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ESRG technical report no. 3

Breeding site fidelity in southern elephant seals of the Falkland Islands

Milano, 25th April 2000

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ABSTRACT

Breeding site fidelity, i.e., the tendency to return to the same breeding site for consecutive breeding attempts, is an important component of mammal life history strategies, and seems almost ubiquitous in *Pinnipedia* species, at least for land breeding ones. Site fidelity may entail significant somatic benefits and costs, and, if coupled with return for first breeding attempt to birth site, may produce a genetic sub-structuring of populations. We present data on female and male site fidelity, together with preliminary information on female phylopatry, of southern elephant seals (*Mirounga leonina*) of Sea Lion Island, the main breeding site of the species in the Falkland Islands. We found a high level of site fidelity at small scale (hundred of metres) in both sexes, although higher in females, even when considering up to five consecutive breeding seasons of the same individual. We discuss the behavioural and genetic implications of site fidelity, emphasizing that it may affect mating tactics, breeding success, and genetic sub-structuring of local populations.

KEYWORDS

Site fidelity, philopatry, breeding strategies, southern elephant seals, *Mirounga leonina*, Falkland Islands

INTRODUCTION

Site fidelity is an important aspect of breeding biology of a species because it may entail both somatic and genetic costs and benefits. It may affect female breeding strategies (e.g., through familiarity with local resources), male mating tactics (e.g., through improvement in location of mates), and both male and female breeding success (Belichon et al., 1996). An individual that is successful in a particular site during one breeding season is expected to return to the same place in the following ones. Breeding site fidelity, if coupled with philopatry (i.e., the return for the first breeding attempt to the birth site), can also imply consequences on the population genetic structure, by producing inbreeding depression (unmasking of deleterious recessive alleles, reduction in global viability of progeny) or by maintaining locally adapted gene complexes. A high degree of site fidelity may have an impact on the genetic diversity of local populations. With a reduced gene flow, due to the restricted dispersal of individuals, the genetic diversity of a species should present a hierarchical organization, with different levels of genetic structure at different levels of organization (Giplin, 1991). The result may be the production of hierarchically structured populations in which socio-spatial units correspond to genetic sub-units of the population (Petit et al., 1997).

Some of the most striking examples of long term, small scale fidelity come from marine mammals (e.g., *Chelonia mydas*: Bowen et al., 1992), and site fidelity seems a typical component of breeding biology of most land-breeding *Pinnipedia* species. Information about fidelity of seals and sea lions is often limited to qualitative assessment at colony level. Moreover, even when finer resolution data was available, the observed fidelity was rarely tested against random settlement models. Data on site fidelity are available for many terrestrial breeding seals (Twiss et al., 1994; Lewis et al., 1996), while for ice breeders only information for the Weddell seal is available (Croxall and Hiby, 1983; Siniff et al., 1998). In this species site fidelity seems to be weaker than in land breeding ones, but this is not unexpected due to the variability of ice condition both within and between breeding seasons, and the greater uniformity of the breeding habitat topography. Comparison of site fidelity among species is not easy, firstly because of variation in methodology and resolution. Moreover, fidelity should be evaluated in relation to the social and mating system, which may put specific constraints on females movements. For example, northern fur seal females show an almost metric precision fidelity, which is favoured by the territorial social organization and the topography of breeding sites (Gentry, 1998). This precision is not achievable in species with non-territorial social systems. For example, in elephant seals, most females breed in harems, and, therefore, their pupping location depends on the harem location, which, in turn, is more constrained by social factors (e.g., capability of the harem holder to herd females: Galimberti et al., 2000 a) than by topographical ones. Fidelity may also presents a variation among populations of the same species, due to variation in demography and topography among breeding colonies. Information of male site fidelity is limited to few species (*Mirounga leonina*: Lewis et al., 1996; *Halichoerus grypus*: Twiss et al., 1994; *Callorhinus ursinus*: Gentry, 1998).

Southern elephant seals (*Mirounga leonina*) of Sea Lion Island (Falkland Islands) show a strong fidelity at colony level. The island is the main breeding site of elephant seals in the Falklands (Galimberti and Boitani, 1999). Only few small groups and isolated females breed elsewhere in the islands (Galimberti et al., 2001), and in a six year long intensive mark-recapture study no marked individual was re-sighted breeding in other places. In this paper, we present information on site fidelity at sub-colony level for female and male elephant seals of Sea Lion Island, we compare fidelity among sexes, and we evaluate the effect of individual phenotype on fidelity.

MATERIALS AND METHODS

Field work was carried out during five consecutive breeding seasons (1995-1999) at Sea Lion Island, which shelters a small and localized population of elephant seals (Galimberti and Boitani, 1999; Galimberti et al., 2001), with a mean of 522 breeding females. All breeding individuals were marked with at least two plastic cattle tags (Jumbo Rototag - Dalton Supplies Ltd) put in the rear flippers, to permit identification in consecutive seasons. Estimation of site fidelity by mark-recapture study in large breeding colonies is difficult because of the high likelihood to overlook females (see also Huber et al., 1991). On Sea Lion Island, the small size of the population, the low likelihood to lost both tags (0.21-0.31% for females; 0.23-0.31% for males), and the intensive re-sighting plan carried out daily in the whole breeding colony, and along the whole breeding season, made errors of identification and/or recording of location very unlikely. To permit rapid recognition during censuses and positioning sessions, animals were also marked with black hair dye. Details about marking and census protocols were reported elsewhere (Galimberti and Boitani, 1999; Galimberti et al., 2000 a). We collected data on 646 females and 84 males, each one recorded for 2-4 breeding seasons. In all, the database included 1463 pairs of breeding seasons for females and 134 pairs of breeding seasons for males. The much lower number for males was due to the heavily unbalanced sex ratio, 9.2-10.1 females per male (Galimberti et al., 2001).

We collected two kind of spatial information, qualitative and quantitative. The former was collected by referencing the position of individuals to a series of landmarks, defined and marked by permanent signposts at the beginning of the study. These landmarks permitted to classify positions of individuals at two spatial level, zone and area. A *zone* was a continuous stretch of 2-6 sandy beaches, used by breeding seals, clearly separated from other zones by rocky areas, never used for breeding. Three different zones were occupied by elephant seals (mean length of coast of zones = 1451 m; total length = 4354 m; Fig. 1). An *area* was a part of the zone clearly delimited by topographical features, but not separated from adjacent areas by habitat not suitable for breeding. In all, 11 of the 17 areas were occupied by breeding seals for one or more seasons, and were considered in the analysis (mean length of coast of areas = 445 ± 195 m; maximum distance between centroids of areas = 1670 m; maximum distance between extreme landmarks of areas = 2049 m). Females formed *harems*, i.e., stable groups of 2-129 individuals at peak haul-out, clearly separated from other groups. Harems could have been considered as an additional level for a qualitative assessment of spatial structure, but we decided to exclude this level because the joining of a specific harem by a female is affected by male social behaviour (Galimberti et al., 2000 b), and, therefore, is not a good index of intrinsic fidelity. Every day during the whole length of the breeding season (12 weeks), we recorded the position of all breeding males (18633 daily records, with a mean of 33-42 records per male per season) and 75-100% of females (65593 daily records, with a mean of 21-24 records per female per season).

Quantitative spatial information was collected using Global Positioning System receivers (ProMark X, Magellan Corporation). We used static differential post-processing to map positions of landmarks and individuals, and dynamic differential post-processing to map profiles of zones, areas and harems (technical details of the GPS was presented in Galimberti and Sanvito, 1999). We generated corrected UTM coordinates using NavStar post-processing software (Magellan Corporation), from which we calculated spatial statistics and generated maps using custom scripts developed in HyperTalk language (Apple Inc.). Due to the small size of our working site and the absence of obstacles, satellite coverage was excellent, and the accuracy of positioning was close to the limit stated by the manufacturer (3 meters RMS: Magellan System Corporation 1995. Professional products: operation manual. San Dimas, CA). GPS data was collected at variable intervals, at least weekly but also daily for some areas, during the 1997 to 1999 seasons only.

The concept of site fidelity has been used with different meanings by different authors, hence consistent operational definitions are needed (Shields, 1987). We defined *site fidelity* as the return to the same *breeding site* during consecutive seasons. The strict meaning of breeding site was different between the two sexes. Female elephant seals are very sedentary after giving birth (Galimberti et al., 2000 b), and, hence, for females, breeding site was equated to *parturition site*, which was assessed by direct observation of parturition, or by examination of the daily individual serial records of female status. Males show an higher mobility during the breeding season, in part related to the status of the male. Harem-holding males usually stop moving after getting full control of an harem, hence spending almost all the breeding season in the same area, which was equated to their breeding site. For non harem holding males, the breeding site was defined as the area in which they were most frequently seen during the central phase of the breeding season, i.e., the three weeks in which most females went into oestrus (Galimberti and Boitani, 1999).

We used the size class of the female as an index of her age, since in southern elephant seals these parameters are closely related (Campagna et al., 1992). We classified females in three size classes, small, medium and large. The classification is repeatable and consistent among observers (Galimberti et al., 2000 a). We classified males in five age classes based on male morphology (sub adult male, SAM, class 1 to 4, and adults, AD). This qualitative classification is repeatable (Galimberti and Boitani, 1999), and should have a good a linear relationship with true age (Deutsch et al., 1994). We classified males as principal males, if they get control of an harem, and secondary, if they did not.

In some analysis, the same individuals appeared more than one time because many individuals were present on land for up to five consecutive breeding seasons, rising some concern for risk of pseudo-replication (Bartz et al., 1998). Although we think that different breeding seasons of the same individual should be considered independent events, due to the between-season variation of individual phenotype and population socionomy, we checked the results of suspect analysis by randomly sampling one entry for each individual. In all cases, we obtained results very similar to the ones of full analysis, and, therefore, we reported only the latter. We reported statistics as mean ± standard deviation, or median ± median absolute deviation for skewed variables. Confidence limits for proportions were calculated using the Blyth-Still-Casella method (Metha and Pathel, 1998). We compared proportions, and tested contingency tables, using exact tests run in StatXact 4 for Windows (Cytel Software Corporation). When exact test were not manageable, we resorted to Monte Carlo estimates of probability, with 20000 re-samplings in all cases. Effect of local demography and individual traits on site fidelity was tested using logistic regression (see also Baker et al., 1995), run in SPSS 6.1 for Power Macintosh (SPSS Inc.).

RESULTS

Site fidelity of females

Breeding was concentrated in the three main zones, that represent 21% of the perimeter of the island (20.4 km). Although most of the rest of the coast of the island is made up by cliffs unsuitable for seal haul-out, 18% is occupied by pebble beaches that are potentially suitable for seals breeding, and were in fact frequently occupied by moulting individuals. Notwithstanding this, the percentage of females breeding outside the main breeding sites ranged from 0 to 0.89% in different years (n = 517-567 females).

We calculated the percentage of females coming back to the same breeding zone during five consecutive breeding seasons on the total number of returned females. This percentage ranged from 71.4 to 72.1, and was homogeneous among years (Likelihood ratio test: G = 0.0660, P > 0.95). Therefore, we pooled different years to get a single estimate of site fidelity, equal to 71.7 % (0.95 CI = 69.3-74.0%). This percentage was different from the expected with an equal probability of return for each zone (Binomial test: expected proportion = 1/the number of zones, P = 0.0000).

Our sample of females included females with 1 to 4 breeding seasons after the first. Most females were continuous breeders, but some of them skipped one seasons. Site fidelity was not different among continuous breeders and skippers (58.6% n = 584 vs 56.5% n = 92, Fisher's exact test: P = 0.7338). On the contrary, there was a variation in fidelity with increasing number of breeding seasons. For females present on land for 2 breeding seasons, the percentage of returns to the same zone of the first breeding attempt was 72.4%. It decreased to 62.5% for 3 breeding season, but was almost equal for 4 (45.4%) and 5 (45.8). The decreasing trend up to 4 seasons was significant (Jonckheere-Terpstra Test, with Monte Carlo sampling: JT statistic = -5.139, P = 0.0000). We tested each set of females with 1, 2, 3, and 4 returns against the expected proportion of females returned to the same area with random settlement and 1-4 returns, i.e., $(1/\text{n° of zones})^{\text{n° of returns}}$. We found significant deviation from the random pattern in all cases (Binomial test: p = 0.0000 for all four independent tests). The difference among observed and expected fidelity increased with the increase of the length of breeding history (from +39.1 to +44.6%).

To evaluate fidelity at finer resolution, we examined returns to the same breeding area. The percentage of females coming back to the same area ranged from 33.3 to 41.9% in different years. Percentages were not completely homogeneous among years, but differences were not significant (Likelihood ratio test: G = 7.231, P = 0.0654); hence, we pooled all data to obtain a single estimate of area fidelity (36.6%, 0.95 CI = 34.1-39.1). Observed area fidelity was significantly higher than expected with random return (Binomial test: expected proportion = 1/the number of areas, P = 0.0000). If settlement for parturition in consecutive seasons was random, we expected the number of areas per female to have a uniform distribution. We tested this hypothesis in a sample of 142 females recorded for 5 breeding seasons. Only 7.8% of females were recorded in the same area during all seasons, but 41.6% were recorded in 2, and only 3.5% changed areas every season. In all, the observed distribution was significantly different from a discrete uniform distribution with values ranging from 1 to 5 (KolmogorovSmirnov test: KS statistic = 0.2380, P = 0.0000).

To quantify fidelity, we calculated mean distances between areas of consecutive breeding attempts (using centroid of areas calculated from GPS data). Distribution of distances were skewed ($g1 = 0.979$ for all distances, $g1 = 0.852$ for females that changed area only), hence we calculated medians. Median distance for all females was 340 ± 340 m, while for females that changed area it was 469 ± 211. If the choice of area for parturition was not related to choice during the previous season, we expected distances to be uniformly distributed between 0 and 1670 m (the maximum possible distance). This was not the case (Kolmogorov-Smirnov test, with Monte Carlo sampling: KS statistic = 0.2380, P = 0.0000), and the distribution was clearly clumped on the left, with decreasing probability of movement between areas with increase distance between them. In all, 83.9% of females gave birth within 500 m from the parturition location of the previous year.

Site fidelity could be related to phenotype of females, and in particular to age (that we equated to size class), experience, and the result of the previous breeding attempt. Site fidelity (at zone level) was higher for females of the large size class (81.1%, n = 302), and decreased for medium (71.5%, n = 228) and small females (64.3%, n = 84). Experience was measured as number of successful breeding seasons before the current breeding attempt. This is a partial measure of experience, because some females where already breeding before the start of the study, but it should be correlated with full experience (Sydeman and Nur, 1994). Experience had no clear effect on fidelity. Although females with 4 previous breeding seasons had a slightly higher fidelity, the sample was very small (81.1%, n = 37 vs 74.5%, n = 609). We classified females as nulliparous, if they did not give birth or lose the pup before weaning, or parous, if they successfully weaned their pup. Site fidelity was lower for nulliparous females, but the sample was very small due to the very high fecundity of elephant seal females (68.8%, n = 16 vs 75.2%, n = 614). We run a logistic regression with fidelity as dichotomous response variable (0 = return to different zone, 1 = return to same zone). Only size class was retained in the final model (Likelihood ratio test: G = 12.670, df = 2, P = 0.0018), and the removal of the other two factors produced a non significant reduction of the fit (Likelihood ratio test for status: G = 0.154, df = 1, P = 0.69; Likelihood ratio test for experience: G = 1.231, df = 1, P = 0.27).

Although available data was scanty, we calculated philopatry, using a small sample of females marked as newborn in 1995 and returned for breeding in 1999. Philopatry was high, with 63.2% primiparous females (n = 38; 0.95 CI = 46.5-77.4) that returned to the same zone of birth, and significantly different from expected (Binomial test: P = 0.0003), although lower than site fidelity of adult females.

Site fidelity of males

Although males showed a much higher mobility than females (unpublished data), during a five year period only two males settled outside the main breeding site, and for one season only, associated with an isolated female and an harem of two.

All the analysis of male data were less powerful than the ones for females, due to the much smaller samples, hence all result should be considered tentative. Zone fidelity for males ranged from 54.1% to 69.2%, and was homogeneous among years (Likelihood ratio test: G = 1.825, P = 0.62). Zone fidelity of pooled data was 61.9% (0.95 CI = 53.6-70.1%). This percentage was significantly higher than expected (Binomial test: P = 0.0000). As a whole, zone fidelity of males was lower than fidelity of females (Fisher's exact test: P = 0.0125). Area fidelity ranged from 23.1% to 37.0%, again with homogeneity between years (Likelihood ratio test: G = 1.830, P = 0.63) and a common estimate (pooled years) of 29.1% (0.95 CI = 21.6-37.3). Male area fidelity was lower than female one (Fisher's exact test: P = 0.0501).

Median distance between breeding sites during consecutive attempts was 357 ± 357 m for all males, while for males that changed breeding site it was 469 ± 216 m. The observed distribution of distances was different from the expected distribution in absence of site fidelity (Kolmogorov-Smirnov test, with Monte Carlo sampling: KS statistic = 0.4042, P = 0.0000). Distribution of distances was not different between the two sexes (Kolmogorov-Smirnov test, with asymptotic estimation of probability: KS statistic = 0.0639, P = 0.73).

There was a gradual increase in zone fidelity with the increase of the age class (from 47.6%, n = 1 for SAM1 to 76.9%, n = 39 for adults; Jonkheere-Terpstra test, with randomization: JT statistic = 1.688, P = 0.0485). Male experience was defined as the number of previous seasons in which the male was observed in the breeding colony during the central phase of the season. Fidelity increased with experience from 56.4% (n = 55) for males with one previous season to 70.0% (n = 10) for males with four seasons. Principal males were more faithful to their breeding zone than secondary males (73.3%, n = 30 vs 58.7%, n = 104). In a logistic regression model, only age was retained as a significant factor (Likelihood ratio test: G = 9.983, df = 4 , P = 0.0416), while removal from the model of other factors produced no reduction of the fit (Likelihood ratio test on experience: G = 0.142, df = 1, P = 0.71; Likelihood ratio test on status: G = 0.610, df = 1, P = 0.4349).

DISCUSSION

The high level of fidelity of both females and males demonstrated that the link to breeding site is an important component of elephant seal breeding strategies. Apart from a generalized tendency to return to the same breeding colony, southern elephant seals of Sea Lion Island consistently choose the same part of the colony for breeding during consecutive seasons. The degree of site fidelity of Sea Lion Island females is comparable to site fidelity in other species for which data is available (a summary of some fidelity measures is reported in Table 1), and it is higher than the level recorded for the elephant seals of the closest population, Valdés Peninsula (the 3 km criterion adopted Lewis et al., 1996 will include almost 100% of the females if applied to the Sea Lion Island population).

Site fidelity was particularly remarkable for females with a long series of breeding attempts. In our study, we analysed females with a maximum of five breeding attempts, that represents about a third of the whole maximum breeding lifespan of females of this species (17 years, start breeding at 4 and living to 21: McCann, 1985; Arnbom et al., 1992). With a less-than-perfect mechanism of return to previous breeding site, we expected an accumulation of errors with increasing number of returns. This was in fact the case, but the decrease was quite slow, and ceased after three returns. This is a preliminary indication that site fidelity improves with experience and that older females have a stronger site fidelity. Males showed a more flexible strategy of choice of breeding site, in part related to male age and status during the previous breeding season, although the small sample size complicates the interpretation of result. This is in accordance with the life history differences between the sexes in this species, in which males, and in particular sub-adult males, clearly adopt a more "risky" breeding strategy than females (Clinton and Le Boeuf, 1993).

In mammals, females are usually the philopatric sex and dispersal is male- biased (Dobson, 1982), although this is not always the case (Clutton-Brock, 1989). Moreover, sex-related variability in site fidelity depends on the type of mating system adopted (Greenwood, 1980). In resource-defence mating systems, males are expected to be more philopatric than females, because familiarity with the site to be defended may increase success in defence of resources. In mate-defence mating systems, males should adapt their spatial distribution to female distribution, and, therefore, their philopatry should be less pronounced. In seals and sea lions, fidelity is, on the contrary, typical of both males and females, although males usually showed a lower fidelity, in particular before sexual maturity (*Halichoerus grypus*: Twiss et al., 1994; *Callorhinus ursinus*: Gentry, 1998). This is in accordance with our results for southern elephant seals, where males show a weaker site fidelity than females, but also an increase of fidelity with the increase of age and status of the male, that reach a maximum for adult harem holders. This is similar to the increase in male fidelity of territorial species, where tenured males show a fidelity similar to breeding females (*Callorhinus ursinus*: Baker et al., 1995; *Halichoerus grypus*: Twiss et al., 1994).

Some of the variation in site fidelity should depend on previous breeding history, with positive breeding attempts reinforcing fidelity. In our sample, the effect of previous breeding failure was difficult to evaluate due to the very high fecundity and weaning success of the vast majority of female. Therefore, the only female phenotypic trait with a sure relationship with fidelity was size class, that should well represent age. In grey seals the most important component for site fidelity is age (Pomeroy et al., 1994). In Weddell seals there is a bigger difference in site fidelity between parturient and non parturient females, with a reduction in fidelity for females which failed to reproduce successfully (Stirling, 1974), an adaptation to breeding habitat. Even if female fidelity for stable fast-ice areas is advantageous, ice condition may change from year to year and so the ability to choose another site in another stable area may improve reproductive success. Hence, the effect of the result of previous breeding attempts should depend on the local variability of breeding habitat, and may be very difficult to detect in a species with low pre-weaning mortality and stable breeding habitat.

Female philopatry and site fidelity may have a significant effect on the genetics of the population. They may produce a sub-structure of groups of related females, which genetic structure may be quite different from the mean of the population. Genetic variance among subgroups will depend on the level of philopatry, and also on the mating system. Polygynous systems produce the maximum genetic variance between groups (Chesser, 1991), and hence the effect of female philopatry and site fidelity should be particularly strong in elephant seals, which have the highest level of polygyny of all mammals. The philopatry observed at Sea Lion Island is at least comparable to the 77% of females giving birth within 4 km from the birth site recorded on Macquarie Island (Nicholls, 1970), and to the 71.4% reported for the northern species (Reiter et al., 1981). Hence, on Sea Lion Island we expect to have some level of genetic sub-structuring of the population. The pattern of combined philopatry and site fidelity of both sexes, which is somehow unusual among mammals, may increase the global effect of site fidelity on the genetic structure of the population (Petit et al., 1997). We are currently trying to verify this hypothesis by analysing microsatellite data from DNA samples collected at the same time of the fidelity study.

ACKNOWLEDGMENTS

We wish to thank Carla and Alberto Galimberti for their continued and strenuous support of our research on elephant seals; Ilaria Marzetti, Alice Camplani, Alessia Gallastroni and Daniela Marasco for their help with data collection; professor Luigi Boitani (Department of Biology, University of Rome "La Sapienza") for the GPS receivers. For field work, we wish to thank: the Falkland Islands Government for allowing us to carry out our research in the Falklands; the Falkland Islands Development Corporation and Mr. D. Gray for allowing us to do the field work on Sea Lion Island. Special thanks go to David and Patricia Gray for their kind and constant help during our residence on Sea Lion Island.

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Species	N	Site fidelity	Habitat	Mating system	Reference
Southern elephant seal	398	86% within 3 Km from previous breeding site	Land	Harem defence polygyny	Lewis et al., 1996
Northern elephant seal	150	70% within 4 km from previous parturition site	Land	Harem defence polygyny	Reiter et al., 1981
Grey seal	59	76% within 80 m from previous pupping site	Land	Scramble competition polygyny	Pomeroy et al., 1994
Harbour seal	36	30% within 0.5 km from previous pupping site	Land	Scramble competition polygyny	Schaeff et al., 1999
Weddel seal	94	59.5% give birth in the same colony of previous year (km scale)	Ice	Territory defence polygyny	Stirling, 1974
Antarctic fur seal	115	80.2% return at least once in the same beach (440 m^2)	Land	Territory defence polygyny	Lunn & Boyd, 1991
Australian fur seal	15	93.3% in the same colony of previous year	Land	Territory defence polygyny	Stirling, 1971
Northern fur seal	7940	78% in the same central breeding area (up to 1 km long)	Land	Territory defence polygyny	Gentry, 1998
Australian sea lion	29	69% within 5 m from previous pupping site	Land	Territory defence polygyny	Higgins & Gass, 1993

Table 1 - Breeding site fidelity of females of pinniped species