

Female strategies of harassment reduction in southern elephant seals

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Female southern elephant seals are expected to adopt behaviours that reduce the costs of male harassment. We studied the strategies and tactics of harassment reduction in two populations, at Punta Delgada (Valdés Peninsula, Argentina) and at Sea Lion Island (Falkland Islands) during five breeding seasons in all. Females synchronized their breeding activities to reduce harassment risk, and rarely bred alone to reduce the likelihood of encounters with subadult males. Females showed a clear preference for larger harems, that guaranteed a reduced harassment risk: movements between arrival on land and parturition were mostly from smaller to larger harems, and the likelihood of abandonment was lower for large harems. Females protested against approaching males in the vast majority of interactions, regardless of the social context and the status of the interacting male, but protest varied with female breeding status and male phenotype. Frequency of protest of individual females decreased linearly from the beginning of oestrus to departure to sea. Interactions with mature males were less protested. The frequency of protest linearly decreased with increase in age class, and mating attempts by males of higher status and dominance rank were less often protested. Most of this variation with male phenotype, however, was due to the higher probability of older and more dominant males to interact with oestrus females that had an intrinsically lower tendency to protest. Protest variation in relation to male phenotype was more parsimoniously explained as a consequence of differential access of males to oestrus females rather than of female selectivity. Protests had a role in disruption of mating attempts, although the phenotype of interactors was more important: adult, large and dominant males disrupted interactions regardless of incitation by female protest.

KEY WORDS: harassment, mating systems, synchronized breeding, harems, female protest, mating disruption, "trade sex for protection" hypothesis, southern elephant seal, *Mirounga leonina*.

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INTRODUCTION

Harassment (for definition see GALIMBERTI et al. 2000a) may entail significant costs for females (CLUTTON-BROCK & PARKER 1995) and may reduce their breeding success and survival (LE BOEUF & MESNICK 1990). Harassment is widespread in mammals (SMUTS & SMUTS 1993) and female behavioural responses to harassment are quite variable, ranging from plain flight (primates: SMUTS & SMUTS 1993; *Equus* spp.: BERGER 1986) to acceptance of mating (*Ovis canadensis*: HOGG 1984; *Mirounga angustirostris*: MESNICK & LE BOEUF 1991). Aggressive retaliation by females is rare in mammals (SMUTS & SMUTS 1993, but see BERGER 1986 for wild horses). Males are usually the larger sex and they often have secondary sexual characters to be used as weapons in agonistic encounters: hence, female aggression may result in a very dangerous reaction by male (PACKER & PUSEY 1983).

Females are expected to adopt strategies (= global, long term behaviours) and tactics (= context specific, short term behaviours) to reduce the likelihood of interaction with harassing males and the risk of harassment (SMUTS & SMUTS 1993). They may concentrate breeding in time and space, to enjoy a dilution effect on harassment rate (BONESS et al. 1995). They may breed in groups under the control of few dominant males, that should be able to keep away other males (TRILLMICH & TRILLMICH 1984). When not able to escape from harassing males, they may tune their behavioural reaction to mating attempts to reduce risk of physical damage ("trade sex for protection" hypothesis: MESNICK & LE BOEUF 1991, LOVELL-MANSBRIDGE & BIRKHEAD 1998). They may also show a suite of behaviours to enhance conspicuousness of the mating attempt to neighbouring males, and to incite their intervention ("female incitation of male competition" hypothesis: COX & LE BOEUF 1977).

Southern elephant seals (*Mirounga leonina*, SES hereafter) are a good subject for tests of hypotheses concerning the female reaction to harassment. Harassment is frequent in this species, and although long term costs seem small, short term effects on female time and energy budgets are significant (GALIMBERTI et al. 2000a). In the northern elephant seal (*M. angustirostris*) females seem to mold their behavioural reaction in such a way to minimize the costs of harassment, in particular by a context specific fine tuning of protest against male approaches, and by facilitation of copulations (COX & LE BOEUF 1977, MESNICK & LE BOEUF 1991). In this paper, we present data obtained from two local populations of SESs, Punta Delgada (Valdés Peninsula, Argentina; DEL hereafter) and Sea Lion Island (Falkland Islands; SLI hereafter), that have a different basal harassment risk due to differ-

ences in demography and sociology (GALIMBERTI et al. 2000a). We analyze the role of synchronized breeding, compare harassment between harem females and isolated females, evaluate preference of females for harems of different size, describe female reaction to male approaches, and evaluate the role of disruption of mating couples and female incitation of male competition.

METHODS

Details about study populations, behavioural observation protocols, definitions, and statistics were presented in a companion paper (GALIMBERTI et al. 2000a). We outline here only specific aspects of methodology not covered in the previous paper.

We estimated synchronization of breeding using dates of parturition and the begin of oestrus, calculated from serial records of individually marked females. We recorded every observed parturition (80-100 per year), and, thanks to the intensive marking and accurate censuses of breeding areas (GALIMBERTI et al. 2000a), we were able to estimate parturition time with a 12 hr precision for most non-observed birth. Distribution of observed and estimated parturition dates were equal. In all, we collected 354-429 parturition dates per year. We estimated the beginning of oestrus from parturition dates by applying a standard partum-oestrus delay of 20 days (GALIMBERTI & BOITANI 1999, see also CAMPAGNA et al. 1993).

To evaluate female preference for harems of different size, we analyzed both movements between harems recorded during observation periods (see GALIMBERTI et al. 2000a), and movements estimated from serial records of marked females. Every day during censuses we identified 75-100% of the total number of females on land using tags and dye marks (GALIMBERTI et al. 2000a), and hence we were able to accurately record most harem shifts.

We define female *protest* as the series of avoidance/aggressive behaviours that SES females show when approached by males, including move away, sand flipping, body slams, swinging of hind flippers, bites on the neck and trunk of the male, and emission of croaking vocalizations. We classified protest in three level of intensity, low (L), medium (M), and high (H) using occurrence and length of different protest modules. Low protest involved only vocalizations and/or short distance movements, high protest involved direct aggression (biting of neck and trunk), repeated shaking of the body and rear flippers, long distance movements; all other episodes were classified as medium protest.

Dominance hierarchies in southern elephant seals are well defined and almost stable during each breeding season (GALIMBERTI 1995). Hence, we define *dominance rank* of a male as the position occupied by the male in the dominance hierarchy as calculated from the results of all agonistic interactions recorded. We applied the iterative method of Gibson & Guinness (GGI; GIBSON & GUINNESS 1980, GALIMBERTI 1995) to wins/losses matrices to calculate a population wide index of dominance.

When statistical hypothesis were directional because of the natural ordering of groups (e.g. age class), we tested differences between groups with exact Cochran-Armitage test with equally spaced scores (= binomial trend test; ARMITAGE 1955, METHA & PATEL 1992) for $2 \times C$ contingency tables, and exact or randomization Jonckheere-Terpstra test (METHA & PATEL 1992) for $R \times C$ contingency tables and continuous variables. In these tests we sometimes corrected effects for a main categorical covariate (e.g. age class) using stratification (METHA & PATEL 1992). Cochran-Armitage test and Jonckheere-Terpstra test were run in StatXact Turbo 2.11 (Cytel Software Corporation). We tested hypotheses on multiway contingency tables using log-linear models. When one of the factors in the table was clearly a dependent variable we employed logit models (AGRESTI 1990). In both cases, significance of individual factors was tested by comparing the likelihood-ratio of the model with and without the specific factor (NORUSIS 1994). We run logit models and logistic regression in SPSS 6.1 for Power Macintosh (SPSS Inc.).

RESULTS

*Strategies of harassment reduction**Do females synchronize breeding to reduce exposure to harassing males?*

Harassment depends on the breeding sex ratio, and synchronized breeding may effectively reduce the risk of interaction with harassing males (GALIMBERTI et al. 2000a). In both studied populations the timing of breeding is very regular across years (DEL: CAMPAGNA et al. 1993; SLI: GALIMBERTI & BOITANI 1999), and the median date of oestrus was almost constant (28-10 in 1995, and 29-10 in 1996 and 1997; MAD = 6 days for all years). Although the length of the period in which at least one female is in oestrus was about 52 days (1995: 55 days; 1996: 52 days; 1997: 50 days), most females came into oestrus during a 3 weeks period, i.e. in about 1/4 of the entire length of the breeding season (in different years 69.8-73.6% of 295-428 females began oestrus in a 3 week period, and 88.4-91.5% in a 4 week). The same result was found considering the total number of females actually in oestrus during each day (73.6-76.0% in 3 weeks and 87.2-90.3% in 4). The distribution of oestrus

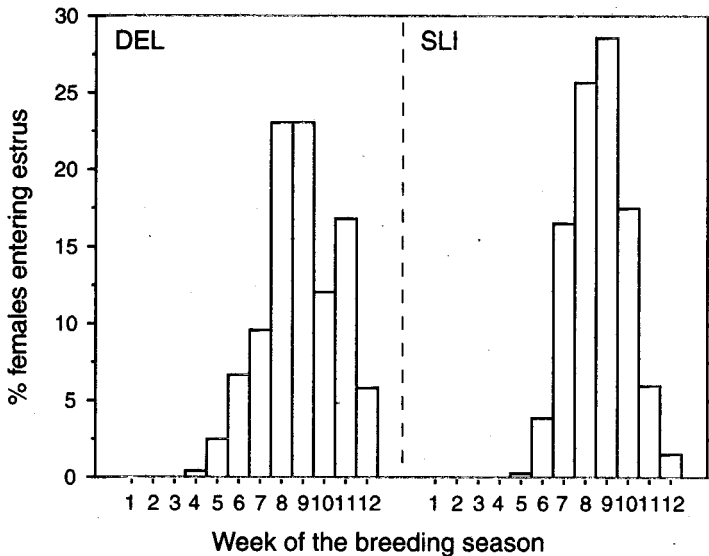


Fig. 1. — Distribution of percentages of females entering oestrus, 1994 for DEL and 1996 randomly chosen to represent SLI (kurtosis_{DEL} = - 0.96, kurtosis_{SLI} = - 0.83; breeding processes in elephant seals are well described by gaussian models, GALIMBERTI & BOITANI 1999, hence synchronization may be described by index of kurtosis of distribution of oestrus). Breeding was slightly less synchronized at DEL, with a longer span with at least one female in oestrus (70 days in 1994) and less concentration of oestrus (58.1%, n = 239 females in 3 weeks; 67.8% in 4; comparison of weekly frequencies, Exact likelihood ratio test: G = 38.5, P = 0.0000). Day of begin of oestrus of individual marked females was calculated from observed parturition date by adding the mean span in days between parturition and oestrus (GALIMBERTI & BOITANI 1999).

across the season was homogeneous at SLI between different seasons (Exact likelihood ratio test: $G = 4.79$, $P = 0.57$), but breeding was less synchronized at DEL (Fig. 1).

We compared geographic variation in the synchronization of breeding using the distribution of births, instead of oestrus, because this information was more readily available. For Valdés Peninsula, CAMPAGNA et al. (1993) report that 60% of the pups are born during the 3 weeks of the maximum concentration of births, while on Sea Lion Island about 75% (73.0% in 1995, 76.8% in 1996) of pups are born during 3 weeks and about 85% (84.7% in 1995 and 86.9% in 1996) during 4 weeks. Both McCANN (1985) for South Georgia and CARRICK et al. (1962) for Macquarie Island report that about 80% of the pups are born in about 3 weeks. Notwithstanding geographic variation, high synchronization of breeding is typical of all elephant seal populations.

Do females show any harem size related preference?

Do females move between harems? Breeding in large harems guarantees a reduced risk of harassment (GALIMBERTI et al. 2000a). We evaluated harem size preference from movements of females that changed harem between arrival and parturition. Twenty one percent of females ($n = 1151$ marked females) changed harem; median length in days between settlement in the first harem and settlement in the parturition harem was 3 days (MAD = 2, $n = 247$). Most shifting females (89.7%, $n = 247$) went directly to the parturition harem, while the rest visited 1-4 harems (median = 1 harem) before settling for the parturition, with a median length of residency in the transfer harems of 1.6 days. No differences in tendency to shift were found between females of different size classes (S = 17.6% of $n = 142$ females, M = 22.5% of 391, L = 22.4% of 576; Exact likelihood ratio test: $G = 1.77$; $P = 0.41$).

Do females choose larger harems? The likelihood of abandonment of a harem before parturition had a negative correlation with harem size and a positive one with rate of harassment (Fig. 2); small harems, with higher per capita harassment rate, were abandoned more often. In a sample of 86 movements between harems observed from departure to arrival, females usually shifted to larger harems (*mean diff. in size* = 13.4 females; Wilcoxon signed rank test: $z = -3.37$, $P = 0.0008$). We then considered all harem shift as detected from daily census. Females moved to larger harems in 63.5% of cases ($n = 301$) and harems at the end of the shift were larger than harems at the beginning (*mean diff. in size* = 10.1 females; Wilcoxon signed rank test: $z = -4.12$, $P < 0.0001$). These movements were in many cases partial movements, i.e. the same female moved again before parturition. Definitive shifts between arrival and parturition were tested using serial records of marked females. In a sample of 205 females that settled in one harem at arrival and then moved to another harem for parturition, 70.0% shifted to a larger harem; mean difference in size between harem of arrival and harem of parturition was 24.3 females (Wilcoxon signed rank test: $z = -8.28$, $P < 0.0001$). This shift towards harems larger at the moment of the movement implied a shift toward harems which also had a larger size at peak haul out (*mean diff.* = 31.8; Wilcoxon signed rank test: $z = -9.10$, $P < 0.0001$).

Do shift to larger harems affect the likelihood of harassment? Destination harems had an higher number of associated males than origin harems at the

moment of the shift (*mean diff.* = 0.31; Wilcoxon signed rank test: $z = 2.78$, $P = 0.0060$); this effect was due to the correlation between harem size and number of associated males (GALIMBERTI et al. 2000a). The increase in number of associated males due to harem shift did not result in an increase of harassment rate (*mean diff.* = 0.006; Wilcoxon signed rank test: $z = -1.41$, $P > 0.15$) due to the dilution effect of the increase in harem size (GALIMBERTI et al. 2000a).

In all, females frequently changed harem between arrival and parturition and they showed a clear preference for larger harems, that guaranteed a lower harassment rate, notwithstanding the increase in number of peripheral males.

Do female choose specific harem holders?

The capability of harems holders to provide protection against harassing males should be related to harem holder (HH) phenotype. Older and bigger males

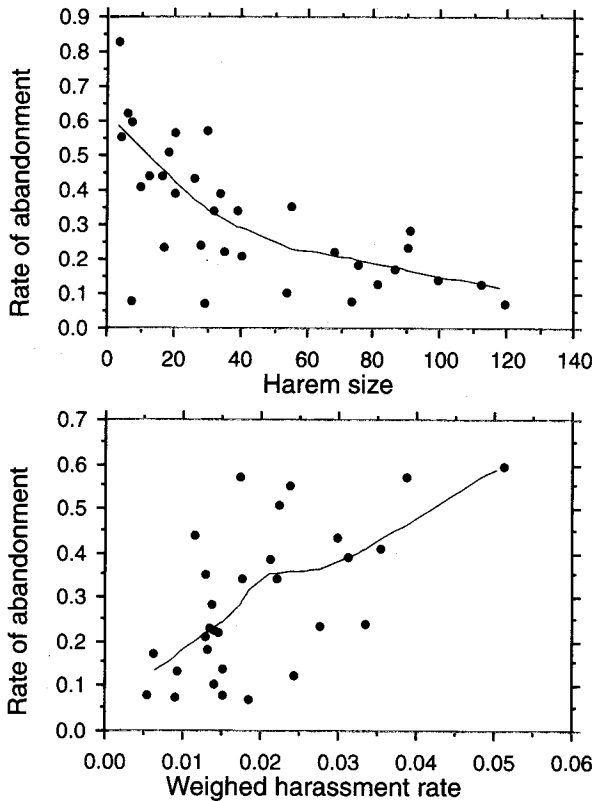


Fig. 2. — Rate of abandonment of harems (proportion of females leaving the harem) on harem size (number of females at peak; Pearson's correlation coefficient, with randomization test: $r = -0.659$, $n = 33$ harems, $P_{10000} = 0.0001$) and weighed harassment rate (mean harassment rate per observation period; $r = 0.615$; $n = 30$ harems, one outlier excluded; $P_{10000} = 0.0002$). Line is LOWESS smoother (tension = 66% of point; TREXLER & TRAVIS 1993).

are better able to control their harems (GALIMBERTI 1995, MODIG 1996). Hence, females may reduce harassment risk by choosing powerful HH. Due to the prevalence of adults between HH, we were not able to effectively test the role of holder age in change of harem by individual females. In 93.1% of 260 changes of harem, the holder of both the source harem and the destination harem were adults. In the remaining changes ($n = 18$) in 77.8% of cases an older male was holder of the destination harem. On the other side, there was variation in size class of HH males. In a sample of 258 changes, the holder of the destination harem was the same size as the holder of the source harem in 32.5% of cases, larger in 47.7% and smaller in 19.8%. We calculated for each year the expected proportions of movement towards smaller and larger holders from year specific size class distribution of HH. The observed proportion of movements towards larger HH was almost equal to the expected in 1995 (0.620 vs 0.625, $n = 79$; Binomial test: $P = 0.48$), slightly smaller than expected in 1996 (0.725 vs 0.850, $n = 69$; Binomial test: $P = 0.003$), and slightly larger than expected in 1997 (0.846 vs 0.725, $n = 26$; Binomial test: $P = 0.13$). In all, no clear trend of movements towards larger males was apparent.

Female behavioural reaction to mating attempts

How do female react to male approaches?

Females protested most interactions in a more or less vigorous fashion (82.4%, $n = 4476$ interactions); in 31.9% of 3299 protested interactions the level of protest was classified as high. Females tried to move away from the male in 52% of 3071 interactions, emitted vocalizations (see BARTHOLOMEW & COLLIAS 1962) in 83.5% of 3102, bit the male in 5.1% of 3058, and resisted to the male approach with movements of the body (mainly shaking of the hindquarters, as in northern elephant seal: LE BOEUF 1972) in 80.1% of 1128. The structural analysis of behavioural sequences confirmed that direct aggression occurred only in few cases: plain move away represented 11.6% of observed behavioural modules ($n = 3670$), aggressive vocalization 17.6%, flipping (which is a stress associated behaviour: LEWIS & CAMPAGNA 1995) 0.76%, shaking of the body 5.8%, bite and strokes 0.3%.

There was a clear variation in the proportion of protested interactions during the breeding season. During the pre-breeding and pre-peak phases of the season a larger proportion of interactions were protested (97.1% of 442 interactions and 89.3% of 905 interactions) than during the peak and post-peak phases (78.4%, $n = 2814$ and 77.1%, $n = 315$).

Is female protest affected by harem size?

We found a quite large variation in the proportion of protested interactions between harems (from 61.3%, $n = 186$ interactions to 96.9%, $n = 260$). We tested the effect of harem size on protest by comparing the frequency of protested interactions between harems of above median size (large harems) and below (small harems). If protest is mostly a tactic to reduce harassment by secondary males (as in northern elephant seals, COX & LE BOEUF 1977), protest should be lower in small harems, which usually had few or no associated secondary males (GALIMBERTI et al.

2000a). Contrary to this expectation, females in small harem protested more frequently than females in large harems (91.8%, $n = 716$ interactions vs 83.8%, $n = 3209$; Fisher's exact test: $P = 0.0000$). Females in small harems were frequently approached by the harem holders also when they were clearly anoestrus. The level of protest was homogeneous between large and small harems (Exact likelihood ratio test: $G = 0.2048$, $P = 0.91$). We tested the effect of harem size on protest also by logistic regression, and we found a negative relationship between the likelihood of protest and total harems size [$b = -0.0113$, $se(b) = 0.0014$; LR test: $\chi^2_1 = 67.0$, $P < 0.0001$].

Do female protests affect mating efficiency?

Is facilitation of intromission frequent? Females protested against males during most approaches, and we never observed female solicitation of copulation, but, on the other hand, sometimes females facilitate intromission by opening their hind flippers, elevating the perineum, and adopting a lordotic posture (as in northern elephant seal: COX & LE BOEUF 1977). Facilitation was observed in 1.35% of cases ($n = 3177$ interactions). Almost all facilitated matings involved an adult male (97.7%, $n = 43$).

Do protests affect the likelihood of intromission? The occurrence of protest was lower for actual matings than for interactions that did not lead to intromission (51.7%, $n = 998$ vs 96.0%, $n = 3169$; Fisher's exact test: $P = 0.0000$). This was true for both adult (51.4%, $n = 951$ vs 95.9%, $n = 2779$; Fisher's exact test: $P = 0.0000$) and subadult males (57.4%, $n = 47$ vs 96.4%, $n = 372$; Fisher's exact test: $P = 0.0000$).

Protest occurred in 96.2% of unsuccessful attempts ($n = 2673$) of harem holders and in 52.1% of successful ones ($n = 940$; Fisher's exact test: $P = 0.0000$). The likelihood of ending with an intromission was much lower for protested approaches than for non-protested ones (HH: 22.3% of 2193 protested approaches vs 85.2% of 677 non-protested, Fisher's exact test: $P = 0.0000$; non harem holders, NHH: 9.5%, $n = 274$ vs 68.2%, $n = 44$, $P = 0.0000$).

Readiness to copulate depends also on the breeding status of the female (see below); a smaller proportion of interactions with anoestrus females resulted in intromission (11.6%, $n = 4767$ interactions with anoestrus females vs 74.1%, $n = 1092$ interactions with oestrus females; Fisher's exact test: $P = 0.0000$). We evaluated the joint effect of female status and protest by entering the two variables in a logit model with success in intromission as the dependent variable; as separate factors, both females status and protest did not fully explain the variation in intromission success, but the dispersion explained by female status was larger than the variation explained by protest (entropy due to model: 690.2 vs 502.7).

Is length of preliminaries influenced by protest? We expected protest to increase the time necessary to reach intromission. Median time in seconds to reach intromission (first intromission in cases with more than one intromission per mating bout) was lower for non-protested interactions than for protested ones (67 vs 124 sec; Mann-Whitney test: $U' = 56306.5$, $n_{\text{Prot.}} = 259$, $n_{\text{Non Prot.}} = 290$, $z = -8.041$, $P < 0.0001$). For adult males median time in seconds to reach intromission was lower for non-protested interactions than for protested ones (66 vs 124.5 sec; $U' = 49316$, $n_{\text{Prot.}} = 244$, $n_{\text{Non prot.}} = 272$, $z = -8.1371$, $P < 0.0001$). The same was true for subadult males but the difference was not significant. For HH males median time in seconds to reach intromission was lower for non protested interactions than for

protested ones (70 vs 122 sec; Mann-Whitney test: $U' = 50575$, $n_{\text{Prot.}} = 241$, $n_{\text{Non prot.}} = 281$, $z = -7.245$, $P < 0.0001$). The same was true for non-holders but the difference was again not significant.

Do females protest change with female breeding status?

Do oestrus females protest less frequently? Anoestrus females protested a larger proportion of interactions than oestrus females (95.5%, $n = 3283$ vs 46.0%, $n = 846$; Fisher's exact test: $P = 0.0000$; see GALIMBERTI et al. (2000a) for oestrus definition criteria). For anoestrus females protest was usually medium (51.6%, $n = 2760$) or high (36.0%), while for oestrus females protest was usually low (58.5%, $n = 386$); distribution of level of protest between the two classes of females was different (Exact likelihood ratio test: $G = 400.2$, $P = 0.0000$). Suckling females protested heavily more frequently (37.5%, $n = 2287$) than both pregnant (29.0%, $n = 424$; Fisher exact test, Bonferroni corrected: $P = 0.0004$) and oestrus (9.6%, $n = 386$; $P = 0.0000$) females.

Is protest during day of departure particularly low? From results obtained in the northern species (COX & LE BOUEF 1977), we expected females to suffer a particularly high risk of harassment and to strongly reduce the level of protest during the day of departure to sea, in which they are particularly exposed to non holder males. There was a clear increase in harassment risk for marked females from day 5 before departure to day 1 before departure, but, contrary to expectations, there was a slight decrease the day of the departure (Fig. 3). There was a clear decrease

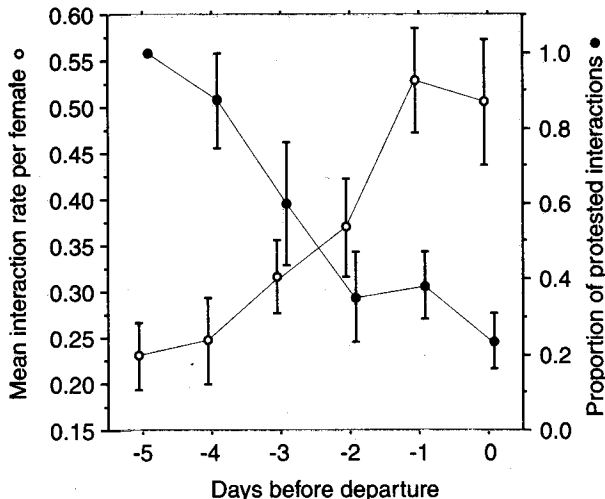


Fig. 3. — Number of interactions per observation period and proportion of protested interactions from day 5 before departure to day of the departure. Mean daily values of marked females (open circles, interaction rate, Repeated measure ANOVA on log transformed data: $F_{5,204} = 7.803$, $P < 0.0001$; filled circles, proportion protested, Repeated measure ANOVA, with randomization, on arcsin transformed proportions: $F_{5,99} = 5.19$, $P = 0.0003$).

in proportion of interactions protested by individual females from day 5 before departure to the day of the departure (Fig. 3), but, again contrary to expectation, this decrease was a gradual and almost linear process, without a dramatic change during the day of the departure.

Are the last copulations of individual females non-protested? The last copulations of individual females usually happened at the harem periphery before departure, or during the departure phase. Hence, last copulations were an ideal subject to test the hypothesis of protest reduction as an anti-harassment tactic, in particular against non-holder males. We expected last copulations to be non-protested in most cases, in particular when NHH were involved.

To standardize differences in the basal tendency to protest of different females, we compared the first and last copulations of marked females. We found a notable reduction in the frequency of protest between first and last copulations both when the involved male was adult (35.2% of 182 last copulations were protested vs 53.4% of 579 first copulations; Fisher's exact test: $P = 0.0000$) and subadult (41.6%, $n = 12$ vs 71.4%, $n = 28$; Fisher's exact test: $P = 0.09$; power analysis: effect size = 0.28; $1-\beta = 0.43$). The reduction in proportion of protested copulations was larger for subadults (-29.8% subadults vs -18.2% for adults), but odds ratio of protest of last versus first copulations was homogeneous between the two age groups (Exact Zelen test for homogeneity: Zelen statistics = 0.2326, $P = 0.72$). There was a reduction in the frequency of protest between first and last copulations for HH (34.3% of 181 last copulations were protested vs 54.5% of 584 first copulations; Fisher's exact test: $P = 0.0000$). On the contrary for NHH, last copulations were protested in a slightly higher percentage of cases (53.8%, $n = 13$ vs 47.8%, $n = 23$; Fisher's exact test: $P = 1$; note the very small sample size; power analysis: effect size = 0.06; $1-\beta = 0.06$).

Protest of first copulation was not particularly high. At SLI, 54.2% of first copulations ($n = 607$) were protested; most often (55.1%, $n = 312$) protest during these copulations was low. The percentage of protested first copulations was not different than the percentage of protested second or successive copulations (54.2%, $n = 607$ vs 51.7%, $n = 998$; Fisher's exact test: $P = 0.35$); the distribution of levels of protest was homogeneous between first copulations and the rest of copulations (Exact likelihood ratio test: $G = 1.448$, $P = 0.50$).

In all, according to expectations, protest of each individual female decreased from first to last copulation, but first copulations as a whole were not particularly protested; hence, this reduction seems the result of a process in which females become accustomed to male approaches, and the most important factor here seems the individual variation in the basal tendency to protest. We found scarce evidence of a specific reduction of protest during last copulations with marginal males: reduction was homogeneous between males age classes, and we found a slight increase of protest were NHH were involved.

Is female protest tuned to male phenotype?

Age class. A higher percentage of interactions was protested for subadult males than for adults (92.1% of 433 interactions vs 84.6% of 3732; Fisher's exact test: $P = 0.0000$); although we found a significant variation in the proportion of protested interactions between age classes, differences were small, the trend of decrease with age was not completely clear, and it depended strongly on the pooling of

females of different breeding status (Fig. 4). The trend was more apparent when comparing subadults pooled in two classes based on physiological maturity (pre-breeding subadults: 100% protested, $n = 46$; breeding subadults: 91.2%, $n = 387$; Exact Cochran-Armitage test: *standardized trend statistic* = -4.448 ; $P = 0.0000$). We found no difference in the proportion of interactions with medium level of protest between adult and subadult males (49.3%, $n = 1395$ vs 49.4%, $n = 170$).

Breeding experience. The effect of male experience was tested by comparing males who held a harem during the previous breeding season (*experienced males*) with males who did not (*inexperienced males*). Interactions with inexperienced males were protested more often (89.8%, $n = 1328$ vs 85.1%, $n = 1959$; Fisher's exact test: $P = 0.0000$), however caution is needed in interpreting this finding due to the very small effect size and the very large samples.

Male status and dominance rank. The frequency of protest was slightly lower for alpha males than for non-alpha males (81.6% of 3718 interactions vs 86.4% of 745; Fisher's exact test: $P = 0.0015$). Differences in the frequency of protest directed towards males of different status was large (Likelihood ratio test with Monte Carlo sampling: $P = 0.0005$), and examination of residuals suggested that secondary males associated with harems had a higher proportion of protested interactions. This was confirmed by testing peripheral plus marginal males vs other males (90.5%, $n = 346$ vs 81.8%, $n = 4030$; Fisher's exact test: $P = 0.0000$).

We evaluated the effect of dominance rank, as measured by GGI, on likelihood of protest by logistic regression: the regression coefficient was negative [$b = -6.067$, $se(b) = 0.795$; LR test: $G_1 = 76.45$, $P < 0.0001$], hence an increase in the rank of the male reduced the likelihood of protest by the female.

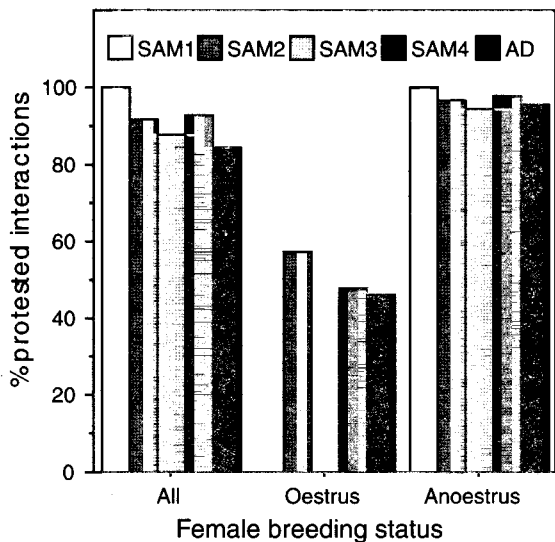


Fig. 4. — Percentage of protested interactions by male age class (SAM1 to AD) for all interactions (Exact Cochran-Armitage test: *standardized trend statistic* = -4.027 ; $P = 0.0001$), interactions with oestrus females only (*standardized trend statistic* = 0.8748 ; $P = 0.40$), and interactions with anoestrus females only (*standardized trend statistic* = -1.342 ; $P = 0.19$).

In all, some of the observed variation of female protest was related to male phenotype. In particular, females protested less when approached by older, more experienced males, with higher status and dominance rank, but in most cases the effect size was small, and trends were not completely clear.

Is male phenotype the most important determinant of protest?

The reduced percentage of protested interactions for adult, dominant males could be simply a by product of their likelihood to interact with oestrus females, that had a lower tendency to protest. Adult males interacted more with oestrus females than did subadults males (15.4%, $n = 7393$ vs 5.1%, $n = 1133$; Fisher's exact test: $P = 0.0000$). Considering oestrus females only, the proportion of protested interactions was, contrary to expectation, higher for adult males, although the difference was slight (46.2%, $n = 816$ vs 38.9%, $n = 36$; Fisher's exact test: $P = 0.50$; note the extreme difference in size of samples). We entered protest as dependent and adulthood and oestrus state as independent variables in a logit model. The most parsimonious model included only oestrus state (fit of the whole model, LR test: $G_2 = 3.606$, $P = 0.16$) and the inclusion of adulthood resulted in a decline of fitting (improvement in the fitting, LR test: $G_1 = 3.301$, $P = 0.70$; negligible increase in entropy explained by the model).

As a better context to test pure female tendency to protest, we considered only uninterrupted mating attempts during which the male was actually able to touch the female. There was only a slight difference in the percentage of protested interactions between subadults and adults (81.1%, $n = 2325$ vs 86.2%, $n = 167$; Fisher's exact test: $P = 0.12$), and no clear trend of decrease with age (e.g. 88.5%, $n = 78$ for SAM4 and 80.0%, $n = 60$ for SAM3; Exact Cochran-Armitage test: *standardized trend statistic* = - 1.619; $P = 0.11$). We then considered only non-disrupted mating attempts with intromission longer than 60 sec. Copulations with subadults were protested in only a slightly larger proportion of cases (55.0%, $n = 40$ vs 52.4%, $n = 767$; Fisher's exact test: $P = 0.87$) and there was no clear trend of decrease in protest between subadults of different age classes (in fact, the proportion of protested interactions was higher for SAM 4 than for SAM3: 61.9%, $n = 21$ vs 33.3%, $n = 12$; Exact Cochran-Armitage test: *standardized trend statistic* = 0.1239; $P = 1$).

In conclusion, although females tended to protest regardless of the interactor, they also had a small tendency to protest more during approaches of subadult, inexperienced males, but the bulk of this effect was due to the lower likelihood of secondary males to interact with oestrus females. Hence, the apparent modulation of protest on male phenotype is better explained as a result of phenotype-limited opportunities to interact with receptive females (that depend on the male dominance system), than as a result of an active female preference for specific males.

Mating disruption and female protest

The reaction of the female to male approaches may have a special role in disruption of mating couples, as suggested for the northern elephant seals (Cox & LE BOEUF 1977). Hence, we carefully analyzed the effect of protest on likelihood of disruption.

Is disruption of mating couples frequent and homogeneous between populations?

Reproductive interactions were disrupted by another male in 11.5% of cases ($n = 8923$). The likelihood of interruption of approaches and mating attempts was higher at PD (17.5%, $n = 2656$ interactions vs 8.9%, $n = 6267$; Fisher's exact test: $P = 0.0000$). The rate of disruption was lower for actual copulations than for mating attempts without intromission both at DEL (5.6%, $n = 834$ vs 29.5%, $n = 1057$; Fisher's exact test: $P = 0.0000$) and SLI (1.9%, $n = 963$ vs 9.7%, $n = 3211$; Fisher's exact test: $P = 0.0000$). This difference is in accordance with the results from South Georgia, although there disruption is more frequent (39% of approaches, and 4.5% of actual copulations; McCANN 1981).

At DEL, we found a gradual trend of a decrease in the proportion of interrupted interactions with the increase in the likelihood of intromission (from approaches, 30.5%, $n = 946$; to mounts, 20.7%, $n = 111$; to actual copulations, 5.6%, $n = 834$; Exact Cochran-Armitage test: *standardized trend statistic* = - 13.36; $P = 0.0000$); this trend was not apparent on SLI where the reduction in disruption was abrupt. At DEL we found a 72.9% decrease in disruption between mounts and copulations, while on SLI the decrease was 95.9%. These results confirmed our general impression that SLI males were much more efficient in controlling the activity of other males.

Does male phenotype affect disruption?

The likelihood of disruption should depend firstly on the resource holding potential of the males involved. Hence, before testing the effect of female protest, we evaluated the effect of male phenotype on the likelihood of disruption.

Is likelihood of disruption affected by the age of the interactors? The majority of disrupted males were subadults both at DEL (70.1%, $n = 461$ interactions) and SLI (59.5%, $n = 556$; Fisher's exact test: $P = 0.0005$); the higher proportion of disrupted adults at SLI was due to the higher presence of adults between secondary males, a result of the higher degree of despotism found at SLI. The percentage of disrupted interactions decreased with age of the disrupted male both at DEL (from 63.6%, $n = 55$ of SAM1 to 7.8%, $n = 1775$ of adults; Exact Cochran-Armitage test: *standardized trend statistic* = - 18.61; $P = 0.0000$) and SLI (from 42.9%, $n = 63$ to 4.2%, $n = 5357$; Exact Cochran-Armitage test: *standardized trend statistic* = - 27.81; $P = 0.0000$).

Is the likelihood of disruption affected by the seasonal status of the interactors? Non harem holders were disrupted more frequently than holders both at DEL (37.0% of 625 interactions by NHH were disrupted vs 11.4% of 2029 interactions by HH; Fisher exact test: $P = 0.0000$) and SLI (37.6% of 1159 interactions by NHH were disrupted vs 2.4% of 5102 interactions by HH; Fisher exact test: $P = 0.0000$). While the proportion of disrupted interactions for NHH was homogeneous between populations, the proportion of disrupted interactions for HH was not (Fisher exact test: $P = 0.0000$). This difference was due to the reduced level of despotism at DEL, that permits less powerful males to achieve the status of harem holders by simply shifting harem or breeding area.

Is the likelihood of disruption affected by the instantaneous status of the interactors? Alpha males were almost never disrupted during their mating attempts both at DEL (0.8% of 1333 interactions were disrupted) and SLI (0.5% of 4763 interactions were disrupted). Apart from the almost null likelihood of disruption of alpha

males, we did not find any strong effect of instantaneous status of the male: alphas were able to disrupt the mating attempts of other males in spite of their proximity to females. Solitary males were disrupted much more frequently at DEL than at SLI (45.3%, $n = 150$ vs 26.1%, $n = 505$; Fisher exact test: $P = 0.0000$): this result is related to the higher density of secondary males at DEL, that promotes competition for marginal breeding opportunities.

Is the likelihood of disruption affected by the dominance rank of the interactors? We evaluated the effect of dominance rank by running a logistic regression of disruption on Gibson-Guinness index. Males with higher dominance rank were less prone to disruption both at DEL [$n = 2516$ interactions, $b = -11.11$, $SE(b) = 0.53$; LR test: $G_1 = 551.6$, $P < 0.0001$] and SLI [$n = 6155$ interactions, $b = -11.35$, $SE(b) = 0.41$; LR test: $G_1 = 847.6$, $P < 0.0001$]. At DEL, mean rank of the disrupted males was 0.48 ($n = 426$ interactions, $SD = 0.097$), while mean rank of the non-disrupted males was 0.62 ($n = 2090$, $SD = 0.097$). At SLI, the mean rank of disrupted males was 0.51 ($n = 530$ interactions, $SD = 0.104$), while the mean rank of non-disrupted males was 0.66 ($n = 5625$, $SD = 0.081$). The disruptor had a higher rank than the disrupted in 95.7% of cases ($n = 418$) at DEL, and in the 95.1% of the cases ($n = 527$) at SLI.

Does the female position in and outside harems affect the disruption rate?

Interactions with harem females were disrupted much more frequently than interactions with isolated females both at DEL (45.8%, $n = 644$ vs 16.2%, $n = 198$; Fisher's exact test: $P = 0.0000$) and SLI (49.8%, $n = 928$ vs 10.5%, $n = 533$; Fisher's exact test: $P = 0.0000$).

At DEL core females were disrupted as frequently as non-core females (44.1%, $n = 222$ vs 46.7%, $n = 422$; Fisher's exact test: $P = 0.56$), while at SLI the frequency of disruption for core females was much lower (33.1%, $n = 151$ vs 52.9%, $n = 748$; Fisher's exact test: $P = 0.0000$).

Is the likelihood of disruption related to female protest?

Protested interactions were disrupted in a higher proportion of cases but the difference was very small (5.7%, $n = 3039$ vs 4.1%, $n = 510$; Fisher's exact test: $P = 0.17$). The percentage of disrupted interactions increased only slightly with the level of protest (low: 4.0%, $n = 481$; medium: 4.5%, $n = 1211$; high: 6.4%, $n = 965$; Exact Cochran-Armitage test: *standardized trend statistic* = 2.274; $P = 0.0259$).

Is the relationship between protest and disruption affected by male phenotype? The relationship between protest and likelihood of disruption was affected by the age of the male. Disruption was more frequent in protested interactions for SAM3 (26.6%, $n = 94$ vs 14.3%, $n = 14$) and SAM4 (28.7%, $n = 164$ vs 25.0%, $n = 12$) while was less frequent for adults (2.7%, $n = 2683$ vs 2.9%, $n = 479$), but differences were small and the associated probability was very large (Exact permutation test, stratified by age class from SAM2 to AD, because all interactions involving JUVs and SAM1s were protested: $P = 0.90$).

We introduced male age and level of protest in a logit model with disruption as the dependent variable. The model with male age only fitted the data very well (LR test: $G_2 = 1.010$, $P = 0.60$); the inclusion of protest level did not result in improve-

ment in the model (increase in entropy explained by the model < 0.1%) and actually reduce the quality of fit. The trend of a decrease in the percentage of disrupted interactions with age was true both in non protested (from 40%, $n = 5$ for SAM2 to 2.9%, $n = 479$ for AD, we recorded no non-protested interactions for SAM1; Exact Cochran-Armitage test: *standardized trend statistic* = - 5.216; $P = 0.0002$) and protested interactions (from 40.5%, $n = 42$ for SAM1 to 2.5%, $n = 2683$ for AD; Exact Cochran-Armitage test: *standardized trend statistic* = - 19.12; $P = 0.0001$). This trend was not stronger for protested interactions (Exact Cochran-Armitage test: *standardized trend statistic* = 1.304, note positive sign; $P = 0.20$). We then compared the decrease in disruption with age between level of protest, to verify if the decrease was steeper for more highly protested interactions, and we found a small but significant difference between levels of protest (Jonckheere-Terpstra test, with Monte Carlo sampling: $P_{100000} = 0.0377$), but contrary to the expectation the trend was more apparent for medium level protest (Medium vs Low, Exact Cochran-Armitage test, Bonferroni corrected: $P = 0.0078$; Medium vs High, Exact Cochran-Armitage test, Bonferroni corrected: $P = 0.0003$) and low and high level protest were homogeneous (Exact Cochran-Armitage test, Bonferroni corrected: $P = 0.73$).

In all, we found that female protest increased the likelihood of disruption, but this effect was small, and it was not molded on the specific phenotype of both the disrupted male and the disruptor. Disruption of mating couples seems to depend mostly on differences of resource holding potential between the males, with little or no effect of female selectivity. Intense protest made approached females much more conspicuous, but HH were very often able to detect intruders in absence of female protest.

DISCUSSION

Notwithstanding the mild ultimate effects of harassment (GALIMBERTI et al. 2000a), SES females showed clear aversive proximate reactions to male harassment, and adopted a suite of behavioural adaptations that reduce the likelihood of interception by harassing males and the risk of dangerous harassment.

Harassment reduction

A basic strategy of harassment defense is synchronization of breeding, i.e. a strong temporal clustering of reproduction. Females that breed at the same time of other females should suffer a lower level of harassment due to the dilution effect of the presence of other females, something analogous to the "predator-swamping" effect that also promotes synchronization (IMS 1990). Land breeding polygynous pinnipeds have concentrated breeding seasons (RIEDMAN 1990, BOYD 1991), and females that breed outside the phase of peak breeding usually experience higher level of harassment and lower breeding success (BONESS et al. 1995). In our study, the breeding season was almost 3 months long, but most females bred in a 4 weeks period. Females that come on land to breed around the peak of the season, experience a higher breeding sex ratio, a net dilution in the risk of contacts with secondary males, and a lower harassment rate (GALIMBERTI et al. 2000a). Although in Pinnipedia synchronization is above all an adaptation to land breeding in unstable

environments (LE BOEUF 1986), it probably had a significant role as an harassment reduction tactic in the evolution of mating systems (BARTHOLOMEW 1970).

The same dilution effect of clustering in time may result from clustering in space. Grouped breeding may entail significant costs to females, and may reduce lifetime breeding success (transmission of diseases: VEDROS et al. 1971; aggression between females: McCANN 1982; mother-pup separation: RIEDMAN & LE BOEUF 1982; accidental damages due to male-male competition: LE BOEUF & BRIGGS 1977, BALDI et al. 1996), however, one of the benefits of grouped breeding that has been suggested as possible counter balancing factor of costs is defense from male aggressive mating tactics (TRILLMICH & TRILLMICH 1984). SES females have a strong tendency to grouped breeding and isolated females are rare both at DEL and SLI. Isolated females have a higher likelihood of encountering marginal males, suffer a higher rate of harassment, and are the main victims of episodes of intense harassment (GALIMBERTI et al. 2000a). Clustering of breeding in both time and space is analog to the "selfish herd" principle of the dilution of predation risk (HAMILTON 1971), and grouped breeding may be a very effective anti-harassment strategy (TRILLMICH & TRILLMICH 1984). In our studied populations large harems guarantee a lower per capita harassment rate, less disruption of activity rhythms, and a lower likelihood of interaction with young, inexperienced males (GALIMBERTI et al. 2000a). About 1/4 of females of all age classes changed harem between arrival and parturition and showed a clear preference for larger harems. Conflict between sexes over optimal harem size is frequent in mammals (e.g. *Marmota flaviventris*: ARMITAGE 1986), but this was not the case in SES: large harems guarantee high mating success to HH males (unpublished data) and were also preferred by females. Both at DEL (BALDI et al. 1996) and at SLI (GALIMBERTI & BOITANI 1999) breeding in large harems does not seem to have the aversive effects on female breeding success typical of grouped breeding in pinniped species (LE BOEUF & BRIGGS 1977).

The grouping of females during the breeding season under the control of a single dominant male should result in a reduction in the likelihood of encountering marginal males, and, hence, in a reduction of short- and long-term breeding costs for the female (LE BOEUF 1991). Seeking the protection of a dominant male is widespread in primates (*Pongo*: MITANI 1985) and has been proposed as a main cause of the evolution of ungulate leks (CLUTTON-BROCK et al. 1992, 1996). This effect should be much more pronounced in species with a high level of polygyny, due to the higher percentage of males excluded from access to females, and due to the danger of aggression, given the large sexual dimorphism.

Variation in agonistic capabilities between males is often large, and this is particularly true in strongly despotic mating systems. Some males are expected to be able to offer females better protection from harassment by marginal males. Females may reduce harassment risk by choosing males with better success in competition, and, hence, clustering may depend on the relationship between the phenotype of breeding group holders and harassment. In SES, the stability of harem control and the capability to keep away marginal males have a notable effect on harassment level (GALIMBERTI et al. 2000a), and should depend on differences in resource holding potential between the alpha and other males associated with the harem. Hence, females may be expected to exert some kind of direct or indirect choice between alpha males on the basis of their phenotype. We found scarce evidence for an effect of male phenotype on female movement between harems. The proportion of shift towards older and larger males was not different from the expected proportions calculated from the distribution of phenotypic traits of the

HH males in the population. In all, females seem to adopt a simple strategy of clustering in both time and space, without fine tuning their choice of breeding unit on the male phenotype of the dominant males.

Female behavioural reaction to harassment

When strategies to escape from harassing males are not effective, females are expected to resort to tactics of harassment risk reduction. Females are able to tune their behavioural reaction during male approach: their reaction to male mating attempts is more or less independent from their physiological status, and they may show receptive behaviours also when not in oestrus (*Panthera leo*: PACKER & PUSEY 1983; Primates: SMUTS & SMUTS 1993). They may choose any mixture of aggressive/receptive behaviour between the two extremes of strong protest and the acceptance of copulation. By protesting mating attempts, females usually attract the attention of other, possibly more dominant, males, thereby inducing attempts of mating disruption (the "female incitation of male competition" hypothesis: COX & LE BOEUF 1977). On the contrary, by reducing protest and showing receptive behaviours during mating attempts, females may reduce the danger of physical damage (the "trade sex for protection" hypothesis: MESNICK & LE BOEUF 1991).

In SES, direct aggression was rarely used by females as an anti-harassment tactic: in species with risk of intense retaliation (due to sexual dimorphism in size and weapons) females tend to avoid direct aggression (PACKER & PUSEY 1983, SMUTS & SMUTS 1993). Females try to use plain move away as an avoidance tactic, but with limited success due to the higher agility of males on land (GALIMBERTI et al. 2000a). Hence, SES females may only fine tune their reaction to males to reduce risk and effects of harassment. Females protested most mating attempts with a suite of behavioural modules, including croaking vocalization (low frequency pulse trains: S. SANVITO pers. comm.). Although females protested "by default" all approaches and facilitation of copulations was rare, we found some evidence that females may tune their responses to males in relation to social context and male phenotype. We wish to emphasize that, contrary to findings in northern elephant seals (COX & LE BOEUF 1977), this variation is a small part of an almost completely unselective protest tendency.

Oestrus females protested less frequently than anoestrus females, and there was a decrease in the level of protest with progress of oestrus. The level of protest was lower for the last copulation of individual females than for their first copulation, but there was no drastic variation in the level of protest during the last day on land. Increase in behavioural receptivity to male approach was a gradual, almost linear process. COX & LE BOEUF (1977) suggest that in northern elephant seals receptivity during the last day on land is exceptionally high, in particular towards secondary males: on the contrary, we found that last copulations with individual females made by secondary male were slightly more protested than first copulations. We found much evidence that protest was less frequent and less intense during interactions involving males with high resource holding potential, as in the northern species (COX 1981). Approaches by adult males were less frequently protested than mating attempts by subadults; mature males and males of higher status also received less protest, and dominance rank was negatively related to likelihood of protest. But this effects were a by-product of the higher likelihood of males with high resource holding potential to interact with oestrus females, who

thus have a fundamental tendency to protest less. Variation in protest between males with different phenotype is best explained by the different opportunities to contact oestrus females. The balance between protest and receptivity during mating attempt seems to depend more on the effect of simple female physiological state than on active or passive choice of specific male phenotypes.

Protest and disruption of mating attempts

Protest could be a valid anti-harassment tactic only if it increases the probability of intervention by more dominant and mature males. COX & LE BOEUF (1977) interpreted protest in northern elephant seals as a form of female incitation of male competition that resulted in a reduction of the likelihood of interaction with marginal males. Female behaviour during mating attempts may serve as solicitation of mate guarding by older, more dominant males and protection against harassing males in different species (*Loxodonta africana*: POOLE 1989; *Columba livia*: LOVELL-MANSBRIDGE & BIRKHEAD 1998). By protesting, females are supposed to enhance the likelihood of intervention by higher rank males (MESNICK & LE BOEUF 1991); this could result in benefits at a proximate level (cessation of interaction with less dominant and less experienced males) and at an ultimate level (passive choice of males carrying "good genes").

Disruption of mating attempts was frequent in both populations studied, although disruption was more common at DEL but more effective at SLI, where main breeding males were more efficient at controlling the activity of other males. Percentages of disrupted interactions, both total and per age class, were lower than in the northern species (COX & LE BOEUF 1977). In Primates rate of disruption seems to be linked to rank per se, and not to specific individual traits (BRUCE & ESTEP 1992), while in both species of elephant seals tendency and capability to disrupt varied also between high ranking males. Disruptors were older, more mature and more dominant than disrupted males, who usually were subadults, and disruption usually happened near harems, while interactions with isolated females were disrupted less frequently.

Protested interactions were disrupted more frequently, but the difference was very slight. The likelihood of disruption increased with decrease of age class, and this trend was almost equal in both protested and non-protested interactions. COX & LE BOEUF (1977) reported for northern elephant seals that the mating attempts of subadults are interrupted earlier due to the effect of protest, and that mating attempts of subadults are always shorter. On the contrary, we did not find a clear trend of increase in duration of interactions with age and mean duration was shorter for adult males both for uninterrupted and interrupted interactions. This was not unexpected because observation of behavioural sequences demonstrated that harem holders test females with rapid approaches while subadult, secondary males could be very persistent in their mating attempts if free to do so. Protest seems to have just a minor effect on the likelihood of interruption by other males, and this result was confirmed by observations of behavioural sequences of disrupted mating attempts: intense protest made approached females much more conspicuous, but often HH males were able to detect intruders in the absence of female protest. In all, we found a limited effect of protest on likelihood of disruption, that depended mostly on differences in RHP of involved males.

CONCLUSION

Our results on southern elephant seals are at somewhat at variance with the results from the northern species (COX & LE BOEUF 1977, COX 1981, MESNICK & LE BOEUF 1991). Northern elephant seal females seem to adopt the same global strategies of harassment reduction as the southern species, although these aspects are not directly tackled in the literature: breeding is very synchronized (LE BOEUF & LAWS 1994), females are grouped in harems (LE BOEUF 1972), and, inside harems, core females are better protected from being harassed by secondary males and enjoy higher pup survival and breeding success (REITER et al. 1981, RIEDMAN & LE BOEUF 1982). This is not unexpected because two species of the *Mirounga* genus have a very similar life history and share many aspects of breeding biology (LE BOEUF & LAWS 1994).

On the contrary, short term tactics of harassment reduction are less developed and effective in southern elephant seals than in the northern species. This variation between the two species seems to depend, apart from differences in methodology and scope of the studies, on variation in the basic demography and sociometry. The breeding areas of northern elephant seals are usually very crowded and the harems are much larger than the ones found in our studied populations (LE BOEUF 1972). More than one male is usually resident in each harem (LE BOEUF 1974), something that very rarely happened during our study, and the density of secondary males is much higher (MESNICK & LE BOEUF 1991). In these more complex breeding conditions, dominance hierarchies are less linear and steady than in our populations (DEL: GALIMBERTI 1995; SLI: unpublished data), harem control is less clear and defined, and secondary males have more opportunities to interact with females (MESNICK & LE BOEUF 1991, GALIMBERTI et al. 2000b). In this situation, female tactics of harassment reduction may have a more important role. The "trade sex for protection" hypothesis, as originally proposed for northern elephant seals, is not as effective in explaining the modulation of female reaction to male harassment in the southern species. The applicability of this hypothesis seems less wide than expected, because female capability to reduce the effect of aggressive male mating tactics strongly depends on local demography and sociometry of breeding areas and units, and may become apparent only in extreme social conditions.

The mating system of southern elephant seals is strongly despotic, mature harem holders have a very effective control of the local breeding situation, even when they have to manage social relationships with a large number of harem females and peripheral males. These conditions put severe limits on female tactics, and females seems to be confined in a role of "making the best of a bad job".

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REFERENCES

- AGRESTI A. 1990. Categorical data analysis. *New York: Wiley*.
- ARMITAGE K.B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies, pp. 303-331. In: Rubenstein D.I. & Wrangham R., Edits. *Ecological aspects of social evolution. Princeton: Princeton University Press*.
- ARMITAGE P. 1955. Tests for linear trends in proportions and frequencies. *Biometrics* 11: 375-386.
- BALDI R., CAMPAGNA C., PEDRAZA S. & LE BOEUF B.J. 1996. Social effects of space availability of southern elephant seal in Patagonia. *Animal Behaviour* 51: 717-724.
- BARTHOLOMEW G.A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24: 546-559.
- BARTHOLOMEW G.A. & COLLIAS N.E. 1962. The role of vocalization in the social behaviour of the Northern Elephant Seal. *Animal Behaviour* 10: 7-14.
- BERGER J. 1986. Wild horses of the Great Basin: social competition and group size. *Chicago: University of Chicago Press*.
- BONESS D.J., BOWEN W.D. & IVERSON S.J. 1995. Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behavioral Ecology and Sociobiology* 36: 1-10.
- BOYD I.L. 1991. Environmental and physiological factors controlling the reproductive cycle of pinnipeds. *Canadian Journal of Zoology* 69: 1135-1148.
- BRUCE K.E. & ESTEP D.Q. 1992. Interruption of and harassment during copulation by stump-tail macaques, *Macaca arctoides*. *Animal Behaviour* 44: 1029-1044.
- CAMPAGNA C., LEWIS M. & BALDI R. 1993. Breeding biology of southern elephant seals in Patagonia. *Marine Mammal Science* 9: 34-47.
- CARRICK R., CSORDAS S.E. & INGHAM S.E. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). IV. Breeding and development. *C.S.I.R.O. Wildlife Research* 7: 161-197.
- CLUTTON-BROCK T.H., MCCOMB K. & DEUTSCH J.C. 1996. Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. *Behavioral Ecology* 7: 373-378.
- CLUTTON-BROCK T.H. & PARKER G.A. 1995. Sexual coercion in animal societies. *Animal Behaviour* 49: 1345-1365.
- CLUTTON-BROCK T.H., PRICE O.F. & MACCOLL A.D.C. 1992. Mate retention, harassment and the evolution of ungulate leks. *Behavioral Ecology* 3: 234-242.
- COX C.R. 1981. Agonistic encounters among male elephant seals: frequency, context, and the role of female preference. *American Zoologist* 21: 197-209.
- COX C.R. & LE BOEUF B.J. 1977. Female incitation of male competition: a mechanism of mate selection. *The American Naturalist* 111: 317-335.
- GALIMBERTI F. 1995. Competizione tra i maschi e selezione sessuale nell'elefante marino del sud (*Mirounga leonina*) della Penisola di Valdés [Intermale competition and sexual selection in southern elephant seals (*Mirounga leonina*) of the Valdés Peninsula; in Italian]. *PhD Thesis, Roma: Università degli Studi di Roma "La Sapienza"*.
- GALIMBERTI F. & BOITANI L. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science* 15: 159-178.
- GALIMBERTI F., BOITANI L. & MARZETTI I. 2000a. The frequency and costs of harassment in southern elephant seals. *Ethology Ecology & Evolution* 12: 345-365.

- GALIMBERTI F., BOITANI L. & MARZETTI I. 2000b. Harassment during arrival to land and departure to sea in southern elephant seals. *Ethology Ecology & Evolution* 12: 389-404.
- GIBSON R.M. & GUINNESS F.E. 1980. Behavioural factors affecting male reproductive success in red deer (*Cervus elaphus*). *Animal Behaviour* 28: 1163-1174.
- HAMILTON W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295-311.
- HOGG J.T. 1984. Mating in bighorn sheep: multiple creative male strategies. *Science* 225: 526-528.
- IMS R.A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist* 136: 485-498.
- LE BOEUF B.J. 1972. Sexual behaviour of the northern elephant seal *Mirounga angustirostris*. *Behaviour* 41: 1-26.
- LE BOEUF B.J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist* 14: 163-176.
- LE BOEUF B.J. 1986. Sexual strategies of seals and walruses. *New Scientist* 1491: 36-39.
- LE BOEUF B.J. 1991. Pinniped mating systems on land, ice and in the water: emphasis on Phocidae, pp. 345-394. In: Renouf D., Edit. Behaviour of pinnipeds. London: Chapman and Hall.
- LE BOEUF B.J. & BRIGGS K.T. 1977. The cost of living in a seal harem. *Mammalia* 41: 167-195.
- LE BOEUF B.J. & LAWS R.H. 1994. Elephant seals: an introduction to the genus, pp. 1-26. In: LE Boeuf B.J. & Laws R.M., Edits. Elephant seals. Population ecology, behavior and physiology. Berkeley, CA: University of California Press.
- LE BOEUF B.J. & MESNICK S. 1990. Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour* 116: 143-162.
- LEWIS M.N. & CAMPAGNA C. 1995. Flipping sand in elephant seals: heat stress or just stress? *World Marine Mammal Science Conference, Orlando, Florida*.
- LOVELL-MANSBRIDGE C. & BIRKHEAD T.R. 1998. Do female pigeons trade pair copulations for protection? *Animal Behaviour* 56: 235-241.
- MCCANN T.S. 1981. Aggression and sexual activity of male Southern elephant seals, *Mirounga leonina*. *Journal of Zoology, London* 195: 295-310.
- MCCANN T.S. 1982. Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). *Animal Behaviour* 30: 268-276.
- MCCANN T.S. 1985. Size, status and demography of Southern elephant seal (*Mirounga leonina*) populations, pp. 1-17. In: Ling J.K. & Bryden M.M., Edits. Studies of sea mammals in South Latitudes. Northfield: South Australia Museum.
- MESNICK S.L. & LE BOEUF B.J. 1991. Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. *Behaviour* 117: 262-280.
- METHA C. & PATEL N. 1992. StatXact-Turbo User Manual. Cambridge, MA: Cytel Software Corporation.
- MITANI J.C. 1985. Mating behaviour of male orangutans in the Kutai Reserve. *Animal Behaviour* 33: 392-402.
- MODIG A.O. 1996. Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour* 51: 1295-1306.
- NORUSIS M.J. 1994. SPSS Advanced Statistics 6.1. Chicago: SPSS Inc.
- PACKER C. & PUSEY A.E. 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist* 121: 716-728.
- POOLE J.H. 1989. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour* 37: 842-849.
- REITER J., PANKEN K.J. & LE BOEUF B.J. 1981. Female competition and reproductive success in Northern elephant seal. *Animal Behaviour* 29: 670-687.
- RIEDMAN M. 1990. The pinnipeds: seals, sea lions and walruses. Berkeley: University of California Press.
- RIEDMAN M.L. & LE BOEUF B.J. 1982. Mother-pup separation and adoption in Northern elephant seals. *Behavioral Ecology and Sociobiology* 11: 203-215.
- SMUTS B.B. & SMUTS R.W. 1993. Male aggression and sexual coercion of female in non-human primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior* 22: 1-63.

TREXLER J.C. & TRAVIS J. 1993. Nontraditional regression analysis. *Ecology* 74: 1629-1637.

TRILLMICH F. & TRILLMICH K.G.K. 1984. The mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biological Journal of the Linnean Society* 21: 209-216.

VEDROS N.A., SMITH A.W., SCHENEWALD J., MIGAKI G. & HUBBARD C. 1971. Leptospirosis epizootic among California sea lions. *Science* 172: 1250-1251.