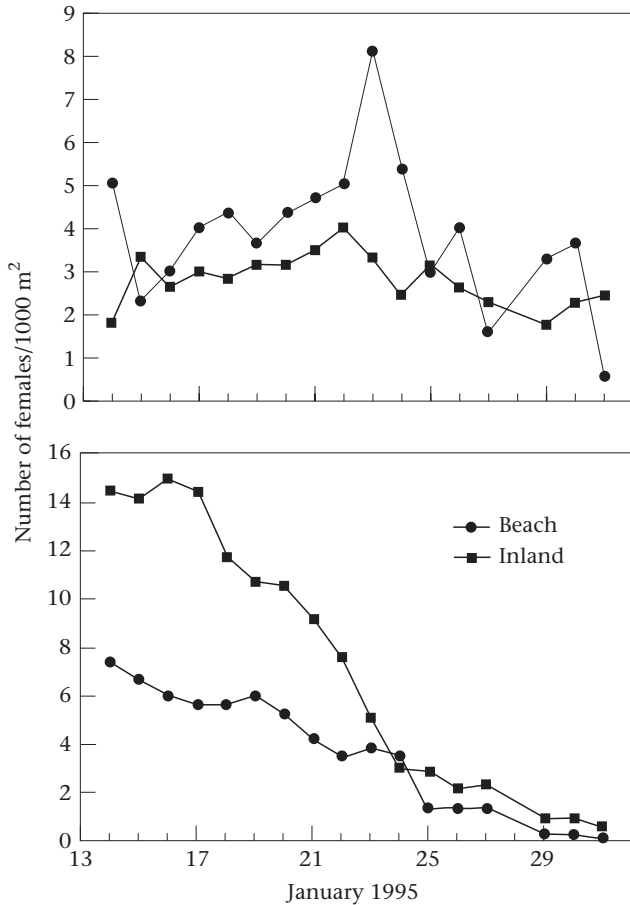


Figure 1. Density of males and females inland and on the beach during 14–31 January 1995.

the greater relative abundance of transient males, rates of male aggression did not vary between sites. The mean number of aggressive bouts/h for inland males was 4.9 ± 0.7 ($N=15$ sampling periods) compared with 5.4 ± 0.6 ($N=15$ sampling periods) for males on the beach (t test: $t_{28}=0.61$, $P=0.5$).

Female movement patterns

Female movement might attract nearby males and thus might lead to a higher probability of nonconsort matings. We examined female movement in relation to location and found no significant effect of location for either between-day (beach: 5.0 ± 0.72 m, $N=10$; inland: 4.5 ± 0.32 m, $N=21$; t test: $t_{29}=0.75$, $P=0.45$) or within-day movement patterns (beach: 1.5 ± 0.16 m, $N=11$; inland: 1.6 ± 0.11 m, $N=21$; t test: $t_{30}=0.26$, $P=0.8$).

Male–female consortships

If females are mating selectively, two possible factors they might use are the amount of time a male spends with a female or how closely he defends her. As locations of animals within the study grid were recorded five to six times each day, we could determine consortships based on male–female associations and calculate turnover rates of consort males. We found no significant difference in

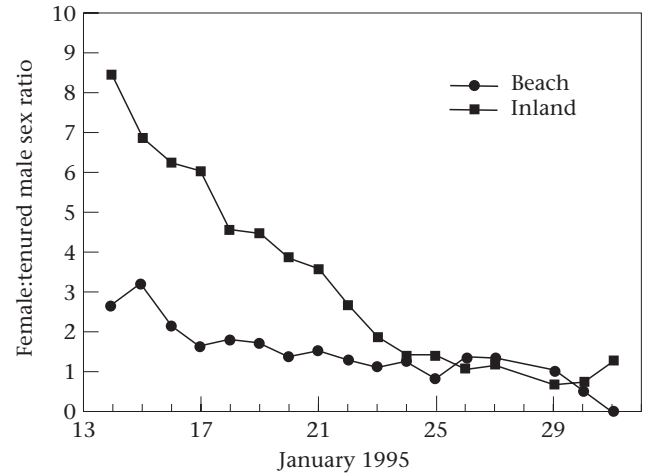


Figure 2. Female-to-tenured-male sex ratio within the defined study site during 14–31 January 1995 ($\bar{X} \pm \text{SE}$: inland = 3.3 ± 0.53 ; beach = 1.4 ± 0.17 , Wilcoxon signed-ranks test: $Z=3.13$, $N_1=17$, $N_2=17$, $P=0.002$).

mean distances between a female and her nearest male for beach and inland females (2.2 ± 0.3 m, $N=10$, versus 2.5 ± 0.3 m, $N=21$; t test: $t_{22}=0.79$, $P=0.43$). Similarly, the mean consortship duration for inland and beach females did not differ significantly (5.8 ± 0.54 days, $N=10$ versus 4.5 ± 0.48 days, $N=22$; t test: $t_{30}=1.47$, $P=0.15$). The mean turnover rate of consort males of inland and beach females did not differ (0.2 ± 0.09 males/day, $N=10$ versus 0.2 ± 0.07 males/day, $N=22$; t test: $t_{20}=0.23$, $P=0.82$).

Copulation behaviour

Fifty-three uninterrupted copulations were observed involving 26 of the 35 females within the study grid. Observations were conducted only during daylight and, therefore, undoubtedly some successful and attempted mounts were missed. Females observed copulating had a mean of 2.0 uninterrupted copulations (range 1–7) with a mean of 1.7 different males (range 1–5) and 2.3 attempted copulations (range 1–6). The first observed attempted copulation for females that had not been observed copulating previously ($N=17$) was 5 days prior to weaning. The first recorded copulation for all females ($N=26$) was 2.5 days prior to weaning.

No significant difference was found in the number of attempted copulations by consort and nonconsort males with regard to location ($G_{\text{adj}}=0.007$, $df=1$, $P=0.93$, Table 3). Nor was there a significant difference in the frequency that beach females were mounted by transient males compared to tenured, nonconsort males ($G_{\text{adj}}=1.54$, $df=1$, $P=0.21$). Beach and inland females showed no difference in the number of copulations by consort and nonconsort males ($G_{\text{adj}}=0.003$, $df=1$, $P=0.96$) or in the number of extraconsort copulations (ECCs) by tenured males and transient males ($G_{\text{adj}}=0.16$, $df=1$, $P=0.68$). The rates of ECCs are consistent with the results of the paternity analysis; beach and inland females combined had a rate of 37.7% ECCs (cf. 43% ECFs).

Table 3. Attempted and successful copulations for females in relation to female location for both consort and nonconsort males

	Consort males	Nonconsort males	
		Tenured males	Transient males
Copulation attempts			
Inland females	18 (56.3)	7 (21.8)	7 (21.8)
Beach females	17 (60.7)	2 (7.1)	9 (32.1)
Successful copulations			
Inland females	22 (61.1)	10 (27.8)	4 (11.1)
Beach females	11 (64.7)	3 (17.6)	3 (17.6)

Numbers in parentheses represent percentages of total successful and attempted copulations for females in each location.

DISCUSSION

Comparisons with Another Colony

The rate of ECFs (43%) among grey seals at Sable Island is consistent with results from a similar study at North Rona, where 36% of fertilizations were by nonconsort males (Amos et al. 1993, 1995). In both studies, consort males were not responsible for siring as many pups of focal females as was expected based on their behavioural status (cf. Anderson et al. 1975; Boness & James 1979; Anderson & Fedak 1985). The similarly high levels of ECFs at both colonies suggest that the level of polygyny in this species based on behavioural measures of copulations or attendance patterns are probably overestimates.

Although it has been suggested that habitat, topography and colony structure influences the degree of behavioural polygyny in pinnipeds (Bartholomew 1970; Stirling 1983; Anderson & Harwood 1985; Boness 1991; Le Boeuf 1991), the extent to which these factors affect the likelihood of ECFs or which males account for these extraconsort paternities is not known. The similarity in levels of ECF between Sable Island and North Rona, which differ substantially in topography and colony structure, suggest that these features are relatively unimportant within the range of variation seen. Females are less clustered at Sable Island and a single male has fewer females to defend access to at any point in time (Boness & James 1979; Anderson & Fedak 1985; this study). However, considerably more transient males roam throughout the colony at Sable Island compared with North Rona. This is probably due to the unrestricted access to inland areas provided by the extensive beach at Sable, whereas North Rona has few access points to the main breeding colony through gullies (Boness & James 1979; Amos et al. 1993, 1995).

It has been suggested for colonial avian species that once breeding densities reach the level at which most breeding individuals are surrounded by neighbours, further increases in densities of animals will not lead to higher levels of ECF (Westneat et al. 1990). This may be the case for grey seals.

Amos et al. (1993, 1995) found that ECFs could not be accounted for by established males on the top of the island, suggesting these females are fertilized by males

either in the gullies through which they must travel to get to sea, or in the water after they have departed. On Sable Island, however, females were observed to mate with both nonconsort tenured males and transient males as they were leaving or while they were still nursing their pups (Boness & James 1979; this study). Thus, both transient males and tenured males may account for ECFs at Sable Island. Unfortunately, as we were unable to relocate females from the study grid for which we had detailed behavioural data, we cannot evaluate the extent to which transient males accounted for ECFs at Sable Island. The lack of higher levels of ECF by females on the beach, where more transient males occur, might suggest the majority of ECFs at Sable Island were by neighbouring tenured males. This would be consistent with the information on ECCs (Boness & James 1979; this study).

Location and Age Effects

There are two possible explanations for the greater rate of ECFs by inland females. First, the greater ratio of females to tenured males in inland areas provides a greater opportunity for nonconsort males to obtain copulations and secondly, inland females must travel further to reach the ocean. Copulations obtained by nearby tenured males or transient males may occur when the consort male is copulating with another receptive female, or is otherwise occupied defending his females from intruding males. Although we did not collect data that would allow us to determine which ECCs occurred while the consort male was preoccupied, it is plausible that these ECCs would occur more often in situations where males are guarding more females. Results from the few females for which we have genetic and behaviour data suggest that this may occur. In each of the three cases, we were unable to exclude the neighbouring tenured male as the father.

Concerning the second explanation for higher ECFs by inland females, as females depart the colony after weaning their pup, they are often approached by males (Boness & James 1979; Boness et al. 1982). Depending on how and where a female travels, she may attract upwards of 10–20 neighbouring tenured and transient males. Although we do not have the data on the proportion of ECFs or ECCs that occur during departure, it is reasonable to expect that females travelling greater distances to reach the water will attract more attention than those females near the shoreline.

Female age and experience are known to be factors in aspects of the reproductive behaviour and success of females in a variety of species (Reiter et al. 1981; Afton 1985; Morton et al. 1990; Gowaty & Bridges 1991; Bowen et al. 1994). We were unable to detect a significant age effect. However, given the low probability of significance ($P=0.11$), despite the lack of power to detect an age effect, we suggest further research in this direction is warranted to follow up on the weak tendency for younger females to have higher rates of ECFs.

Possible Benefits to Females

We did not set out directly to test the possible benefits of ECFs to females. Nevertheless, our results, in

conjunction with prior studies of the reproductive behaviour of grey seals, provide some insights into whether female grey seals might be gaining benefits. Hypotheses concerned with material or immediate benefits (e.g. increased food resources: Cronin & Sherman 1976; Gray 1997b; increased paternal care of young: Burke et al. 1989; Birkhead & Møller 1992; Wagner et al. 1996) would not apply to grey seals because females fast throughout the breeding period and there is no evidence to suggest that males in any way contribute to the care of offspring. However, it is possible that female grey seals might gain genetically from ECFs.

Of the three hypotheses most often cited to explain how ECFs might provide females with genetic benefits (i.e. being fertilized by a male with a higher genetic quality, maximizing genetic diversity among offspring, and ensuring that eggs are fertilized; Westneat et al. 1990; Birkhead & Møller 1992; Lifjeld 1994; Gray 1997a), maximizing genetic diversity can be excluded because grey seal females, like all pinnipeds, give birth to only a single offspring each breeding event. Our data seem inconsistent with the other two hypotheses. We see no reason why females located on the beach should be less likely to seek ECFs than those inland if females were either attempting to ensure fertilization by mating with multiple males or trying to be fertilized by a genetically better mate. Also, if females seek ECFs to improve the genetic quality of their mate, we might have expected to find a negative relationship between ECFs and length of time the consort male had been in attendance of the female. However, if females were able to assess male quality rapidly, then length of tenure might not be expected to be a factor. If there were an age (or experience) component to gaining genetic benefits, we would expect older females to have higher rates of ECFs. Although we can make no conclusive claim based on our analysis of age, because of the low statistical power, we found no significant difference between the rates of younger and older females and the slight difference that existed was the opposite of what was expected.

While more targeted studies are clearly needed, it seems most likely that ECFs in grey seal females at Sable Island are a product of either forced copulations by aggressive and highly sexually motivated males and/or a result of females submitting to copulation attempts to avoid injury (see Mesnick & LeBoeuf 1991). This best fits the finding of inland females having a higher rate of ECF than beach females.

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