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The frequency and costs of harassment in southern elephant seals

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Notwithstanding the important role of male harassment of females for theories of the evolution of mating systems, accurate estimates of its frequency and costs are available for only a few species. In this paper, we quantify the frequency of harassment in southern elephant seals, compare occurrences of harassment inside and outside harems, and estimate the costs of harassment in two populations at Sea Lion Island (Falkland Islands) and Punta Delgada (Valdés Peninsula). Southern elephant seal males are much larger than females, have enlarged canines, and are much more agile on land; hence, females have a small probability of escape from approaching males and may suffer intense molestation. Most males had limited access to females due to the despotic mating system, and their libido was high. Females were approached by males at high frequency, mostly when out of oestrus. The harassment level was negatively related to the ratio of breeding females to breeding males, and females breeding at the peak of the season suffered a lower level of harassment. Females of large harems were harassed less, and their likelihood of interact with secondary males was lower. The activity of harem females was less disrupted, and females in large harems had a higher proportion of resting time. Isolated females suffered more herding episodes, and were approached more frequently by secondary males. The main short-term cost of harassment was disruption of the females' activity schedule; harassment level and total active time were positively related. Suckling bouts were rarely interrupted by male harassment. Mother and pup separations caused by males interaction were rare, short-lasting, and rarely permanent. There was little effect of harassment on weanling weight, physical damage of females was rare, and there was only a slight non-significant negative relationship between harassment level during one season and the likelihood of surviving to the next.

KEY WORDS: harassment, mating systems, costs of reproduction, southern elephant seal, *Mirounga leonina*.

INTRODUCTION

Harassment of females may play a key role in the evolution of breeding systems (REYNOLDS 1996). Harassment is thought to promote the evolution of strongly polygynous mating systems if clustered females suffer a lower level of harassment, due the dilution effect of grouping (CLUTTON-BROCK et al. 1992, 1993). In species where female choice is absent or weak, harassment is postulated to be the only way to convert the results of male-male competition into actual gains in reproduction (SMUTS & SMUTS 1993). The short- and long-term costs of harassment are supposed to shape both long-term breeding strategies (e.g. synchronized breeding: BONESS et al. 1995) and short-term mating behaviour (e.g. facilitation of mating attempts: MESNICK & LE BOEUF 1991).

We define *harassment* as the use by males of aggressive behavioural modules (like herding, pushing, biting, chasing) when approaching females during the breeding season. Our definition of harassment includes a wide range of phenomena labelled in various ways (e.g. molestation, forced copulation, disruption of mating couples). Most definitions presented in the literature include motivational components. For example, our definition of harassment overlaps in part with "sexual coercion" as defined by CLUTTON-BROCK & PARKER (1995), which includes motivational aspects [like "induce (females) to mate" or "punish females that refuse to mate"]. We adopted a general definition based on male behavioural modules to avoid the practical and theoretical problems of distinctions based on motivation. In elephant seals, male aggression directed towards females during the breeding season is related *only* to mating, there is no confounding effect of competition between the sexes for any kind of resource, and the likelihood of aggression is completely asymmetric between the sexes.

Forms of harassment are quite varied: females may be chased, bitten and wounded (*Equus* spp.: RUBENSTEIN 1986). Even when physical damage is not heavy, energy costs for mothers and pups may be high (*Cervus elaphus*: CLUTTON-BROCK et al. 1982; *Dama dama*: CLUTTON-BROCK et al. 1992; *Halichoerus grypus*: BONESS et al. 1995; *Kobus leche*: NEFDT 1995). In every case there is at least a basic cost, disruption of the activity rhythm and time budget (DALY 1978, PARKER 1979). In some species a significant effect on the survival of females or their pups has been demonstrated (*Panthera leo*: PACKER & PUSEY 1983; *Mirounga angustirostris*: LE BOEUF & MESNICK 1990).

Quantitative information about harassment in mammals is scarce (SMUTS & SMUTS 1993). Harassment is common in Primates (NYEMEYER & ANDERSON 1983), especially in polygynous species with multimale groups (SMUTS & SMUTS 1993), and is frequent also in polygynous ungulates (CLUTTON-BROCK et al. 1992, 1993). Heavy harassment of females is quite common in Pinnipedia mating systems (*Neophoca cinerea*: MARLOW 1975; *Otaria byronia*: CAMPAGNA et al. 1988; *Monachus schauinslandi*: HIRUKI et al. 1993a). Harassment in pinniped species is sometimes intense and may affect female reproductive success (HIRUKI et al. 1993b). In northern elephant seals, mating harassment is widespread (LE BOEUF 1972), may result in serious damage to females (LE BOEUF & MESNICK 1990), and has a significant effect on female breeding strategies (RIEDMAN & LE BOEUF 1982).

Female southern elephant seals (*M. leonina*; SES hereafter) gather in large groups during the breeding season. Each group has one or more associated males (MCCANN 1981) and one of them has usually a more or less complete control of the harem. Hence, the mating system is very despotic and only a few males have free access to breeding females. This shortage in mating opportunities is coupled with a very high level of libido in all males, related to a high level of serum testosterone (GRIFFITHS 1984). SES males may attempt to mate with dead females, weanlings, yearlings and small juveniles (ROSE et al. 1991), and even individuals of other species (FOLLIS & MORTENSON 1995). Moreover, males are larger than females (LE BOEUF & LAWS 1994), they have enlarged canines, and they constantly show behavioural patterns of herding and biting while interacting with females. Hence, males should be a significant source of harassment for females, and sexual coercion could be an important component of male mating tactics. Preliminary evidence indicates that this is the case (MCCANN 1981, 1982). Preliminaries are short in SES breeding behaviour, and males are often able to overpower females; cases of forced copulation happen regularly, although not frequently. Hence, male-female interactions are potentially a very risky business for the female. For a female one or few copulations should be all that is needed for successful breeding activity: extra copulations and non-mating interactions with males have no functional value for the female and may represent a significant cost. Hence, most male-female interactions are a form of harassment from the point of view of the female.

To be an important selective force and to be able to shape the behaviour of females, harassment must be intense, frequent and costly. Data on the frequency of harassment is available for just a few species, and accurate estimates of the costs of harassment are difficult to obtain (LE BOEUF & MESNICK 1990, CLUTTON-BROCK & PARKER 1995). In this paper, the first of a series on harassment in SES, we analyze harassment in the small and localized population of Sea Lion Island (Falkland Islands) and we carry out some comparisons with data collected at Punta Delgada (Valdés Peninsula), which shelters a population with a different socionomy and with topographically different breeding areas (see Methods section). We have three main goals: to quantify the frequency of harassment, to evaluate the effect of different social contexts on harassment, and to estimate the short- and long-term costs of harassment.

METHODS

The populations. We carried out observations of male-female interactions during three breeding seasons (September-November, 1995-1997) at Sea Lion Island (Falkland Islands; 52°26'S, 59°05'W; SLI hereafter), and during two breeding seasons (August-October, 1993 and 1994) at Punta Delgada (Valdés Peninsula, Argentina; 42°26'S, 63°38'W; DEL hereafter). Although the observational protocol was similar between the two populations, data collection at DEL was less complete than at SLI, and, hence, many hypotheses were tested using SLI data only. The results refer to SLI except where explicitly stated.

During the study, the SLI population increased from 517 breeding females in 1995 to 563 in 1997; the number of breeding males (see below) ranged from 52 to 60, and the mean seasonal breeding sex ratio (= n of mature females/n of breeding males; BSR hereafter) ranged from 9.2 to 10.1. The median harem size (see below) at peak presence of females on land was 32 females and the median number of peripheral males associated with harems (calculated from daily values) was 0.21. At DEL, we monitored 521 females and 52 breeding males in 1993 and 613 females and 60 breeding males in 1994 (BSR was about 10 in both years). The median harem size was 47 females and the median number of peripheral males per harem was 0.69. The most notable difference in socionomy between DEL and SLI populations was that almost 3 times as many peripheral males were associated with harems at DEL, and this produced a more intense competition for mating opportunities between non-harem holding males (unpublished data). At DEL, there was also a higher turnover of breeding males. The SLI population is small, localized and almost isolated, and hence males have very few opportunities to move to other breeding areas. On the contrary, at DEL secondary males frequently moved in and out of our study area, switching to adjacent areas and harems. Additional information about the study populations may be found elsewhere (SLI: GALIMBERTI & BOITANI 1999; DEL: CAMPAGNA & LEWIS 1992, CAMPAGNA et al. 1993).

Behavioural observations. At SLI we marked all breeding males and females by putting nylon cattle tags (Jumbo Rototags, Dalton Supplies Ltd) in the interdigital membrane of the hind flippers, and we marked all males and the majority of females (70-85%) with commercial black hair dye (New Rolcolor Creme Professional, Nuova Ropel Srl). Recognition of individuals during interactions was high (the male was recognized in 99.7-100% of all interactions, the female in 49.4-83.1%), in particular during copulations (male: 100%, female: 71.1-95.8%). At DEL females were not tagged and were dye marked only in 1994; males were tagged and dye marked as on SLI.

We recorded behavioural interactions using an all occurrences sampling norm and a continuous recording norm (ALTMANN 1974) during observation periods of 2 hr length (hence our basic data were rates calculated per period: ALTMANN & ALTMANN 1977). We calculated individual time budgets from data recorded with a scan sampling norm and an instantaneous recording norm. During 4586 hr of observation, we recorded 12591 male-female interactions (3816 at DEL, 8775 at SLI), including 2590 copulations (1218 at DEL, 1372 at SLI). Due to practical constraints, it was not always possible to collect complete data for all interactions; therefore, we were not able to use all interactions to test every hypothesis, and sample size varied between different analysis. We coded behavioural events using a standard ethogram (MARZETTI 1997), analogous to the one described for the northern species (LE BOEUF 1972). To evaluate the costs of harassment we recorded all occurrences of interruption of suckling bouts, separation of the pup from the mother, and wounding of females during male-female interactions. We recorded rare events (e.g. heavy harassment episodes, severe wounding of females) with an ad libitum sampling norm during the whole length of our time in the field. We carried out observations during the day, except for a small sample of observations with night vision equipment (32 hr in all); activity was equal between day and night (see also BALDI et al. 1996), as in the northern species (SHIPLEY & STRECKER 1986).

To collect data in different breeding situations, we observed all the harems in our study areas (4-5 km of coast at DEL; 7.2 km of coast at SLI); we spent almost the same observational time at each harem (9-12 harems per breeding season; 3-168 females per harem), except for very small harems that had a short duration. In 1996 one medium sized harem (58 females) was observed intensively (all females were marked and the recognition rate for females during interactions was 100%). We repeated some analysis with data from this harem only, but the emerging patterns for this harem were equal to those from the whole set of harems, hence we present results from the whole set only. Demographic parameters of the whole population and of each harem were calculated from data collected during daily counts of the whole area occupied by breeding elephant seals; during censuses we also collected information about every marked male and female of the population (see GALIMBERTI & BOITANI 1999 for details on the census methods).

General definitions. We define *breeding season* as a 12 week period that includes the arrival of the first breeding males and the return to sea of the last breeding females; this period is centred around the *peak haul out* (= the day in which we counted the maximum number of females on land), which is almost constant across years (GALIMBERTI & BOITANI 1999). We define *breeding male* as any male that is present in the breeding areas (*breeding area* = a portion of beach with at least one breeding female) for at least 1 week. We define *breeding female* as any female that resides in a harem and has a regular breeding history (came to land, stayed in a harem for at least 3 weeks, mated, returned to the sea): this definition includes pregnant females that regularly give birth (96.6-98.3% of all females) and yeld females, but excludes a few transient females that occasionally appear on the beaches for few hours to few days. We define *harem* as a group of two or more females, and *harem size* as the number of females in the harem based on daily counts; in a season long analysis, harem size is the maximum size reached during the season (usually at peak haul out, but not always because different harems may reach maximum size on different days). We classified harems as *small* (size < median size, calculated for each season) or *large* (size ≥ median size).

Male phenotypic traits. We classified males by their age in six age classes: *juveniles* (JUV), *subadults* class 1 to 4 (SAM1 to SAM4), and *adults* (AD). The rationale for this classification is presented elsewhere (GALIMBERTI & BOITANI 1999). True age is expected to be almost linearly increasing between consecutive age classes. We employed eyeballed standard body length (≈ 2.6 m; SBL) as an approximate measure of distance between individuals (BALDI et al. 1996). We classified males by status at the beginning of each behavioural interaction by evaluating the distance (measured in SBL) from the female group; we recognized five categories: *alpha* (0 distance, inside female group), *beta* (inside female group, but less inside than the alpha), *peripheral* (1 to 5 standard body lengths from females), *marginal* (6 to 10 SBL), *solitary* (more than 10 SBL). We also classified males on a seasonal basis as *harem holders* (HH) and *non-harem holders* (NHH; equivalent to "marginal males" of McCANN 1981): harem holders were the alpha males of established harems for at least two consecutive daily censuses.

Female phenotypic traits. We classified females by their size in three classes: *small* (S), *medium* (M), and *large* (L). The rationale for this classification is presented elsewhere (GALIMBERTI & BOITANI 1999). Size is a good index of age in female elephant seals (CAMPAGNA et al. 1992b). We also classified females as *isolated* or *harem* (at least one other female at a distance ≤ 10 SBL). Inside harems we classified females as *core* (at least one other female on all sides, not directly exposed to peripheral males) and *external* (no other female on at least one side, directly exposed to peripheral males). We evaluated the *oestrus* status of the female at the beginning of each interaction using her external morphology (females fast during the breeding season, and this produces visible changes in body shape) and the development of her pup (size, fatness, fur colour). These criteria are independent from the behavioural reaction to male approach, avoiding the risk of circularity, and are in accordance with an estimation of oestrus based on parturition dates and mean delay between parturition and oestrus (as from GALIMBERTI & BOITANI 1999; see also CAMPAGNA et al. 1993).

Indices of harassment and mating activity. To quantify the frequency of harassment we calculated two indices. The first one was the number of interactions per female per observation period (simple harassment rate, SHR). Different kinds of interactions had different length, and length is a good measure of the level of harassment suffered by the female (MARZETTI 1997). Hence, we calculated another index: the number of interactions per female per observation period with each interaction weighed by the median length of the specific kind of interaction, setting the weight for the longest (copulations) to 1 (weighed harassment rate, WHR). To measure the control of the females by males we used a females/days index (FDI), calculated as the daily number of females held by a male summed for all the days of his presence on land (CLUTTON-BROCK et al. 1982). We calculated mating success as the number of copulations observed per 100 hr of observation (MS_{100}; CAMPAGNA et al. 1993). We used ENFI (Estimated Number of Females Inseminated; LE BOEUF 1974) as an estimate of seasonal reproductive success.

Statistics. In many cases, we tested hypothesis by contingency table analysis of social interaction counts. This procedure may suffer statistical problems due to non-independence between interactions involving the same individuals (MACHLIS et al. 1985). However, the problem is particularly relevant when small groups are studied, and, therefore, less relevant to this study, where we present data collected from many social units, involving a large number of males and a very large number of females (see above, section "The population"). Each male-female dyad contributed to the data sets only for a very small share of the overall number of interactions (Observed dyads SLI, 1995-1997: 2194 male-female dyads excluding interactions with non-identified females, with a mean 2.7 interactions per dyad; Observed dyads DEL, 1994 only: 639 male-female dyads, with a mean 1.8 interactions per dyad); hence, we expected the inflation of test probabilities due to non-independence to be scarce. The alternative, i.e., to calculate mean or median values to attain independence (MACHLIS et al. 1985) and avoid pseudo-replication (HURLBERT 1984), itself presents significant drawbacks. First, the level to be used to calculate mean values, i.e., the peseudo-replicated unit, is not easy to define; in the present study, it could be the dyad, the individual, or the harem, with much subjectivity in making the choice (see, e.g., LOMBARDI & HURLBERT 1996 vs WILSON & DUGATKIN 1996). We think that the right unit to analyze dyadic social behaviour is the dyad, not each individual of the dyad, because the social behaviour and the social relationship expressed during the interaction is not a property of each individual, but an emerging property of the two (see, e.g., BARRETTE 1993). Second, the use of mean values implies that the inter-unit (e.g., inter-individual) variability has no biological/statistical meaning, something that is quite unlikely (see, e.g., BENNETT 1987), and untenable for our data sets. Third, there are practical problems, e.g. deciding which estimator of central location to use, in particular with skewed distributions and small data sets (like our inter-dyad or inter-individual data sets), and how to apply the method to nominal attributes (that comprise a large part of the variables analyzed in this paper). In all, the advantages of the simple use of interactions more than balance the negative effects of quasi-independence.

Data from different years were pooled in most cases, after checking homogeneity with a Kruskall-Wallis test (with randomization for small samples), while data from the two populations were usually analyzed separately. We presented statistics as mean and standard deviation, or median and median absolute deviation (MAD) for asymmetric variables. Due to the high frequency of unbalanced samples and heavy tailed distributions, we limited as much as possible the use of asymptotic inference (ADAMS & ANTHONY 1996, MUNDRY & FISHER 1998), and we extensively employed exact non-parametric tests (SIEGEL & CASTELLAN 1988, METHA & PATHEL 1992) or randomization tests (MANLY 1997). We reported exact probabilities for exact tests, actual probabilities and the number of resamplings (as subscript) for randomization tests, and approximate probabilities for standard parametric and non-parametric with normal approximation tests. Probabilities were two-tailed unless stated. With small sample sizes and dubious statistical tests, we carried out post-hoc power analysis (THOMAS & JUANES 1996) with $\alpha = 0.05$. Effect size for the different tests was calculated as from COHEN (1988). In many cases (randomization and non-parametric test), we were unable to calculate the power of the specific test, and we presented power analysis for the equivalent parametric test as the best approximation we were able to provide.

We ran parametric tests in StatView 4.5.1 (Abacus Concepts Inc.) and Systat 5.2.1 (Systat Inc.), and exact/randomization tests in RT 2.0 (MANLY 1996) and StatXact Turbo 2.11 (Cytel Software Corporation).

RESULTS

General aspects of harassment

How elephant seal males harass females

Copulatory behaviour in our populations was equal to that reported for South Georgia (LAWS 1956, MCCANN 1981). Apart from simple chasing, two main components of male behaviour are of particularly high relevance for female harassment: herding and neck-biting (McCann 1981, Marzetti 1997).

Southern elephant seal males are much larger than females, and they are able to overpower them. While females seems to have an agility advantage at sea, on land they are much less agile and slower than males. Herding modules (module = fixed action pattern) comprised 11.9% of all occurrences in a large sample of behavioural modules (n = 3670). Herding was often very intensive; in 8.9% of cases males put their whole chest on the back of the female, and in 2.7% of cases a pushing behaviour (the male slamming the female's back with his whole chest) was observed. Herding was an effective behavioural tactic: 87.2% of 611 herding episodes resulted in control of the female's movements by the male. Most of herding episodes were due to adult (95.0%, n = 1060), HH males (81.6%, n = 1052); harem holders were particularly effective during herding (89.5% of success on 514 tries vs 74.7% of 95 tries by secondary males; Fisher exact test: P = 0.0000); they employed herding both to recruit females to harems (14.1%, n = 854 herdings) and to stop the movement of females away from harems (85.9%). Herding efficiency improved with age (from 50% of success for SAM3 to 88.2% for adults; Exact Cochran-Armitage test: *standardized trend statistic* = 3.711; P = 0.0016).

Males have enlarged canines (in particular the lower pair) and they very often showed neck-biting behaviour during mounts and copulations. Some form of biting was recorded in 17.1% of the interactions (n = 3444). Biting was more frequent during copulation (19.9%, n = 422 vs 2.7%, n = 2619; Fisher's exact test: P = 0.0000) and in interactions involving alpha males (18.4%, n = 2754 vs 11.6%, n = 683; Fisher's exact test: P = 0.0000). Some alpha males consistently showed almost continuous neck-biting during successful matings, even when the female's behaviour was completely receptive. There was a trend for the frequency of biting to increase with age (from 2.3%, n = 43 for SAM1s to 17.9% n = 2974 for ADs; Exact Cochran-Armitage test: *standardized trend statistic* = 2.874; P = 0.0043).

Pure aggression by males towards females, without a typical sequence of approach/mount behaviours was very rare (0.25% n = 8758). Such aggression was seen in both adult and subadult males, but more frequently for the latter (0.95%, n = 1162 vs 0.14%, n = 7596: Fisher's exact test: P = 0.0001). This confirms that harassment in elephant seals is strongly related to mating, and that males, even young subadults, are usually able to get sufficient control of the female to begin the mating sequence.

Despotism in the mating system and harassment

The intensity of harassment should depend on a high level of libido in males combined with limited opportunities for access to receptive females. The level of despotism in the mating system on SLI was very high. Across three breeding seasons the females/days index had a median value of 5 and ranged from 0 to 3541 (n = 137 breeding males), with a very skewed distribution (g_1 = 2.798). Also the distribution of MS_{100} and ENFI were very skewed (g_1 = 2.534 and 2.851), and the inter-individual variation was very large (CV = 1.984 and 2.367). A large percentage of breeding males was not able to copulate (38.6% in 1995, 59.6% in 1996 and 58.7% in 1997), and the majority of males, including some HH males, achieved only 10 copulations or less (81.8% in 1995, 80.6% in 1996, 80.4% in 1997). At DEL (n = 112 males) despotism in access to females was lower. DEL and SLI populations had almost equal mean ENFI (10.5 vs 11.2; t-test, with randomization: *mean diff.* = – 0.723, P_{10000} = 0.81) but DEL had a significantly lower variation between individuals (CV = 1.67 vs 2.37; F-test, with randomization: *variance ratio* = 0.433, P_{10000} = 0.0000) and the opportunity for selection (ARNOLD & WADE 1984) was almost double at SLI (I = 5.60 vs 2.77).

The percentage of the first copulations for each female by harem holders was very similar in the two populations (91.9%, n = 99 at DEL vs 92.5%, n = 716; Fisher's exact test: *P* = 0.83), but the percentage of all copulations realized by NHH males was significantly greater at DEL (23.1%, n = 876 vs 11.1%, n = 1367; Fisher's exact test: *P* = 0.0000). The percentage of copulations by secondary males involving a harem female (including peripheral females) was also greater at DEL (58.9%, n = 202 vs 38.2%, n = 152; Fisher's exact test: *P* = 0.0002). In all, the lower asymmetry in the distribution of mating opportunities at DEL was mainly due to a lower effectiveness of the despotic tactics of the alpha males.

Females of DEL population interacted more with NHH males than those from SLI (35.0%, n = 2430 interactions vs 19.0%, n = 8701; Fisher's exact test: *P* = 0.0000). This was true both for harem (29.7%, n = 2176 interactions vs 14.6%, n = 7799; Fisher's exact test: *P* = 0.0000) and non-harem females (81.5%, n = 248 interactions vs 57.8%, n = 894; Fisher's exact test: *P* = 0.0000).

Is the frequency of harassment sufficiently high to be a notable selection pressure?

At SLI the median seasonal male-female interaction rate (number of interactions per 2 hr observation period) was 2 interactions (MAD = 2, n = 1837); at DEL the median interaction rate was almost triple, 6 interactions (MAD = 5, n = 456), significantly higher than at SLI (Mann-Whitney test: U' = 546492, z = – 10.2, *P* < 0.0001). The per female interaction rate was also lower at SLI (median = 0.030, MAD = 0.030) than at DEL (median = 0.115, MAD = 0.093), and again the difference was significant (Mann-Whitney test: U' = 519467, z = – 7.95, *P* < 0.0001).

The "mean" female interacted with males about 2.5 times per day (or about 67.5 times during the mean length of their presence on land of 27 days, see GALIMBERTI & BOITANI 1999). Only 11.7-13.1% of the interactions involved a female that appeared receptive from a behavioural point of view. About 1/4 of all interactions of the marked females (1995: 28.2% of 180 females, 1996: 25.7% of 312, 1997: 24.0% of 326) were concentrated during the oestrus span, as calculated from the parturition date (GALIMBERTI & BOITANI 1999; see also GALIMBERTI et al. 2000). Hence, although females interacted more than expected during oestrus (3 days; Binomial test for 1995, 1996, 1997: expected proportion = 0.11, *P* < 0.0001 in all cases), most interactions were concentrated in the remainder of their residence on land, and had no role in actual fertilization.

Is harassment related to fluctuations in the local sex ratio?

We expected the baseline per female rate of harassment to depend on the rate of encounters of each female with the pool of breeding males, and hence on the breeding sex ratio. Daily variations in BSR was synchronized between years (cross correlations always greater than 0.97, with maximum correlation at lag equal to 0 days) and similar between populations (r = 0.96). At SLI, the BSR was about 10 females per male (9.2-10.1 in different years). It ranged daily from 0.1 to 11.3 and had a gaussian shaped variation with a maximum between week 6 and 7 (see also GALIMBERTI & BOITANI 1999).

The seasonal variation of harassment rate was symmetric across years (SHR: r = 0.75-0.81, maximum cross correlation with lag equal to 0 days; WHR: r = 0.84-0.98, maximum cross correlation with lag equal to 0 days). The SHR had an inverted gaussian variation across the breeding season, with high values at the beginning of the season (local maximum in the 2nd week = 0.69), low values at mid season (global minimum in the 6th-7th week = 0.10), and high values again at the end of the season (global maximum in the 11th week = 1.11). A similar seasonal variation was found for WHR (local maximum in the 2nd week = 0.40; global minimum in the 6th week = 0.03 and 7th week = 0.04; global maximum in the 11th week = 0.08). The harassment rate was negatively correlated to BSR in both populations (Fig. 1), however it was not related to the number of breeding males on land (r = – 0.024-0.116; $P_{10000} > 0.50$ for all comparisons).

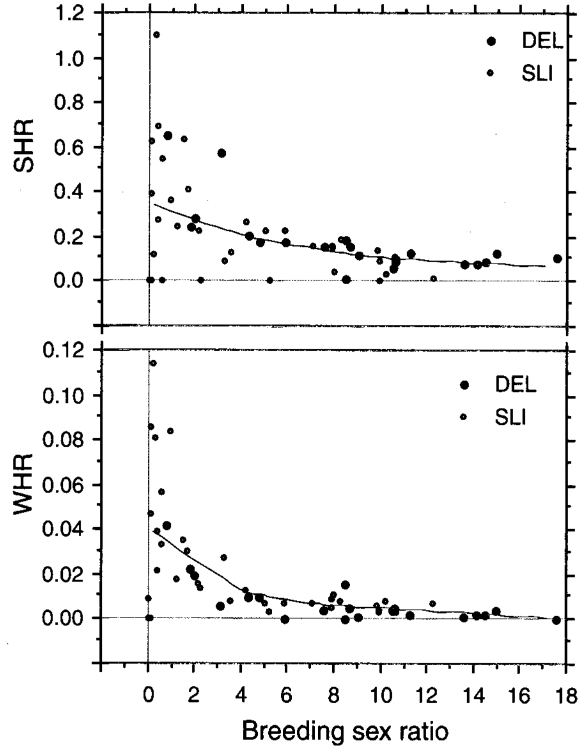

Fig. 1. — Simple harassment rate (SHR, top) and weighed harassment rate (WHR, bottom) plotted against the breeding sex ratio. Scatterplots of weekly values, at DEL (n = 20 harems of 2 breeding seasons; SHR-BRS: Pearson coefficient of correlation, r = – 0.684, $P_{10000} = 0.0002$; WHR-BRS: r = – 0.690, $P_{10000} = 0.0003$) and SLI (n = 36 harems of 3 breeding seasons; SHR-BRS: r = – 0.399, $P_{10000} = 0.0153$; WHR-BRS: r = – 0.525, $P_{10000} = 0.0006$; comparison between r values: SHR, $P_{10000} = 0.005$; WHR, $P_{10000} = 0.02$). Line is LOWESS smoother (tension = 66% of point; TREXLER & TRAVIS 1993), on pooled data from both populations.

Is harassment related to the socionomy of the breeding areas and harems?

Does the harassment rate vary between breeding sites? There was a large variation in the harassment rate at various breeding sites within the same population; we found 2.5 times variation of mean SHR between breeding areas at SLI (range = 0.18-0.47) and a 5 times variation at DEL (range = 0.11-0.57). Th variation in WHR was smaller (DEL: 0.006-0.040; SLI: 0.012-0.019). There was also a large variation in harassment rate between different harems both at DEL (SHR: 0.056-0.270; WHR: 0.009-0.098) and SLI (SHR: 0.080-0.545; WHR: 0.005-0.051).

Is the variation in harassment related to the socionomy of the harems? A large part of the context specific variation in harassment was related to variations in local demography and socionomy. Females were prone to two main sources of harassment: HH males and secondary, NHH males. Risk of harassment from HH males should depend mostly on the number of females available to each holder, i.e. on harem size, while harassment from secondary males should depend mostly on both harem size and the number of competing males. The variation in the mean daily number of males associated with different harems was large, in particular at SLI (SLI: CV = 1.415, n = 33 harems; DEL: CV = 0.750, n = 35). SLI harems had a significantly lower number of associated males than DEL harems (median = 0.212 vs 0.692; Exact Mann-Whitney test: U' = 799, P = 0.0061). Harems larger than the median had a larger number of associated males (Fig. 2) and the mean number of associated males was linearly related to harem size (Spearman correlation coeffi-

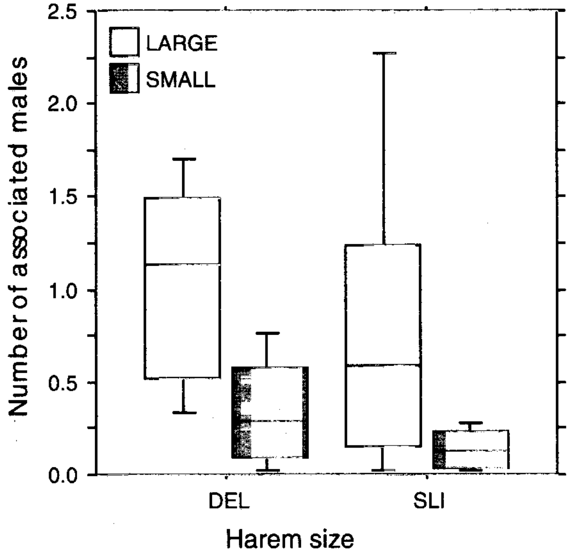

Fig. 2. — Boxplots of the number of associated males of small (S) and large (L) harems, split by population (DEL: median_L = 1.13 MAD_L = 0.34 N_L = 22, median_S = 0.29 MAD_S = 0.21 N_S = 11; Exact Mann-Withney test: U' = 209, P = 0.0004; SLI: median_L = 0.59 MAD_L = 0.47 N_L = 19, median_S = 0.11 MAD_S = 0.10 N_S = 16; Mann-Withney test, with randomization: U' = 249, P = 0.0009). Distributions were calculated as the mean seasonal number of associated males per harem; large harems are harems with a size at peak greater than the yearly median of harems size, small harems are harems with a mean size smaller then or equal to the yearly median.

cient, with randomization test: $r_S = 0.729$, n = 68 harems, $P_{10000} = 0.0005$). The correlation was significant in both populations, but it was slightly larger at DEL ($r_S = 0.820$, n = 33, $P_{10000} = 0.0004$ vs $r_S = 0.674$, n = 35, $P_{10000} = 0.0005$). The number of males per female was less correlated with harem size, and the correlation was significant only at SLI (DEL: $r_S = 0.274$, $P_{10000} = 0.12$; SLI: $r_S = 0.388$, $P_{10000} = 0.0275$).

Is there an interaction between the number of peripheral males and harem size in the determination of harassment rate? The mean number of interactions per observation period was positively related to harem size (Multiple linear regression, with randomization test on regression coefficients: $\beta = 0.674$, $P_{10000} = 0.0002$), but not to the mean number of associated males ($\beta = -0.184$, $P_{10000} = 0.59$) or the mean number of associated males per female ($\beta = 0.118$, $P_{10000} = 0.22$). The harassment rate was not related to the absolute or the relative number of associated males (SHR: $P = 0.81$ and $P = 0.12$; WHR: $P = 0.54$ and $P = 0.73$), but it was negatively related to harem size (SHR: $\beta = -0.236$, $P_{100000} = 0.060$; WHR: $\beta = -0.559$, $P_{10000} = 0.0072$). The weighed harassment index was also positively related to two indices of instability of harem control, the number of alpha males that controlled the harem during the season ($\beta = 0.302$, $P_{100000} = 0.0429$) and to the number of transition of alpha male ($\beta = 0.301$, $P_{10000} = 0.0385$). The effects of harem structure on harassment are summarized in a path diagram (Fig. 3).

Notwithstanding the larger number of associated males, large harems guaranteed a lower harassment rate, due to the larger number of females over which the harassment is distributed. Harassment was also lower in large harems due to the stability of control: in fact, harems with frequent changes of harem holders had an higher harassment rate, and large harems are usually controlled by males with higher resource holding potential, that are better able to maintain steady harem control.

Harassment inside and outside harems

Does harassment depend on male status and qualities?

DEL females had higher probability of interacting with NHH males than SLI females (36.7% of n = 2426 interactions vs 22.9% of n = 8694; Exact likelihood ratio test: G = 178.0, $P = 0.0000$).

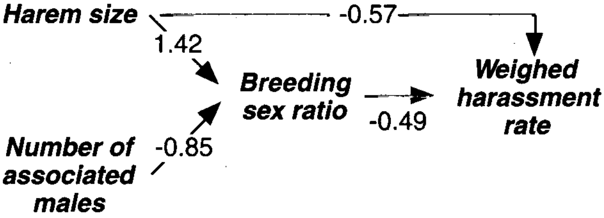

Fig. 3. — Descriptive path diagram of the effect of harem structure on harassment. Values are path coefficients calculated on standardized variables (Crespi & Bookstein 1989). Harem size had both a direct negative effect on harassment rate and an indirect negative effect through is positive effect on the breeding sex ratio; the number of associated males had only an indirect positive effect on harassment rate due to its negative effect on BSR; BSR had a negative effect on on harassment rate.

As expected,. harem females interacted more with the main breeding males (DEL + SLI data: 85.1%, n = 11575 interactions) while non-harem females interacted more with secondary males (46.5%, n = 1246); the proportion of interactions with secondary males was significantly greater for non-harem females (Fisher's exact test: $P = 0.0000$). Of the interactions involving harem females (n = 10349) 80.5% were accomplished by the alpha of the harem. Main breeding males interacted with isolated females in a lower proportion of cases (7.4% of n = 10638) than did secondary males (28.3% of n = 2399; Fisher's exact test: $P = 0.0000$).

There was a notable variation in the absolute interaction rate between harem holders (1995: 0.17-2.32 per hour of observation; 1996: 0.14-2.74; 1997: 0.34-2.14); hence females held by different males were prone to different harassment pressures. Some of the variation in the likelihood of harassment inside harems seems to depended on the "personality" of the alpha male: for example, in a 73 female harem of 1996, the interaction rate was very low because of the very high resource holding potential of the alpha male, that kept away peripheral males, combined with his very low tendency to interact with females; the same pattern was shown in another harem held by the same male in 1997.

Is harassment affect by female position in the harem?

In a sample of 9710 harem interactions, 56.3% involved core females (50.2% of 6265 interactions at SLI and 67.3% of 3445 at DEL; Exact likelihood ratio test: G = 268.2, $P = 0.0000$). From data on harem structure, we calculated that a mean of 30% of females were external. Hence, if interactions are homogeneously distributed between core and external the expected proportion of interactions involving externals should be 0.3: external females interacted more frequently than expected in both populations (Binomial test: $P = 0.0000$ in both cases).

Core females had a lower likelihood of interacting with secondary males: 6.6% of the interactions of core females (n = 5461) involved secondary males, while 24.9% of the interactions of external females (n = 4242) involved secondary males (Exact likelihood ratio test: G = 651.7, $P = 0.0000$); 9.3% of the interactions of core females (n = 4664) involved non-alpha males, while 35.1% of interactions of external females (n = 3838) involved non-alpha males (Exact likelihood ratio test: G = ·862, $P = 0.0000$). There was a clear trend in the percentage of interactions with secondary males which increased from core, to external, to isolated females (Fig. 4, left). Notwithstanding the confounding effect of the increase of interaction rate with age, whatever the contest, there was a significant trend of increase with age in the proportion of interactions with core females (Fig. 4, right).

Is the harassment of isolated females particularly intense and dangerous?

Do females frequently breed alone? Isolated females with pups were rare on SLI. Four types of occurrences of isolated females after parturition were observed: females that gave birth alone and remained alone during the whole suckling period; females that gave birth alone and then joined a harem; females that gave birth in a harem but lactated alone; females left alone at the end of the breeding season after the break-up of the harem system. The percentage of females that were alone at parturition was 0.97% (n = 517 females) in 1995, 1.90% in 1996 (n = 527) and

3.73% in 1997 (n = 563). Every year the majority of females that give birth alone then joined a harem before coming into oestrus (100% in 1995, 80% in 1996 and 66.7% in 1997). Isolated females sometimes gave birth in very unsuitable places, and then moved with their pups for long distances (more than one km) to reach a harem, taking up to 4 days to reach their destination. Therefore, the proportion of females that remained alone during the whole period of suckling was always very small: none in 1995, 0.38% in 1996 and 1.24% in 1997. Only one female, in 1997, gave birth inside a harem and carried on suckling alone for 95% of the suckling period . During each breeding season 1.1-1.8% of females remained alone at the end of the season.

Is harassment on isolated females very intense? Due to their rarity, isolated females represented a scarce mating opportunity for NHH males, but notwithstanding this, the few isolated females were often harassed, and the longest episodes of harassment (up to more than 12 hr in length) involved isolated females. The median length of interaction was greater for isolated females than for harem females (108 vs 69 sec; Mann-Whitney test: U' = 587685, n_{Isolated} = 338, n_{Harem} = 2727, z = – 4.532, $P < 0.0001$). The median length of body contact between male and female was longer for interactions with isolated females (192 vs 81 sec; U' = 8584.5, n_{Isolated} = 41, n_{Harem} = 281, z = – 3.525, $P < 0.0005$). In interactions including different contact phases, the median length of each phase was longer for isolated females (95.5

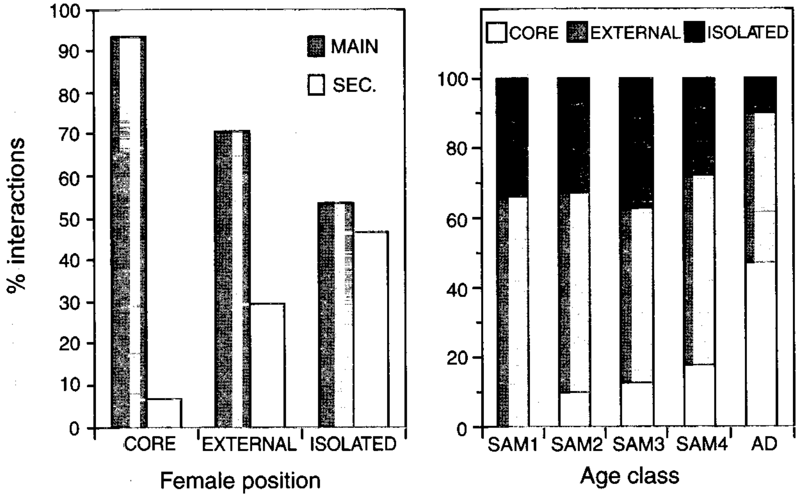

Fig. 4. — Position of the female and the phenotype of interacting males. Left: bar chart showing the percentage of interactions involving females with different positions within the harems (core, external and isolated females), by male seasonal status (main breeding males, secondary males; increase of involvement by secondary males with decrease in centrality of position, Exact Cochran-Armitage test: *standardized trend statistic* = 37.01; $P = 0.0000$). Right: stacked bar chart showing the percentage of interactions involving males of different age classes (SAM1 to AD) by position of the female within the harems (higher representation of subadult classes in interactions involving isolated females, Exact Cochran-Armitage test: *standardized trend statistic* = – 19.21; $P = 0.0000$; lower representation of subadult classes in interactions involving core females, Exact Cochran-Armitage test: *standardized trend statistic* = 14.36; $P = 0.0000$).

vs 42 sec; Exact Mann-Whitney test: $U' = 871.5$, $n_{Isolated} = 13$, $n_{Harem} = 85$, $P = 0.02$; note small and unbalanced samples; power of equivalent t-test: $1\text{-}\beta = 0.64$).

Isolated females were herded more often than harem females (31.1%, n = 904 vs 9.9%, n = 7860; Fisher's exact test: $P = 0.0000$). Isolated females interacted 3 times more with subadults than did harem females (31.7%, n = 901 vs 11.1%, n = 7853; Fisher's exact test: $P = 0.0000$); the larger proportion of interactions with subadult males for isolated females was true for all kinds of interactions, but the difference was particularly large for the most harassing interactions (pure aggression: 85.7% due to subadults for isolated females vs 12.8; herding: 12.5 vs 2.4%). In all, isolated females were harassed for longer than harem females (sometimes for exceptionally long periods), they were herded more frequently, and they interacted more with subadult males.

Does isolated females react differently to harassment? Both harem and isolated females tried to escape from harassing males by move away, but isolated females did that more frequently (71.6%, n = 261 interactions vs 50.2%, n = 2795; Fisher's exact test: $P = 0.0000$) and moved more (median = 10.3 steps vs 5.9; Mann-Whitney test, with randomization: $U' = 12572$, $n_{Isolated} = 30$, $n_{Harem} = 622$, $P_{10000} = 0.006$; note unbalanced samples; power of equivalent t-test: $1\text{-}\beta = 0.80$). Isolated females protested less frequently than harem females, but the difference was small (80.8%, n = 317 vs 85.8%, n = 3850; Fisher's exact test: $P = 0.0202$). SES females tended to protest always, regardless of their status. Female vocalization was observed less frequently during male approaches towards isolated females (77.7%, n = 265 vs 84.2%, n = 2819; Fisher's exact test: $P = 0.0202$).

Is harassment by secondary males concentrated on isolated females? Differences between SLI and DEL were found in the frequency of interactions and matings by NHH males with isolated females. The percentage of interactions by NHH males was higher at DEL than at SLI (36.9% of 2433 interactions vs 23.3% of 8749; Fisher's exact test: $P = 0.0000$); the percentage of matings by NHH males was also higher at DEL (23% of 883 matings vs 11.2% of 1370; Fisher's exact test: $P = 0.0000$). Hence, harassment on isolated females due to secondary males was higher and isolated females where a better source of matings for secondary males at DEL than at SLI. The trend of increase in frequency of interactions with age class was different between harem and non-harem females, with all subadult classes more represented in interactions with the latter (Fig. 4, left).

Effects of harassment

Does harassment disrupt female activity budgets?

The first effect of harassment should be disruption of time budgets; in particular, we expected harassment to increase activity time and hence reduce the time available for resting. SES females spent most of their time on land resting (88.7 ± 7.3% of total time on land, n = 697 females; see also McCann 1982). To evaluate the variation of time budgets among harems, mean harem values were obtained from the time budgets of identified females; we first calculated mean values for individual females and then mean harem values (number of females used in calculations: 3-42 per harem). Active time varied between harems (Kruskall-Wallis test, 1995: $H_{10} = 48.2$, $P < 0.0001$; 1996: $H_{10} = 80.8$, $P < 0.0001$; 1997: $H_{11} = 23.1$, $P < 0.0171$). The mean active time of females was lower in large harems (= harems bigger than the median harem size) than in small harems (2.6%, n = 18 vs 3.5%, n = 11; t-test, with randomization, on arcsine transformed proportions: *mean diff.* = – 0.94; P_{200000} = 0.03) and active time decreased with both harem size (Pearson correlation coefficient, with randomization test: r = – 0.478, n = 29, P_{10000} = 0.008) and the breeding sex ratio (r = – 0.479, P_{10000} = 0.008). Male activity disrupted female activity: mean active time had a positive correlation with the intensity of harassment (r = 0.424, P_{10000} = 0.02).

The most serious effect of harassment on activity rhythms should be interruption of suckling, but this was very rare on Sea Lion Island, happening in just 3.1% of the cases (n = 258 interactions involving females with pups). The stopping of suckling due to interaction with males was less frequent than that due to female aggression or the generic diversion of pup attention (unpublished data).

Does harassment result in the separation of mother and pup?

Mother-pup separation (pup farther than one SBL away from the mother) was quite rare, happening in 29.3% of male-female interactions (n = 437). The median length of separation was 4 min (MAD = 2), and the maximum was 20 min. In a larger sample of interactions (n = 2983) clear separation, lasting more than 1 min, was recorded in just 6.1% of cases. No cases of permanent separation were observed, with just one exception: in 1997 a mother was separated from her pup by a secondary male just after parturition, the pup was adopted by another female (who gave birth almost simultaneously with the first one), and the true mother was not able to recover her pup (while the adoptive mother weaned both pups).

The likelihood of separation depended on the kind of interaction: the frequency of separation was minimal for simple approaches (25.4%, n = 260) and maximal for herdings (58.1%, n = 31); the difference in the proportion of separations was significant (Fisher's exact test: *P* = 0.0000). The length of separation from the pup was correlated with the length of the interaction (Spearman correlation coefficient with randomization test: rs = 0.54; n = 78; P_{10000} = 0.0005), and depended on the interaction type, with longer separations for mounts (8.7 ± 0.8 min, n = 13) and copulations (7.0 ± 0.7, n = 17; one factor ANOVA, with randomization test: *P* = 0.0000).

There was no effect of female position on the likelihood of separation: the same proportion of interactions resulted in separation for harem and non-harem females (29.4%, n = 422 vs 26.7%, n = 15; Fisher's exact test: *P* = 1), and for core and non-core females (33.3%, n = 84 vs 34.1%, n = 229; Fisher's exact test: *P* = 1); there was also no effect of female reaction to male approach on the likelihood of separation (36.4%, n = 33 for non-protesting females vs 47.2% n = 142 for protesting females; Fisher's exact test: *P* = 0.33; see GALIMBERTI et al. in press for a definition of protest).

A larger proportion of separations resulted from interactions with adult (33.0%, n = 367 vs 10.0%, n = 70; Fisher's exact test: *P* = 0.0000), harem holding (34.0%, n = 359 vs 7.7%, n = 78; Fisher's exact test: *P* = 0.0000) males; we also found a gradual increase in the proportion of separation with increase in age class (from 6.3% of younger subadults to 33.0% of adults; Exact Cochran-Armitage test: *standardized trend statistic* = 31.73; *P* = 0.0017), and a decrease in the proportion of separations with decrease in male status (from 34.3%, n = 344 for alphas to 7.7%, n = 26 for solitary males; Exact Cochran-Armitage test: *standardized trend statistic* = – 4.40; *P* = 0.0000).

Does harassment affect female breeding or survival?

The effect of harassment on weaning weight. We compared mean weanling weights (see GALIMBERTI & BOITANI 1999 for details of the weighing protocol) of weanlings born in different harems to a global measure of harassment, the mean seasonal per female interaction rate. We found a small, non-significant negative correlation (Pearson correlation coefficient, with randomization test: $r = -0.1776$, $n = 9$ harems, $P_{10000} > 0.64$); the correlation was in the expected direction but the effect size was very small (power of the equivalent parametric test: $1\text{-}\beta = 0.21$).

The wounding of females. The rate of wounding of females during interactions with males was low: wounds that produced obvious scars were observed in 2.9% of 2082 interactions; in 85.7% of these cases we observed just superficial abrasions, that lasted for a few days. Bites where concentrated in the fore part of the body: 65.5% of these wounds were in the neck area, while 18.8% were concentrated in the nape, and just 3.1% on the back. Females have a thick dermal shield in the neck area (LE BOEUF & MESNICK 1990), but neck bites were more frequent during copulations (superficial wounds were observed in 11.3% of 247 copulations but in only 1.6% of 1665 interactions of other kinds; Fisher's exact test: $P = 0.0000$), and female usually mate at the end of their presence on land, when, due to fasting, they have lost about 1/3 of their weight and hence have reduced protection in the neck area.

According to LE BOEUF & MESNICK (1990), two kinds of bite are particularly dangerous in northern elephant seals, a bite on the head that may result in brain damage and a bite on the back that may result in puncture of the extradural vein. Crushing of female skulls was reported for SES of Macquarie Island (CARRICK & INGHAM 1962). We observed bites in the nape area quite often, but we had no indication of serious damage due to these bites. In 1997 one female was severely bitten in the head area, but she was anyway able to wean her pup and return to sea. In 1997 two females received deep wounds, both of them in the dorsal area, one of them by a secondary male and the other by the alpha of the smallest harem. These wounds, deeper than usual and resulting in the removal of a thick dermal layer, were much less deep than the scars due to sharks and killer whales found in many adult, healthy individuals. Both females successfully weaned their pup notwithstanding the wounds, and all of them survived until the next breeding season. During three breeding seasons at SLI, we recorded no cases of female death due to male harassment, and the same was true for two breeding seasons at DEL.

Most of the wounds were not caused by secondary males but by adult (3.3%, $n = 1707$ vs 0.8%, $n = 373$; Fisher's exact test: $P = 0.0045$) and experienced males (4.4%, $n = 1089$ vs 1.2%, $n = 991$; Fisher's exact test: $P = 0.0000$). This result, although contrary to customary expectations, was not unexpected because on SLI wounding happened mainly during copulations, which were monopolized by adult males.

The effect of harassment on female survival. At harem level, there was a slight negative correlation between harassment and the likelihood of survival to the next season, but the correlation was non-significant (Spearman correlation coefficient, with randomization test: $r_S = -0.460$, $n = 8$ harems, $P_{10000} = 0.24$; the power of the equivalent parametric test was very low: $1\text{-}\beta = 0.20$). We verified the effect of harassment on the survival of individual females in a sample of 278 females that bred in 1996, 79.1% of which survived until 1997. The mean harassment level in 1996 for survivors was only slightly lower than that for non-survivors (SHR: 0.15 ± 0.12, $n = 220$ vs 0.18 ± 0.11, $n = 58$; t-test, with randomization: *mean diff.* = 0.024, $P_{10000} = 0.14$; power analysis: effect size = 0.21, $1\text{-}\beta = 0.42$; WHR: 0.047 ± 0.046 vs 0.055 ± 0.049; t-test, with randomization: *mean diff.* = 0.0085, $P_{10000} = 0.24$; power analysis: effect size = 0.18, 1-β = 0.33). In two logistic regressions with survival to 1997 as a dependent variable there was a negative effect of harassment on survival, but it was very slight and non-significant [SHR: b = – 1.57, se(b) = 1.15; LR test: χ_{21} = 1.81, $P = 0.18$; WHR: b = – 3.54, se(b) = 2.89; LR test: χ_{21} = 1.43, $P = 0.23$].

DISCUSSION

Breeding demography and the dilution of harassment risk

Grouped breeding may entail significant costs to females (BARTHOLOMEW 1970) and it may also reduce lifetime breeding success (RIEDMAN & LE BOEUF 1982). One of the benefits of grouped breeding is defense from male aggressive mating tactics, through a dilution effect and the disruption of marginal males by higher ranking males (TRILLMICH & TRILLMICH 1984). To promote grouping through a dilution effect, harassment should be related to the ratio between the number of females and the number of harassing males, that will in turn depend on local demography and socionomy. In SES we found evidence that local demography affects harassment both at population and harem level. At population level, the frequency of harassment was negatively related to the breeding sex ratio: hence, due the gaussian shaped variation of breeding sex ratio across the breeding season, females that breed in different phases of the season were exposed to very different levels of harassment. At harem level, females breeding in larger harems suffered a lower level of harassment, both by alpha males and by secondary males. Reduction in harassment by the alpha was due to a pure dilution effect, while reduction in harassment by secondary males was due to both a dilution effect and disruption by more dominant males. We examined a large spectrum of harems, with a more than 10-fold variation in harem size, and hence our results are a strong indication of the positive effect of female clustering on harassment reduction.

A confirmation of the effect of grouping comes from an examination of harassment on females that breed alone. Isolated breeding is a risky strategy for pinniped females (*Otaria byronia*: CAMPAGNA et al. 1992a). Isolated females were quite rare in our studied populations, and most females that gave birth alone strenuously tried to reach an harem. Notwithstanding their rarity, isolated females were harassed more frequently and for longer than harem females, they also interacted more with subadult males, and were involved in the longest and most dangerous episodes of harassment.

Harassment as a male mating tactic

To serve as a successful mating tactic, male use of force during mating attempts should be effective. Herding, although quite common in pinnipeds mating systems, is usually not very effective (MILLER 1974, BONESS 1991). Herding is peculiar to *Mirounga* among the Phocidae (it occurs rarely in *Halichoerus grypus*: CAMERON 1967), while is quite common in Otariidae. It is used frequently and effectively to recruit females in *Callorhinus ursinus* (BARTHOLOMEW & HOEL 1953), frequently but less effectively in *Arctocephalus* spp. (BONNER 1968, MILLER 1974, VAZ-FERREIRA et al. 1984) and *Neophoca cinerea* (MARLOW 1975), while it is infrequent and ineffective in *Phocarctos hookeri* (MARLOW 1975).

SES males are able to effectively control female movements by herding. In our study populations, herding was employed frequently by both main breeding males and secondary males. Alpha males were very effective in herding females, and they were able to recruit females to harems and to stop escaping females. Biting was employed by alpha males during most copulations as a way to control protest by the female, and to maintain intromission. In general, harem females suffered a frequent but not intense harassment by alpha males, that were not able to recognize oestrus by chemical cues and resorted to approach as a method of testing breeding status of females by their behavioural reaction (McCann 1981). By a combination of herding and biting secondary males were able to force copulation: although copulations with anoestrus females were rare, males were able to achieve intromission even with very reluctant females. Hence, harassment in southern elephant seals seems to be a true, and somewhat effective, mating tactic, as in other mammal species (Smuts & Smuts 1993).

The costs of harassment

To be a significant pressure in the evolution of female breeding behaviour, harassment should be costly for females. One of the most striking difference between our results and previous work on northern elephant seals (Le Boeuf & Mesnick 1990, Mesnick & Le Boeuf 1991) concerns the cost of harassment. Harassment may result in-short term costs (disruption of activity rhythms and time budget, interruption of suckling, temporary separation from the pup) and in long-term costs (definitive separation from the pup, reduction of maternal investment, physical damage to the female, reduction in the likelihood of survival). In our study, male-female interactions often resulted in a significant disruption of the female activity pattern, and in particular in a reduction of resting time. This was the only clear cost of harassment. Interruption of suckling bouts was rare and short-lasting and separation of pups from the mother was also rare, was not-long lasting, and, with very few exceptions, never definitive (see also Baldi et al. 1996). While in the northern species, that breed mostly on crowded beaches, separation due to male harassment is an important source of pup mortality (Riedman & Le Boeuf 1982), in our studied populations density was low, the harems were smaller than in the northern species, and mortality was very low and mostly due to still births (DEL: Baldi et al. 1996; SLI: Galimberti & Boitani 1999). Harassment had no effect on the likelihood of weaning the pups successfully, except for isolated females, that were rare and usually able to complete lactation. These mild effects of harassment on female breeding success are likely to be related to the low crowding of the breeding areas. The effects of harassment were not studied in detail in any high density SES population, but most subantarctic populations, with higher density of females and larger and more crowded harems, have higher pups mortality rates (Galimberti & Boitani 1999). Serious physical damage of females due to male aggression was an exceptional phenomenon in our study populations, and we collected no indications of possible death of females related to male behaviour.

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