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Timing of breeding of female southern elephant seals of the Falkland Islands

Repeatability and correlates

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ABSTRACT

Seasonality and synchrony of reproduction are fundamental aspects of breeding strategies in many mammal species, being related to breeding success and offspring survival. Almost all pinniped species show a clearly defined breeding season and strong synchronization of reproduction. For synchrony and seasonality to be the result of an evolutionary process, timing of breeding should have a significant heritability and should be related to fitness. In *Pinnipedia*, although abundant data is available on timing of breeding at population level, there is scanty information on timing at individual level. In particular, there is a lack of repeatability measures for components of timing of breeding, and of measures of the relationships between timing of breeding and reproductive success. In this paper, I present data for a large sample of female southern elephant seals (*Mirounga leonina*) from the main breeding site of the Falkland Islands. I calculate repeatabilities of breeding events across seasons, analyze the effect of female phenotypic traits on timing of breeding, and explore the relationships between timing and female parental investment. I found high repeatabilities for breeding events, but scarce support to the hypothesis that synchronization has a significant effect on female breeding performance.

KEYWORDS

Timing of breeding, synchrony, repeatability, parental investment, southern elephant seal, *Mirounga leonina*, Falkland Islands

INTRODUCTION

Timing of breeding is a primary target of the action of natural selection (Bronson 1988), and it is a very important component of breeding strategies. It is tightly related to efficiency of parental investment (Smith 1976), survival of offsprings (Ims 1990 a), and, ultimately, reproductive success (Ims 1990 b). Together with spatial dispersion, timing of breeding is the most important correlate of mammalian mating system and male mating tactics (Clutton-Brock 1989). Timing of breeding of many land mammals is characterized by seasonality (*i.e.*, there is a clearly delimited breeding season), regularity (*i.e.*, the pattern of breeding is the same in different years), and synchrony (*i.e.*, most females give birth in a very short time window, shorter that the whole breeding season). In most cases, the level of synchrony is much higher than expected from seasonal variation of gross aspects of environment alone (Boness *et al.* 1995). Seasonality and synchrony of breeding are assumed to be strategies to maximize breeding opportunities in a changing social and ecological environment. Reproduction is timed to enjoy the best environmental conditions for offspring survival, *e.g.*, in relation to food availability or predation risk (Rutberg 1987). In most mammalian species, timing of breeding is hence modulated by a combination of endogenous and exogenous factors, including photoperiod and hormonal reactions to it (Bronson 1989).

In *Pinnipedia*, the physiology of timing of breeding is similar to other mammalian orders (Bronson 1989, Boyd 1991), and seasonality and synchrony are ubiquitous, with almost all species sharing a similar pattern. All pinnipeds present an yearly breeding cycle, a concentrated breeding season with most females giving birth during few weeks, a single estrus phase, and a long embryonic diapause, that permit to have estrus close to parturition, an obvious advantage for marine species that breed on land (Daniel 1981). The only exception are the biannual cycle of the walrus (*Odobenus rosmarus*: Fay 1981), the non-annual and non-seasonal cycle of the Australian sea lion (*Neophoca cinerea*: Higgins 1993), and the prolonged breeding season of *Monachus* spp. (Johanos *et al.* 1994, Aguilar *et al.* 1995). Timing of breeding was probably a main target of selection during evolutionary history of *Pinnipedia* (Bartholomew 1970), leading to the concentration of post-birth maternal investment in a short period (reduced up to four days, *Cystophora cristata*: Bowen *et al.* 1985). There is abundant evidence that in *Pinnipedia* seasonality and synchronization have a proximate causation in photoperiod, and an ultimate causation in the optimal allocation of breeding effort (Boyd 1991). This is particularly true for *Phocidae* breeding in unstable habitats, like pack ice, that present conditions favorable for reproduction just for few days every year (Le Boeuf 1986).

Phenotypic selection acts at individual level, and the evolutionary response to selection requires additive genetic variance in the target trait, i.e., the trait must have a significant heritability (Falconer 1989). Synchronization of breeding observed at population level is the result of selection acting on individual breeding strategies, and timing components of these strategies should be therefore heritable and related to fitness. Heritability of complex traits is difficult to estimate in long living species and without experimental manipulation. In many case, the best result that could be achieved is the estimation of repeatability, that represents an upper limit for heritability (Falconer 1989). In *Pinnipedia*, notwithstanding the abundant data on timing of breeding at population level (Oftedal *et al.* 1987, Boyd 1991), information on timing at individual level is scarce, and measures of repeatability are lacking. In this paper, I present data on timing of breeding of a small and localized population of southern elephant seals (*Mirounga leonina*), located on Sea Lion Island, the main breeding site in the Falkland Islands (Galimberti and Boitani 1999). I summarize information on synchronization of breeding at population level, I calculate repeatabilities for different aspects of timing, I analyze the effect of phenotype on timing of breeding , and I explore its relationship with parental investment and breeding success.

METHODS

Field work was carried out during five consecutive breeding seasons (1995-1999) at Sea Lion Island, the main breeding place of southern elephant seals in the Falklands. The island shelters a small and localized population (Galimberti and Boitani 1999), with a mean of 522 breeding females. Every year, all breeding females and all pups were marked with cattle tags (Jumbo Rototag - Dalton Supplies Ltd) put in the rear flippers, to permit identification in consecutive seasons, and with black hair dye, to permit rapid recognition during censuses and observations. Details on the marking protocol are reported elsewhere (Galimberti and Boitani 1999).

Data on timing of breeding events (arrival to land, parturition, first and last copulation, departure to sea) came from two sources, daily serial records of individual females and direct observations. On each day of the 12 weeks of the breeding season, one observer counted the seals while walking along all breeding beaches during low tide, noting details on marked females, including their breeding status (pregnant, lactating, temporarily separated from pup, alone without pup, alone during the pre-departure phase). To check for presence of breeding females outside the main study area (less than 1% of total females each year), a weekly census was carried out by walking along the cliff-tops of the entire perimeter of the island. Breeding events were recorded regularly during observation periods of 2-hours standard length (5722 periods in all, 862-1294 per breeding season). During the rest of the time spent in the field, every breeding event was recorded *ad libitum*, paying particular attention to signs of recent arrivals (wet isolated females, with diatoms in the facial area) and births (large blood spots on the sand, rests of placentae, crowds of marine birds).

The whole data set comprised 913 females, present on land for one to five breeding seasons (1 season: 13.6%, 2: 14.4%, 3: 19.7%, 4: 24.0%2, 5: 28.3%), for a total of 1906 females seasons, and a mean of 2.09 season per female. I included in the data set only females for which the parturition date was known, and excluded the few females with unusual breeding histories (short term presence on land without parturition, or with still birth or abandonment of the pup). Excluded females were less that 1% of the full data set. During the five years of study, 2139 arrivals, 1994 births, and 2188 departures were observed, or safely placed in a 24 hours window using serial records. I checked the error of estimation from serial records using the subset of females with observed breeding events. For parturition, error had a mean value of 0.242-0.357 days in different years, with estimated date always in the range ± 2 days form true date (and 99% estimated dates in the range ± 1 day). Distribution of error of estimation of parturition was homogeneous between years (Jonkheere-Terpstra test, with randomization: standardized JT statistics = 0.8442, P_{20000} = 0.3967), and the pooled mean error was 0.285 ± 0.478 days (n = 1066). I transformed dates to Julian day (*i.e.*, the number of days from the beginning of the year) and to relative day (*i.e.*, ± number of days from the day of maximum haul out of females, which was 19 October in 1995 and 1996, and 20 October in the period 1997-1999).

I calculated repeatabilities of breeding events using individual values in consecutive breeding seasons. Repeatability is equivalent to the intraclass correlation coefficient (Sokal and Rohlf 1981), and it measures the proportion of variance between hierarchical level of classification (in our case within and between individuals). Repeatabilities were calculated from variance components, using formulas presented in Lessells and Boag (1987), who pointed out that repeatability is often incorrectly calculated from mean squares. Although repeatabilities could be calculated with unbalanced within-individual samples, I split the data set and calculated repeatabilities separately for females with two, three, four and five breeding seasons. I tested significance of repeatability indices using F ratios, as in one-way ANOVA.

To examine the effect of individual phenotype on timing, I used parturition as a global index of timing, instead of repeating the analysis for every breeding event. I chose parturition because it is the event with the smaller variation around the mean (Galimberti and Boitani 1999). I considered four phenotypic trait: primiparity (YES/NO), seasonal breeding status (MILK/YELD), size class, and relative experience (= the number of previous breeding seasons). In the southern elephant seal there is a threefold variation in female size (Fedak *et al.* 1996), which allows a rough classification of females into size classes by visual inspection (Campagna *et al.* 1992). Females were classified in five main classes (extra small, small, medium, large, extra large) and eight intermediate classes, obtaining a 11-levels classification, that was then converted to ranks for analysis. Size classes are repeatable both within and between observers (Galimberti and Boitani 1999, Galimberti *et al.* 2000).

To examine the effect of timing on female parental investment, I calculated or measured five aspects of investment. From direct observation of breeding events and serial records, I calculated the length of presence on land, which is an estimate of fasting effort, and the length between birth and weaning, which is an estimate of lactation effort. From weighing data, obtained with a protocol described elsewhere (Galimberti and Boitani 1999), I calculated weight at birth and weight at weaning. Weights were available for the 1998 and 1999 seasons only, and with smaller samples than for the other variables (Birth weight: N = 181; Weaning weight: N = 299). Sex of pups was recorded during handling operations or during consecutive censuses of all weanlings of the population (N = 774 females and 879 males). When testing the effect of timing on investment, I controlled the effects of phenotypic traits, because timing and phenotype of females are likely to interact (*e.g., Rangifer tarandus*: Adams and Dale 1998).

The analysis of the effect of phenotypic traits on timing of breeding was complicated by the fact that most females of the data set were present on land for more than one breeding season, usually continuously, but sometimes with gaps (every year a small number of females skip breeding, unpublished data). Therefore, I had a longitudinal, repeated measure, data set, with unbalanced repetitions and gaps. Longitudinal data presents specific statistical problems due to correlation of the different observations for values of the response variable within each individual (Diggle *et al.* 1994). Moreover, unbalanced data with gaps are not amenable of analysis by standard repeated measure techniques. Hence, I resorted to generalized estimating equations (GEE), which are an extension of generalized linear models developed to take into account intra-cluster (*i.e.*, intra-individual in our case) correlation (Zeger and Liang 1986). GEE models have three main advantages: the capability to model response variables with non-normal distribution (all distribution of the exponential family are manageable); the applicability to unbalanced data set including singletons; and the estimation of standard errors using robust procedures. The robust standard errors are quite insensitive to mis-specification of parameters of the model, and in particular of the structure of the intra-cluster correlations (Zeger and Liang 1986). GEE models should be used when intra-individual correlation is to be considered noise, and the target of estimation are the population-averaged parameters that link independent variables to the response. They are optimal when there is a large number of clusters (> 30) and a small number of replicates per cluster (Ziegler *et al.* 1996). They were, therefore, particularly suited to my data set (913 clusters with 1-5 observations per cluster). Before running all models, I checked the presence of non linear relationships between the response and quantitative regressors using scatterplots with a LOWESS smoother (Trexler and Travis 1993). I presented asymptotic test of selected parameters of GEE models. These tests are approximate, but should be considered adequate when sample size are large and probabilities are low, as in our case. Models fit was carefully checked using the usual regression diagnostics. All analyses, except nonparametric tests, were carried out using STATA version 5.0 (STATA Corporation), and in particular the *xtgee* module for GEE models (Horton and Lipsitz 1999). Nonparametric tests were carried out using StatXact 4.0 (CYTEL Corporation). For these tests, I calculated probabilities using Monte Carlo sampling instead of normal approximations (number of resampling written as P subscript).

RESULTS

Regularity and synchrony of breeding at population level.

Females haul out showed the same regular patter during five consecutive breeding seasons (1995-1999; see also Galimberti and Boitani 1999). I found a very high concordance both of daily counts of females and of daily proportions of the maximum number of females hauled out in different years (Kendal coefficient of concordance, with randomization test: $W = 0.9923$, $P_{20000} = 0.0000$). I found an high concordance of the number of arrivals, parturitions and departures per Julian day of the season (Arrivals: $W = 0.9070$, $P_{20000} = 0.0000$; Parturitions: $W = 0.9092$, $P_{20000} = 0.0000$; Departures: $W = 0.9375$, $P_{20000} = 0.0000$). I found analogous results using relative days.

I measured synchrony as percentage of births in time windows of different length, calculated from cumulative distributions of daily values. Most births were concentrated in a short time window of about three weeks. I found that, during five consecutive seasons, a mean of 25.0% of females gave birth in a 7 days period, 55.5% in 2 weeks, 73.6% in 3 weeks, and 86.9% in 4 weeks ($N = 297$-406 births per year). To check homogeneity of synchrony, I compared proportion of births in different years by contingency table analysis, finding an homogeneous result in all cases (Likelihood ratio test, with randomization: 7 days: $G = 0.8927$, P20000 = 0.93; 2 weeks: $G = 2.227$, $P_{20000} = 0.70$; 3 weeks: $G = 3.239$, $P_{20000} = 0.52$: 4 weeks: $G = 3.972$, $P_{20000} = 0.41$).

Repeatability.

Repeatabilities and their significance are summarized in Table 1. Repeatabilities for the various timing components were very similar between females with 2, 3, 4 or 5 breeding season, and hence I present results for females with 4 breeding seasons only. This was the best compromise between number of replicates per individual and number of individuals. In the table, calculation were based on Julian day, but relative day produced almost equal results. I present data for the three main events (arrival to land, parturition, departure to sea), together with first and last copulation, but in this last cases samples were small and results should be considered tentative, at best.

Phenotypic correlates of timing of breeding.

I examined the effect of phenotypic factors on Julian day of parturition by running a GEE model with year, primiparity, females status, female size, and female breeding experience as independent variables. Dichotomous variables were coded using dummy variables. Parturition day had a symmetric normal distribution, as checked by symmetry plots, kernel density plots, and Shapiro-Wilk tests of normality ($V = 1.305$-1.880, $P = 0.0777$-0.2631 during various years). Hence, I choose gaussian error distribution with identity link, and I set an exchangeable correlation structure. I run this and following models using robust error, and I replicated calculations using different correlation structure (independent and unstructured) to check robustness of parameter estimation to this assumption (Horton and Lipsitz, 1999). Parameter estimates, robust standard errors, and confidence limits are presented in Table 2. Only size class had a significant effect on parturition day ($z = 7.010$, $P < 0.0001$) with bigger females giving birth later in the season. For the rest of the parameters standard errors were large, in particular for dichotomous variables. I found no year effect. Very similar results were found after changing the working correlation structure, as expected due to the intrinsic robustness of GEE method.

Timing of breeding and female parental investment.

I evaluated the effect of parturition day on two time components of female parental investment, the total length of presence on land and the duration of lactation, two variables that are by themselves correlated (r = 0.6280). To control for the effect of year and phenotype, I used a GEE model, with the component of parental investment as response and the parturition day as regressor, together with year and the four phenotypic traits used above. The length of presence on land had a symmetric normal distribution (Shapiro-Wilk test: V = 0.707-1.777, P = 0.0869-0.7925), and, hence, I fitted a model with gaussian error distribution and identity link function. Results of the fitting are presented in Table 3. Robust standard errors were large for all parameters, except than for day of parturition and size class. Parturition day had a negative significant effect on duration of presence on land (z = -9.407, P < 0.0001), while size class had an equally significant (z = 8.496, P < 0.0001) but positive effect. Analogous results were found for lactation length.

To examine of effect of timing on sex of the pup, I run a GEE model using sex (female = 0, male = 1) as response, a binomial error distribution, and the canonical logit link. All the parameters of the model, including the parturition day, had very large standard errors and confidence limits including zero, and also the approximate test on the whole model was non significant ($\chi2 = 3.62$, df = 5, P = 0.6058), contrary to all other models analyzed.

Birth weight and weaning weight had a normal distribution (Shapiro-Wilk test: V = 0.524, P = 0.9307 for birth weight, and V = 0.502, P = 0.9472 for weaning weight). Samples were smaller than for other responses, and the level of intra-individual replication was lower (Birth weight: mean number of replicates per individual = 1.12; Weaning weight: mean number of replicates per individual = 1.21). I employed anyway GEE for both responses to maintain homogeneity in the analysis, running the models with a gaussian error distribution and an identity link function. These analysis in part confirmed the results for time component of parental investment (Table 4). Size had a significant positive effect on both birth weight (z = 4.097, P < 0.0001) and weaning weight (z = 12.336, P < 0.0001), and day of parturition had a negative effect on weaning weight only (z = -5.160, P < 0.0001). Two differences respect to timing component emerged. We found a significant year effect for both birth weight (z = 3.998, P < 0.0001) and weaning weight (z = 2.519, P = 0.0120), with larger standard error in the latter case. This is in accordance with evidences of a variation in the distribution of weights among years (unpublished data). I also found a positive significant effect of experience on weaning weight (z = 2.310, P = 0.0210), although in this case standard error and confidence limits were very large, and, hence, this result should be considered tentative.

DISCUSSION

Notwithstanding the importance attributed to synchronization of breeding in *Pinnipedia* species, few quantitative information are available, apart from the abundant literature on timing at population level. Control of timing of breeding in pinnipeds is subject to both endogenous and exogenous factors. Photoperiod plays an important role (Temte 1994), but also availability of resources and climate constraints have a notable effect (Boyd 1991, Hind and Gurney 1998). If synchrony of breeding is the result of an evolutionary response to a natural selection pressure directed to the optimal allocation of breeding to enjoy the best environmental conditions (Boyd 1991), two assumptions should be met. Firstly, timing at individual level should be heritable, because only the presence of a genetic additive variance for a trait permits an evolutionary response to a phenotypic selection pressure on the trait. Moreover, timing should be related to fitness, *i.e.*, to some aspect of female parental investment and breeding success. The operation of selection in contemporary populations is not necessarily related to past evolutionary history, but the study of current action of selection may enlighten possible selection processes of the past (Reeve and Sherman 1993).

This study is an attempt to evaluate repeatability of timing of breeding in southern elephant seals, a good candidate for this kind of study due to the regularity of the breeding pattern observed at population level. Repeatability sets a rough upper limit to heritability, although the relationship among the two parameters is complex, in particular for behavioral traits (Aragaki and Meffert 1998). The level of repeatability calculated for timing of individual breeding events in the Sea Lion Island population is on the high side of the range of published values for different kinds of traits (Falconer 1989), with all values greater than 0.73. Repeatability estimates were consistent across four samples of females with increasing number of replicates, experiencing a wide variation of environmental conditions. Hence, I considered our estimates a good index of true repeatability of timing in our study population. As a whole, timing was highly repeatable, and it offers a good opportunity for estimation of heritability.

Repeatabilities mix a component due to endogenous and exogenous non genetic factors with a component due to additive genetic variance. The relative amount of the two component may vary independently, producing high repeatabilities with low heritabilities (Blanckenhorn and Perner 1994). Hence, the next step should be to estimate heritabilities of timing of breeding events, *e.g.*, by offspring-parent regression (Falconer 1989). Currently, just a small sample of female pups marked at the beginning of this study already entered the reproductive stage. From this sample, I obtained a preliminary result that point towards an heritable component of timing of parturition, but data is too scanty to deserve a formal presentation. Unfortunately, due to the quite large dispersion of parturition date, I expect that a very large sample of mother-daughter couples will be needed to achieve a good power in this analysis.

Results on correlates of timing should be considered cautiously, because of the intrinsic problems in the analysis of longitudinal unbalanced data. Notwithstanding this, the combination of large sample size in most analysis, and the use of robust methods taking into account within individual correlation, overcame most problems. Of the phenotypic trait considered, only size had a relationship with timing of parturition, with larger females breeding later in the season, size being a consistent index of age in southern elephant seal females (Campagna *et al.* 1992). Early arriving females usually suffer a more intense harassment by males (Galimberti *et al.* 2000). Harassment of females by males may be a significant cause of reduction of female fitness, both by an increase of female mortality and a reduction of maternal investment (*Mirounga angustirostris*: Le Boeuf and Mesnick 1990; *Monachus schauinslandi*: Hiruki et al. 1993). Hence, harassment was proposed as a primary cause for the evolution of synchronization of breeding (Boness *et al.* 1995). At Sea Lion Island, females that breed in the central phase of the season, when most other females are breeding, enjoy a lower harassment pressure, but harassment itself seems to have a milder effect that reported in other species, including the northern elephant seal (Galimberti *et al.* 2000). If synchronization of breeding is related to optimal allocation of parental investment, we should expect a non linear relationship between day of parturition and indices of parental investment, because most females are synchronized to give birth in the central part of the season, when harassment is reduced. On the contrary, the inspection of scatterplots with LOWESS smoothers gave no evidences of non-linear effects of parturition day. In GEE models, parturition day showed a linear effect on measures of breeding effort and success. The coefficients were negative for all models run, and they were significant for models with time spent on land, duration of lactation, and weanling weight as responses, although the effect size was quite small in all cases. Early arriving females not only were on land for longer, and had an higher lactation effort, but also produced bigger weanlings. Weight at weaning is probably related to survival in southern elephant seals (Burton *et al.* 1997), and hence should be a good index of female breeding success, although contrasting results were found in the northern species (Le Boeuf *et al.* 1994, Elliott and Le Boeuf 1998). As a whole, our expectation of maximum breeding effort and success in the middle phase of the season was not met.

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Variable	r	F	df	P
Arrival	0.7318	11.9169	119,360	< 0.0001
Parturition	0.7801	15.1881	100,303	< 0.0001
Departure	0.7764	14.8893	124,375	< 0.0001
First copulation	0.7991	16.9077	31,96	< 0.0001
Last copulation	0.8116	18.2362	31,96	< 0.0001

TABLE 1 - Repeatabilities of breeding events, calculated on Julian day of the event (r = repeatability; F = F-ratio of the univariate ANOVA; df = degrees of freedom; P = probability of the univariate ANOVA).

Variable	Coef.	Robust SE	Lower CL	Upper CL
Year	-0.2171	0.2408	-0.6890	0.2548
Primiparity	2.2443	1.5761	-0.8447	5.3334
Status	-0.2204	1.5772	-3.3116	2.8708
Size	0.6616	0.0996	0.4664	0.8568
Experience	0.3573	0.2644	-0.1609	0.8755

TABLE 2 - Parameters of GEE model for Julian parturition day (CL = 95% confidence limit).

Variable	Coef.	Robust SE	Lower CL	Upper CL
Presence on land				
Julian day	-0.0968	0.0100	-0.1164	-0.0771
Year	0.0739	0.0838	-0.0903	0.2381
Primiparity	-0.2210	0.5440	-1.287	0.8452
Status	-0.0821	0.6880	-1.430	1.2664
Size	0.3245	0.0418	0.2425	0.4065
Experience	0.1587	0.0969	-0.0312	0.3487
Length of lactation				
Julian day	-.0736774	.0093171	-.0919385	-.0554162
Year	.0671291	.0640468	-.0584003	.1926586
Primiparity	-.3578825	.3158631	-.9769629	.2611978
Status	.0902363	.8804493	-1.635413	1.815885
Size	.289901	.0289155	.2332276	.3465743
Experience	-.0592301	.0720322	-.2004106	.0819504

TABLE 3 - Upper half: parameters of GEE model for length of presence on land. Lower half: parameters of GEE model for length of lactation.

Variable	Coef.	Robust SE	Lower CL	Upper CL
Birth weigth				
Julian day	-0.0435	0.0542	-0.1497	0.0627
Year	4.2707	1.0682	2.1770	6.3644
Primiparity	-3.8664	2.1717	-8.1229	0.3900
Size	1.4788	0.3609	0.7714	2.1862
Experience	0.2071	0.5725	-0.9150	1.3291
Weaning weigth				
Julian day	-0.6091	0.1180	-0.8405	-0.3778
Year	4.7250	1.8758	1.0486	8.4015
Primiparity	-2.2816	4.4267	-10.9578	6.3946
Size	6.9127	0.5604	5.8146	8.0112
Experience	2.3045	0.9978	0.3489	4.2603

TABLE 4 - Upper half: parameters of GEE model for birth weight. Lower half: parameters of GEE model for weaning weight.