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Harassment during arrival on land and departure to sea in southern elephant seals

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During the breeding season female elephant seals spent most of their time on land inside harems. When they arrive on land before joining harems, and when they leave harems to return to sea, they are exposed to secondary males and may suffer intense harassment. Hence, arrival and departure present an ideal opportunity to test hypotheses concerning female tactics of harassment reduction. We studied harassment during arrival and departure in two southern elephant seal populations at Punta Delgada (Valdés Peninsula; DEL hereafter) and Sea Lion Island (Falkland Islands; SLI hereafter). Females were less likely to be intercepted by males during arrival than during departure. They also arrived mostly at high tide, thereby reducing the distance from water to the harems. Interception rate and harassment during departure were higher at DEL, where male density and the breeding sex ratio affected the likelihood of interception; on SLI, the socionomy had a small effect. Harassment was higher at low tide at DEL but not at SLI, because tide level variation was larger at DEL and this resulted in a larger variation in the distances of the harems from the water. Females departed more often than expected at high tide at DEL but not at SLI. In both populations females departed directly to sea, rarely stopping before reaching the water, and they never sought contact with males. Social distraction during departure significantly reduced the likelihood of interception. Departures were more frequent during periods of high social activity, and females departing just after other females were less prone to harassment. Accepting copulations with secondary males may reduce the dangerous effects of harassment: interactions occurring during departure were less frequently protested, but we found no indication that departing females were facilitating copulations in a special manner. Quantity and quality of protest during departures was similar to protest during the last days of residence of the females in the harem.

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

INTRODUCTION

Male harassment of females during breeding interactions is a widespread phenomenon that may entail significant cost for the female. Hence, females are expected to adopt behavioural tactics to reduce the rate and costs of harassment (SMUTS & SMUTS 1993). In elephant seals (*Mirounga* spp.) females that come to land for breeding spent most of their time inside harems. Grouped breeding and choice of larger harems are an affective ways of reducing harassment risk and costs (GALIMBERTI et al. 2000a). On the contrary, when arriving on land, before joining harems, and when leaving harems, to come back to sea after weaning, females are exposed to a high harassment risk. In particular, they may be approached by young, marginal males, that are particularly dangerous due to their high libido, their low opportunity to approach females in the very despotic mating system, and their only partially mature mating behaviour (MESNICK & LE BOEUF 1991). Hence, the arrival and departure of female elephant seals seem a very good opportunity to test hypotheses concerning harassment reduction tactics.

In northern elephant seals (*M. angustirostris*) harassment during departure is particularly intense and dangerous, and may result in the death of the female, although this is a rare phenomenon (LE BOEUF & MESNICK 1990). Almost all northern elephant seal females are intercepted during departure, a large percentage of the them mate at least once before reaching the water, and females are sometimes badly wounded during mating attempts (COX & LE BOEUF 1977, MESNICK & LE BOEUF 1991). The breeding behaviour of secondary males is usually very aggressive, and females had few opportunities to escape approaching males (LE BOEUF 1972). Departing females seem to fine tune their behavioural reaction to reduce the risk of physical damage, and on the basis of this observation a "trade sex for protection" hypothesis was proposed (MESNICK & LE BOEUF 1991): females should reduce protest and facilitate intromission if this implies a reduction of risk of being severely wounded and an increase in the likelihood of being protected from other approaching males.

The mating system of southern elephant seals (*M. leonina*; SES hereafter) is very similar to that of the northern species (MCCANN 1981). The level of despotism and the libido of the males are as high or higher, and hence the harassment of females outside harems is expected to be very intense (GALIMBERTI et al. 2000b). We present data on arrival and departures of females in two populations of SES, Punta Delgada (Valdés Peninsula, Argentina; DEL hereafter) and Sea Lion Island (Falkland Islands; SLI hereafter). In a previous companion paper, we found harassment risk to strongly depend on local demography (GALIMBERTI et al. 2000b) and on specific social context (GALIMBERTI et al. 2000a). Hence, we analyzed harassment during arrival and departures in two populations with different topography and tide regime, demography and socionomy, and level of despotism in the mating system (DEL: CAMPAGNA et al. 1993, GALIMBERTI 1995; SLI: GALIMBERTI & BOITANI 1999). We evaluate the level of harassment during arrival and departure, we relate harassment differences to variations in the abiotic and social environment, and we tested various hypotheses concerning female tactics of harassment reduction.

METHODS

We carried out detailed observations of female arrival and departure during two breeding seasons (1993 and 1994) at Punta Delgada and during three breeding season (1995-1997) at Sea Lion Island. Details of the populations, behavioural observation protocols, definitions, and general statistic procedures were presented in a companion paper (GALIMBERTI et al. 2000b). We outline here only aspects of methodology specific to arrival/departure data collection and analysis.

We collected data for 133 arrival at SLI, and we also analyzed a sample of 42 arrivals at DEL for which only information about time, place and tide level was available; we collected data for 349 departures, 120 at DEL and 229 at SLI. We recorded, for arrivals and departures, details about time, place and tide level; the number of males in the area, the number of males that competed for the female, the number of males that interacted and mated with her; the number of interactions and actual copulations; the length of the episode; the presence/absence of mate guarding. We recorded details of the identity, size class and the status of the female, and the identity, age class, size class, status, and the dominance rank of all the males that competed for the female. We also recorded detailed information about the kind, result, and the level of female protest for every mating attempt. We were not always able to record all the data for each arrival or departure event, hence sample size varied between the analyses. We defined high tide as the 3 hr (± 90 min) period around maximum tide level as calculated from tide tables. To verify the effect of tide level on various events, we calculated tide level at time of each event from tide tables (SERVICIO DE HIDROGRAFIA NAVAL 1993, 1994; PROUDMAN OCEANOGRAPHIC LABORATORY 1995, 1996, 1997) applying an harmonic model.

We tested differences between DEL and SLI using the Fisher exact test for categorical variables (run in StatXact Turbo 2.11, Cytel Software Corporation), and the t-test with randomization (MANLY 1997) for continuous variables (run in RT 2.0, MANLY 1996). We analyzed the effect of environmental and social factors on the likelihood of interception (as binary variables: yes/no) using logistic regression, with test of coefficients based on change in the log likelihood (HOSMER & LAMESHOW 1989). We run logistic regression in SPSS 6.1 for Power Macintosh (SPSS Inc.). We analyzed the relationships between social/environmental factors and harassment variables using OLS regression with a randomization test on coefficients (MANLY 1997). Regression results include standardized coefficients (β) to facilitate comparison of the relative magnitude of effects of independent variables. We run OLS regression tests in RT 2.0.

RESULTS

Harassment during arrival

Is interception during arrival frequent?

At SLI, in 40% of 100 arrivals at least one male tried to intercept the female, and in 35% interception was successful. In this sample of arrivals a mean of 0.58 ± 0.84 males tried to intercept the female, and 0.44 ± 0.69 males interacted with the female. Arriving females were usually pregnant females who protested heavily during mating attempts. In spite of this, some very rare cases were observed in which females copulated during the arrival phase: two females in 1996 (one returned to the sea immediately after copulation) and three females in 1997 (two departed immediately after copulation).

Is harassment risk equal during arrival and departure?

At SLI interception risk during arrivals was lower than during departure. The percentage of intercepted arrivals was lower than the number of intercepted departures (23.3% n = 100 vs 40.6% n = 229; Fisher's exact test: $P = 0.0009$). Males tried to intercept females less frequently during arrival than during departure (40.0% n = 100 vs 83.8% n = 211; Fisher's exact test: $P = 0.0000$), and they were less frequently able to actually approach the female (35.0% n = 100 vs 72.0% n = 211; Fisher's exact test: $P = 0.0000$). The mean number of males that tried to intercept females was lower during arrival (0.56 vs 1.77, t-test with randomization: $P_{10000} = 0.0000$), as was the mean number of males that actually intercepted femals (0.44 vs 0.93, t-test with randomization: $P_{10000} = 0.0000$) and also the mean number of interactions with the female (0.27 vs 1.04, t-test with randomization: $P_{10000} = 0.0000$). In all, the risk of harassment was much lower for arriving females than for departing ones.

Do females exploit tide level variation to reduce harassment during arrival?

Evidence was found that DEL females regulate the timing of arrival to reduce the distance to the harems. In a sample of 42 arrivals recorded in 1994 and observed from beginning to end, 81% happened during high tide (Binomial test: $P = 0.0001$). Due to the large variation of tide level at DEL (see below), arrival during high tide allowed females to leave the water close to the harems. All low tide arriving females were intercepted (n = 8), while just 30% of high tide arrivals were intercepted (n = 34; Fisher's exact test: $P = 0.0002$). On the contrary, on SLI the likelihood of interception during arrivals was not different between low and high tide (21.7% n = 92 vs 26.8% n = 41; Fisher's exact test: $P = 0.51$). There were no differences between low and high tide arrivals in the number of competing males (t-test, with randomization: *mean diff.* = 0.31, $P_{10000} = 0.11$), nor the number of interacting males (*mean diff.* = 0.24, $P_{10000} = 0.12$), nor the number of interactions (*mean diff.* = 0.03, $P_{10000} = 0.80$). Of 133 arrivals recorded at SLI, 31% happened during high tide, a proportion not significantly different from the expected (Binomial test: $P = 0.33$).

Harassment during departure

Is the socionomy outside harems different from the socionomy inside?

Sex ratio inside harems was heavily biased towards females (mean 50 females per male and up to 108 at DEL; 43 females per male and up to 119 at SLI), while outside harems during departure there were more males than females (mean: 13 males per female and up to 22 at DEL; 6 males per female and up to 15 at SLI). The social habitat to which the female is exposed changed dramatically during departure. Inside harems, females were surrounded by other females and interacted mostly with just one male, the harem holder (DEL: 69.0%, n = 2176 interactions; SLI: 83.2%, n = 7798), and beta males were rare in our studied populations (at SLI just 3 harems during the whole study had one beta male for 2 or more consecutive days).

Is the risk of interception different between populations?

The risk of interception during departure was higher at DEL: 59.2% of 120 departing females were intercepted outside the harem vs 40.6% of 229 at SLI (Fisher's exact test: $P = 0.0011$). The most substantial difference between the populations was the location where females were intercepted: at DEL 80.3% of 71 departing females were intercepted while still on land, whereas at SLI only 21.5% (n = 93) were intercepted on land (Fisher's exact test: $P = 0.0000$). At DEL, in a sample of 60 departures with copulations by secondary males, 80.0% happened on land, while, in an analog sample of 67 departure at SLI, just 23.9% of the copulations where accomplished on land (Fisher's exact test: $P = 0.0000$).

A very large difference in harassment risk during departures was found between the two study populations. All indicators of harassment had higher values at DEL than at SLI: DEL females were involved more frequently in departures with mating attempts and actual copulation were chased by more males, interacted and copulated more, and with more males, had longer departures, and had more chances to interact with subadults and secondary males (Fig. 1).

Does the risk of interception change in time and space?

We expected the risk of interception to be higher during the last phase of breeding season, because the density of secondary males remained high while the number of females was reduced. The percentage of interceptions was in fact higher during the post peak phase, but the difference was very small at DEL (62.5% , n = 8 vs 58.9%, n = 112) and, although larger, was non-significant at SLI (47.8%, n = 23 vs 39.7%, n = 204; Fisher's exact test: $P = 0.50$). The percentage of intercepted departures was homogeneous during different weeks of the breeding season (Exact likelihood ratio test: $G = 3.6$, $P = 0.85$). All indices of harassment level were homogeneous between phases of the season (ANOVA tests, with randomization: $F = 0.34$-1.84, $P > 0.15$ for all test). The risk of interception was almost homogeneous between the main breeding zones both at DEL (45.8-72.7%; Exact likelihood ratio test: $G = 5.35$, $P = 0.45$) and at SLI (42.4-42.6%; Exact likelihood ratio test: $G = 0.003$, $P = 1$). In all, the risk of interception and harassment was homogeneous in time and space.

Determinants of the risk of interception and harassment

Effect of local demography and socionomy. There was a large difference between DEL and SLI in the local demography at the moment of departure. At DEL departures occurred in areas with greater number of breeding males (13.7 ± 4.25 males, n = 86 vs 5.7 ± 2.91, n = 101; t-test with randomization: *mean diff.* = 8.0; $P_{10000} = 0.0001$), greater number of secondary males (10.9 ± 3.72 vs 4.5 ± 2.88;

mean diff. = 6.2; P_{10000} = 0.0000) and lower sex ratio (5.2 ± 3.29 vs 9.3 ± 10.90; *mean diff.* = – 4.0; P_{10000} = 0.0000).

There was a significant effect of demography on the risk of interception in both populations, but different factors were involved. At DEL, the likelihood of interception depended mostly on the density of females; it was related with the number of females [Logistic regression: n = 87 departures; b = 0.019, se(b) = 0.005; LR test: G_1 = 15.61, P = 0.0005] and the sex ratio [b = 0.366, se(b) = 0.091; LR test: G_1 = 22.88, $P < 0.0001$]. On the contrary, at SLI, the main demographic determinant of likelihood of interception was simply the number of males [n = 102 depar-

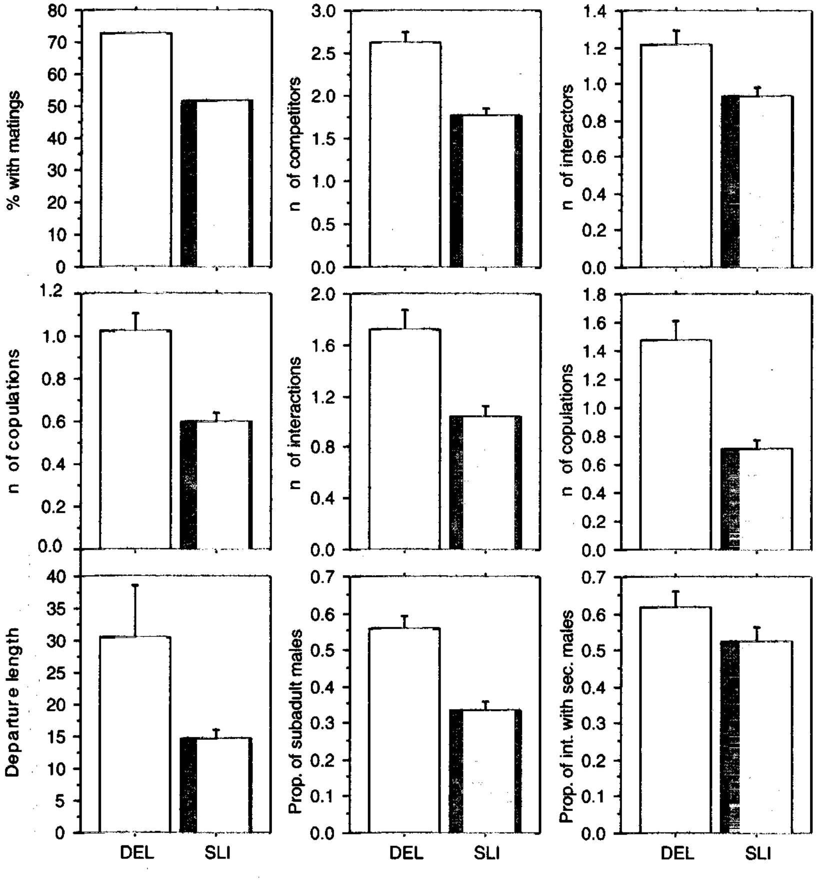

Fig. 1. — Bar chart of harassment variables (mean ± SE) during departures at DEL (n = 117 departures) and SLI (n = 211; percentage with actual matings, including copulations of the alpha inside the harem just before departure: 72.7% vs 51.9%, Fisher's exact test: P = 0.0003; number of males who competed: 2.61 ± 1.51 vs 1.77 ± 1.32; t-test, with randomization: *mean diff.* = 0.85; P_{10000} = 0.0000; number of males who interacted: 1.21 ± 0.89 vs 0.93 ± 0.74; *mean diff.* = 0.29; P_{10000} = 0.0016; number of males who copulated: 1.03 ± 0.87 vs 0.60 ± 0.64; *mean diff.* = 0.43; P_{10000} = 0.0000; number of male-female interactions: 1.73 ± 1.69 vs 1.04 ± 1.271; *mean diff.* = 0.69; P_{10000} = 0.0001; number of copulations: 1.47 ± 1.51 vs 0.71 ± 0.88; *mean diff.* = 0.76; P_{10000} = 0.0000; departure length: 30.6 ± 26.7 min vs 14.6 ± 13.6; *mean diff.* = 16.0; P_{10000} = 0.0038; proportion of subadults among interacting males: 0.56 ± 0.34 vs 0.33 ± 0.35; *mean diff.* = 0.23; P_{10000} = 0.0000; proportion of interactions with secondary males: 0.62 ± 0.43 vs 0.52 ± 0.46; *mean diff.* = 0.093, P_{10000} = 0.11).

tures; b = 0.162, se(b) = 0.074; LR test: G_1 = 5.07, P = 0.0244], and in particular the number of secondary, non-harem holder (NHH) males [b = 0.183, se(b) = 0.076; LR test: G_1= 6.35, P = 0.0153].

Demography had an effect also on harassment risk, and again different aspects of demography were involved in the two populations. At DEL, the density of females was positively related to the number of competiting males (Linear regression, with randomization test on slope: n = 87 departures; β = 0.261, P_{10000} = 0.015) and the number of interacting males (β = 0.294, P_{10000} = 0.0057), but not to the number of copulating males (β = 0.016, P_{10000} = 0.55). At SLI, the density of secondary males was positively related to the number of competiting males (Linear regression, with randomization test on slope: n = 97 departures; β = 0.224, P_{10000} = 0.028) and the number of interacting males (β = 0.188, P_{10000} = 0.049), but not to the number of copulating males (β = 0.156, P_{10000} = 0.12).

Effect of environmental factors: tide level. There was a significant difference between the two study populations in the variation of water level between low and high tide across the whole breeding season (3.25 ± 0.88 m, n = 679 at DEL vs 0.98 ± 0.33, n = 971 at SLI; t-test: t1648 = 73.2, P < 0.0001): the variation of water level during tides at DEL was more than 3 times than at SLI. This result was in accordance with available data on the mean amplitude of tides, which ranges between 2.93 and 4.28 m in various places of the Valdés Peninsula and between 0.88 and 1.89 in the Falklands (SERVICIO DE HIDROGRAFIA NAVAL 1993). Due to this high variation in water level and local topographical features, females of the DEL population experienced a larger variation in the distance between the harem and the water. The mean tide level at departure was, as expected, higher at DEL (2.4 ± 1.12, n = 119 vs 1.0 ± 0.41, n = 211), but also the variability in tide level was much larger (F test, with randomization: *variance ratio* = 7.53, P_{10000} = 0.0000); hence, DEL females experienced a wider range of tide conditions during departures.

Great differences between populations were found in the effect of tide on the risk of harassment during departure: at DEL all harassment variables had lower values during high tide departures, while at SLI no difference between high and low tide was detected (Fig. 2). At DEL, the actual tide level was negatively related to the likelihood of interception [Logistic regression: n = 119 departures; b = – 1.17, se(b) = 0.24; LR test: G_1 = 34.78, P < 0.0001], while no effect of tide level was detected at SLI [n = 221 departures; b = – 0.065, se(b) = 0.337; LR test: G_1 = 0.037, P > 0.84]. At DEL (n = 116 departures) tide level was negatively related to the level of harassment, having a significant effect on the number of competiting males (Linear regression, with randomization test on slope: β = – 0.615, P_{10000} = 0.0001), the number of interacting males (β = – 0.301, P_{10000} = 0.0001), the number of copulating males (β = – 0.326, P_{10000} = 0.0001), the number of male-female interactions (β = – 0.556, P_{10000} = 0.0001) and the number of copulations (Fig. 3). On the contrary, no effect of tide level was detected for SLI departures (n = 202 departures; P > 0.24 for all variables). There were no differences in socionomy between high and low tides departures both at DEL and SLI (t-test, with randomization: P > 0.80 for all demography variables and both populations), hence the effect of tide was a direct one.

Effect of environmental factors: distance of the harems from water. The distance of the harems from water was almost homogeneous at SLI, and harems far on land were usually rare and small, with one notable exception. In 1996 there were two large harems in the same area, one close to the water and the other 800 m away from the water; the same secondary males frequented the periphery of both

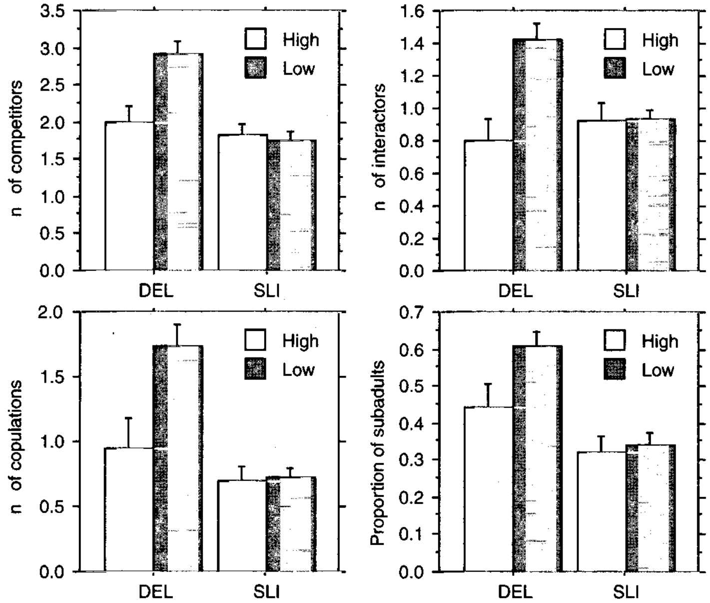

Fig. 2. — Bar charts of harassment variables (mean ± SE, except first chart) during high and low tide departures at DEL ($n_{HIGH} = 41$, $n_{LOW} = 79$; number of competiting males: 2.00 ± 1.95 vs 2.92 ± 1.48; t-test, with randomization: *mean diff.* = – 0.92, $P_{10000} = 0.0011$; number of interacting males: 0.80 ± 0.86 vs 1.42 ± 0.85; *mean diff.* = – 0.63, $P_{10000} = 0.0003$; number of copulating males: 0.62 ± 0.71 vs 1.23 ± 0.87; *mean diff.* = – 0.62, $P_{10000} = 0.0002$; number of interactions: 2.03 ± 1.65 vs 1.16 ± 1.30; *mean diff.* = 0.88, $P_{10000} = 0.0054$; number of copulations: 1.73 ± 1.50 vs 0.95 ± 1.41; *mean diff.* = 0.78, $P_{10000} = 0.0070$; proportion of subadult males: 0.61 ± 0.32 vs 0.44 ± 0.35; arcsine transformed proportions: *mean diff.* = – 0.62, $P_{10000} = 0.0002$) and SLI ($n_{HIGH} = 63$, $n_{LOW} = 165$; $P > 0.70$ for all variables).

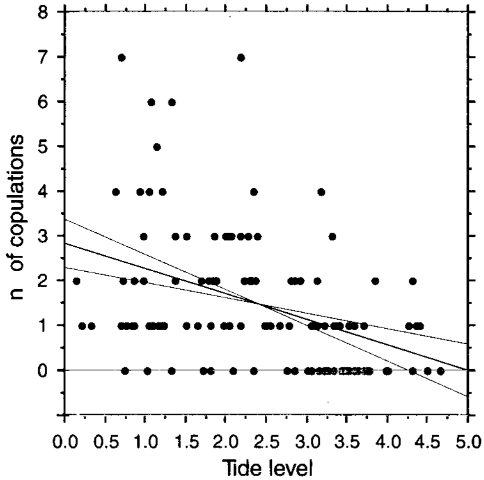

Fig. 3. — Number of copulations during departure on tide level at the beginning of the departure (m) at DEL; line represent OLS regression with 95% parametric confidence interval on the slope (n = 116 departures; $\beta = -0.566$, Randomization test on slope: $P_{10000} = 0.0001$).

harems. Females departing from the harem more distant from the water suffered an higher risk of harassment (Fig. 4).

Effect of social distraction. As a whole, social activity was higher at DEL than at SLI (male-male interactions: FABIANI 1996; male-female interactions: GALIMBERTI et al. 2000b). The total number of social events per observation period with at least one departure was higher at DEL than at SLI (40.2 ± 21.1, n = 87 vs 29.6 ± 19.3, n = 101; t-test, with randomization: *mean diff.* = 10.6, P_{10000} = 0.0005). While the frequency of male-female interaction was almost homogeneous between the populations (13.7 ± 6.9, n = 87 vs 12.7 ± 7.9, n = 101; *mean diff.* = 1.02, P_{10000} = 0.035), male-male interactions were more frequent at DEL than at SLI (26.6 ± 16.3, n = 87 vs 17.0 ± 14.9, n = 101; *mean diff.* = 9.6, P_{10000} = 0.0001).

Social distraction had a slight effect on the likelihood of interception during departure. At DEL, the likelihood of departure was not related to the intensity of male-female interactions [Logistic regression: n = 87 departures; b = 0.013, se(b) = 0.032; LR test: G_1 = 0.171, P = 0.68] or male-male interactions [b = – 0.020, se(b) = 0.014; LR test: G_1 = 2.14, P = 0.14]; the same was true at SLI for male-female interactions [n = 101 departures; b = 0.011, se(b) = 0.027; LR test: G_1 = 0.169, P = 0.68] and male-male interactions [b = 0.023, se(b) = 0.014; LR test: G_1 = 2.77, P = 0.10].

At DEL, there was a negative correlation between social distraction and the indices of the risk of harassment, but the effect size was always very small, although in the expected direction for all variables. The male-female interaction rate was related to the number of competiting males during departures (Pearson's

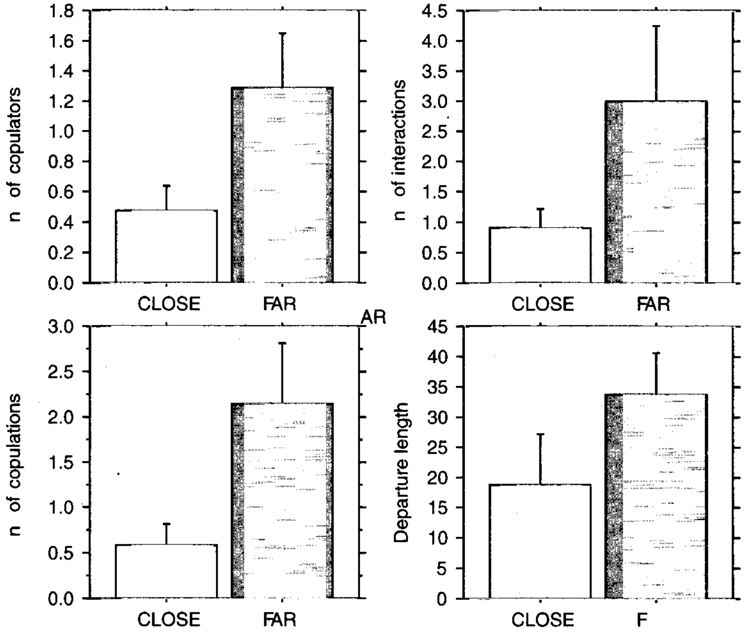

Fig. 4. — Bar charts of harassment variables (mean ± SE) during departures from two harems of the same area, one (n = 7 departures) close to the water, the other (n = 19) 800 m away (number of interactions: 3.00 ± 3.27 vs 0.90± 1.41; t-test, with randomization: *mean diff.* = 2.10, P_{100000} = 0.0253; number of matings: 2.14 ± 1.78 vs 0.58 ± 1.02; *mean diff.* = 1.56, P_{100000} = 0.0098; number of copulating males: 1.29 ± 0.95 vs 0.47 ± 0.70; *mean diff.* = 0.81, P_{100000} = 0.0349; duration of departures: 33.8 ± 13.8 min, n = 4 vs 18.9 ± 22.1, n = 7; *mean diff.* = 14.9, P_{100000} = 0.25; power analysis for equivalent parametric t-test: effect size = 0.78; 1–β = 0.31).

correlation coefficient, with randomization test: r = – 0.187, n = 87, P_{10000} = 0.083), the number of interacting males (r = – 0.192, P_{10000} = 0.074), the number of copulating males (r = – 0.223, P_{10000} = 0.038), the number of interactions (r = – 0.254, P_{10000} = 0.017), and the number of of matings (r = – 0.271, P_{10000} = 0.011).

To evaluate more directly the effect of social distraction on the likelihood of interception and harassment, we calculated the number of male-male and male-female interactions during the 15 min before each departure. Correlations between the number of male-male interactions before departure and all indicators of harassment (number of competiting males, number of interacting males, number of copulating males, number of interactions and number of copulations) were very week in both populations (r < 0.1). Also the number of male-female interactions before departure was not related to the indices of harassment.

A multivariate logistic regression model (with forward selection based on the likelihood ratio statistics) using absence/presence of interception during departures as response was fitted to evaluate the relative importance of environmental factors in determining the risk of interception. Only the adult sex ratio and tide level were retained in the final model for DEL; the effect of adult sex ratio (LR test: G_1 = 21.81, $P < 0.0001$) was more important than the effect of tide level (LR test: G_1 = 16.45, $P = 0.0001$). The same model was fitted to SLI data, but the inclusion of independent variables did not improve the null model.

In all, many environmental and social factors affect the risk of interception and harassment, but different ones were involved in the two population. The effects were greater at DEL than at SLI, because DEL represented a more extreme situation from the point of view of both abiotic and social factors.

Has mate guarding any effect on harassment?

Alpha males tried to guard (= protect the female from approaches of other males) departing females in 41.8% of 349 departures. DEL alphas tried to guard females in a slightly larger percentage of cases (46.7% of 120 departures vs 39.3% of 229), but the difference was not significant (Fisher's exact test: $P = 0.21$). There was no effect of environmental variables on the likelihood of mate guarding during departure, neither at DEL nor SLI, with the the exception of adult sex ratio at SLI: the inclusion of this variable in a logistic model improved the fit with respect to the null model (LR test: G_1 = 6.854, $P = 0.0088$). At SLI, mate guarding by the alpha was more frequent in areas with an higher density of secondary males.

Mate guarding was very effective in the short-term (dominant males were able to disrupt the mating attempts of subordinates in all cases, GALIMBERTI et al. 2000a), but not always definitive. At SLI, secondary males had the same likelihood of intercepting a female even when she was guarded by the harem holder (secondary males intercepted the female in 56.3% of 71 departures without mate guarding and in 57.1% of 70 departures with mate guarding; Fisher's exact test: P = 0.99). They also had the same likelihood of mating in both situations (secondary males mated with the female in 51.9% of 52 departures without mate guarding and in 50.9% of 57 departures with mate guarding; Fisher's exact test: $P = 0.99$). Mate guarding was limited in time and space, and the defense of departing females was effective only within a close distance from the harem.

Harem holders interacted frequently with departing females, both at DEL (50.3%, n = 93 departures) and SLI (56.0%, n = 141 departures), and they frequently copulated during departures, both at DEL (48.2%, n = 85) and SLI (44.0%, n = 109). At DEL secondary males interacted more (72.0%, n = 93 departures vs 56.7%, n = 141) and copulated more (64.7, n = 85 vs 51.4%, n = 109) with departing females than at SLI, but this increase was not associated with a decrease in the activity of alpha males towards departing females. The greater opportunities for secondary males at DEL were a direct result of the longer interval between the alpha leaving the departing female and the female disappearing into the sea.

Does male rank affect departure sequences?

We expected a stratification in the rank of males involved in departures, i.e., a lower rank for males that merely compete and a higher rank for males that mate. If the female interacts more than once with males of different rank, we expected the higher ranking males to interact first. We calculated dominance (IGG) for competing males and copulating males for all departures with at least two males in attendance and at least one of them copulating. The mean dominance rank, percentile transformed to permit comparison between populations, of males interacting with females during departures was lower at DEL (0.543 ± 0.090, n = 48 vs 0.605 ± 0.062, n = 50; t-test with randomization: *mean diff.* = – 0.62, P_{10000} = 0.0004), confirming the better access to females of marginal males at DEL. The rank of copulating males was higher than rank of males that merely compete for the female without intercepting her both at DEL (0.539 ± 0.92 vs 0.465 ± 0.116, n = 49 departures; Paired t-test, with randomization: *mean diff.* = 0.074, P_{10000} = 0.0029) and SLI (0.610 ± 0.79 vs 0.529 ± 0.102, n = 41; *mean diff.* = 0.082, P_{10000} = 0.0003).

The results concerning the relationship of rank with the order of interaction were less clear. At DEL, the rank of the first male interacting with the departing female was only slightly higher than the rank of the last male, with a large dispersion (0.553 ± 0.132 vs 0.542 ± 0.112, n = 48; Paired t-test, with randomization: *mean diff.* = 0.011, P_{10000} = 0.64; due to the small effect size, 0.0738, the power of this test was very low: $1-\beta$ = 0.10). On the contrary, at SLI, the rank of the first male was higher than the rank of the last (0.622 ± 0.96 vs 0.577 ± 0.091, n = 50; *mean diff.* = 0.045, P_{10000} = 0.0096). This difference depends on the higher level of despotism at SLI: the control of the harems by a small number of very powerful males is so effective that even males with high resource holding potential are forced to exploit marginal mating opportunities, such as departing females.

Do females adopt tactics of harassment risk reduction?

Do females depart more frequently at high tide? Due to the higher risk of interception and harassment during low tide departures, we expected females to concentrate their departure attempts at high tide. At DEL females departed in 34.2% of cases (n = 120) at high tide, a proportion significantly higher than the 1/4 proportion expected from our definition of high tide (Binomial test: P = 0.0134). On the contrary, SLI females departed at high tide in 27.6% of cases (n = 228), a proportion only slightly larger than expected (Binomial test: P = 0.20).

Do females depart more during the night? Females may depart at night to reduce risk of interception. We tested this hypothesis using census data from a large harem where all the females were clearly marked by hair dye; this harem was counted daily early in the morning and late in the evening, with 12 hr between the two censuses. In a series of 11 nights and 11 days during the peak phase of the season exactly half of the females (n = 20) departed during the day and half during the night. This was not unexpected because observations made at night confirmed that the breeding activity was almost equal to the day; there was no difference in the total number of social interactions between 1 night observation period (using night viewing equipment) and 1 day observation period for the same harem (≤ 24 hr between the two) for 15 days scattered throughout the season (Paired t-test, with complete enumeration: $P = 0.10$).

Do females choose the fastest route to sea? Due to the increase of harassment risk with an increase in the distance from water, females were expected to depart to sea using the shortest route. In fact, almost all females (> 99%) of our sample took a straight route to sea. There were only three exception to this rule during three breeding seasons, and all of these three females were intercepted by secondary males that mated with them 2 or more times. The circumstance of these departure were always quite particular. For example, in 1997 one female left the harem moving along the beach instead towards the sea, and she was intercepted by two secondary male and herded deep in land, she suffered the most intense episode of harassment observed in our population, and she departed almost 24 hr later from another side of the island.

At DEL, all harems were in front of the sea, but on SLI every breeding season we observed one or two harems deep in land (distance form water > 500 m). Females from these harems, that have no a direct view of sea, also chose the most direct route. Sometimes (3% of cases) females stopped their departure before reaching the water, with no apparent reason and without any intervention by male. In some cases, this stop resulted in interception by males that, without it, would not have be able to reach the female. In other, quite rare, cases females stopped their departures due to calls of their pup.

Do females exploit social distraction? Although social distraction seems to have a small effect on the risk of interception, females may concentrate their departures during periods of maximum activity in and around the harem, to ensure that the majority of males associated with the harem are busy. The effect of the global interaction rate, the male-male interaction rate and the male-female interaction rate on the likelihood of departure was evaluated by logistic regression. Only observation periods with at least one female ready to return to the sea (as calculated from actual departure dates of the marked females) were considered, and the effect of the number of females in the departure phase was controlled by including this factor in the logistic model. The inclusion of the number of interactions (excluding interactions involving departing females) greatly improved the fit with respect to the basic model including only the number of females ready to leave (LR test: $G_1 = 27.87$, $P < 0.0001$). Females departed more frequently than expected during periods of intense social activity. This effect was due mainly to male-female interactions (LR test: $G_1 = 29.40$, $P < 0.0001$), and not to male-male interactions (LR test: $G_1 = 1.60$, $P = 0.21$).

Females may reduce the risk of harassment by departing at about the same time. These synchronized departures to sea are quite frequent in otariid species that alternate suckling phases and feeding trips for long periods (e.g. *Otaria byronia*: CAMPAGNA & LE BOEUF 1988). Synchronized departures (time between the two departures ≤ 5 min) were not frequent, either at DEL (5.0%, n = 120) or SLI (5.7%, n = 229). Notwithstanding the very small sample size (n = 19 couples of departures, pooling DEL and SLI), the comparison of harassment between successive departures gave evidence that harassment was somewhat reduced at the second departure. There was a reduction in the mean number of males that competed for the departing female (Paired t-test, with complete enumeration: *mean diff.* = – 0.833, P = 0.0313), in the mean number of males that interacted (*mean diff.* = – 0.778, P = 0.0582), and in the mean number of males that copulated (*mean diff.* = – 0.889, P = 0.0254).

Is female protest adjusted to reduce harassment risk during departures? We expected females to tune their behavioural reaction to approaching males during departures to reduce harassment risk. In particular, females may reduce risk of dangerous harassment by avoiding protest and facilitating copulation. Departing females protested a smaller proportion of interactions than other females (36.5%, n = 85 vs 82.5%, n = 4413; Fisher's exact test: P = 0.0000), and this was true also after splitting non departing females in solitary (88.9%, n = 271; Fisher's exact test: P = 0.0000) and harem (83.1%, n = 3370; Fisher's exact test: P = 0.0000).

The low level of protest of departing females seems to depend mostly on a gradual reduction of tendency to protest during the last phase of permanence on land of each female, independent from the specific departure context (GALIMBERTI et al. in press a). Notwithstanding this, we evaluated the effect of protest by examining the sequence of male-female interactions during each departure. In sequences of interactions in which protest for all interactions of the sequence was recorded, there was a prevalence of completely non protested sequences (62.1%, n = 153; a lower proportion than found in the northern species, MESNICK & LE BOEUF 1991), but also completely protested sequences were frequent (24.2%). The percentage of completely non protested sequences was higher at DEL (73.0%, n = 63 vs 54.4%, n = 90; Fisher's exact test: P = 0.0274). The proportion of protested interactions in each sequence was lower at DEL (0.21 ± 0.37, n = 63 vs 0.39 ± 0.46, n = 90; t-test, with randomization: *mean diff.* = – 0.18, P = 0.010), and also the proportion of protested copulations was much lower (0.14 ± 0.31, n = 60 vs 0.32 ± 0.45, n = 76; *mean diff.* = – 0.184, P = 0.0080). In all, DEL females, intrinsically exposed to higher harassment risk, seems to protest less against approaching males during departures.

The analysis of protest tuning during departures is complicated by individual variation in tendency to protest (GALIMBERTI et al. 2000a). We tried to account for this factor by analyzing sequences of interactions of each departure. There is a increasing gradient of harassment risk in the sequence of interactions, because more powerful and experienced males usually interact first. Hence, if reduction of protest is a tactic to reduce risk of bad harassment by marginal males, we expected protest to decrease along the sequence of interactions. We explored the presence of trends in level of protest in sequences of interactions by comparing first and last interactions: in 66.7% of 66 sequence level of protest was equal, 16.7% higher and 16.6% lower. In sequences with variation of level of protest, there was a decrease trend from the first to the last in 40% of cases (n = 20) and an increase trend in 60%. No trend of variation of protest was apparent during departures in which the female interacted three or more times. In all, we did not find any evidence of a specific modulation of protest during departures.

DISCUSSION

SES females spend most of their time on land inside harems. Here, the main source of harassment is the harem holder, females enjoy a reduction in the harassment rate due to the dilution effect (GALIMBERTI et al. 2000b), and are protected from the harassment of secondary males by HH males (Galimberti et al. 2000a). On the contrary, while arriving on land, before joining a harem, and while returning to sea, at the end of breeding, females are on their own, exposed to NHH males and without any dilution or protection effect. Hence, while harems are a good context to test the hypothesis of a strategic, season wide decision (e.g., preference for larger harems), arrival and departure are the optimal context to test hypotheses about short-term tactics of harassment reduction.

For northern elephant seals, Mesnick & Le Boeuf (1991) concluded that opportunities to escape from approaching males during arrival and departure are low, that most females are intercepted by one or more males, and hence that females resort mainly to the tactic of harassment reduction after being intercepted because they are not able to escape. In our studied populations the rate of interception was lower than the near 100% reported for the northern species (Cox & Le Boeuf 1977, Le Boeuf & Mesnick 1990), and about half of the females were able to depart without being intercepted by males. Indices of harassment (the number of males in attendance and the percentage of departures with copulation) were also lower.

For the northern species, Mesnick & Le Boeuf (1991) concluded that females were not able to fully exploit the environmental conditions in order to reduce the risk of interception. Females tactics seems somehow more effective in SES: females were able to reduce the distance travelled on land during departure by leaving at hide tide at DEL, where the tide level had a significant effect on the distance of the harems from water. On SLI, they did not depart more frequently at high tide, but there the variation in distance from water due to the tide was small. On the contrary, on SLI, when departing from harems formed deep in land, females chose the most direct route to the water even though they were without direct sigh of the sea. Females did not depart more frequently at night (Mesnick & Le Boeuf 1991), but this was not unexpected because activity was homogeneous between day and night, and available evidence demonstrates that elephant seals have very good vision in low brightness conditions (Levenson & Schusterman 1997). The differences between DEL and SLI confirmed that the functional significance of some behavioural tactics may emerge only in extreme environmental conditions.

The effect of social activity on the likelihood of interception was almost zero in both populations, notwithstanding the huge difference in the frequency of social interactions between them. Also the effect on harassment risk was small and seen only at DEL. In all, social distraction was not very effect at reducing risk during departure. Notwithstanding this, females tended to depart more frequently during periods of high social activity, and females that departed just after other females were subjected to a reduced harassment. The main problem here seems the short range of female reactivity: each individual female tends to react only to events that happen at close distance (few metres) from her, lacking the strategic vision needed to fully exploit social distraction.

In all, females were not so effective in escaping from males. Their tactical options are limited: they are less agile on land than males and retaliation against male aggression is very dangerous due to smaller size of their body and weapons. Their behaviour during departures seems to be an example of the "to make the best of a bad job" strategy. Moreover, females fast while on land and have a huge energy expenditure due to lactation (Fedak et al. 1994), hence their departure to sea should be timed quite strictly by plain physiological determinants.

Mesnick & Le Boeuf (1991) attributed a particular importance to reduced protest during departures as an harassment reduction tactic: by reducing protest and facilitating intromission, northern elephant seals females reduce the risk of being heavily harassed and gain protection from locally dominant males ("trade sex for protection" hypothesis). A low level of protest during departure was also found in the southern species, but evidence for a specific tactic based on protest reduction were weak. Females gradually reduce protest from the beginning of oestrus to the day of departure, and this process is almost linear. Most departures with more than one interactions were associated with absent or low protest, but about $^1/_4$ of departures was globally very protested. Protest during the last day of residence in a harem was similar in quality and quantity to protest during departure. There was also no clear trend in the variation of protest level in sequences of interactions during departures. Facilitated copulations were observed not only during departures but also inside harems. In all, low protest during departure is more parsimoniously interpreted as the prosecution of a trend in the reduction of protest from the beginning of oestrus (due to physiological variations, habituation to male approaches, exhaustion of females), than as a specific female tactic of harassment risk reduction directed towards the approaches of subadult secondary males.

The whole pattern of male avoidance shown by female southern elephant seals has two components: while the strategic component (synchronization of breeding, formation of harems, preference for larger harems) presents a modest variation between populations (GALIMBERTI et al. 2000a), and even between species of the same genus *Mirounga*, the tactic component (timing of departure to sea, protest and receptivity) is very plastic, and presents a notable variation between, and within, populations. Due to the plasticity of the behaviour of seals and the variation in breeding conditions, a full understanding of the reproductive behaviour requires the study of a wide array of breeding contexts.

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