Aquatic Mammals 2001, **27.2,** 92–104

Modeling female haul-out in southern elephant seals (*Mirounga leonina*)

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Abstract

It is difficult to achieve good estimates of population size for pinnipeds by direct counts, because a part of the population is at sea at any time. In southern elephant seals (*Mirounga leonina*), the estimation of population size is carried-out by applying a correction factor, calculated from life tables, to the number of females hauled-out during the breeding season. Different models have been proposed in the literature to estimate the total number of females. In this paper, we consider the model proposed by Rothery & McCann (1987) for the South Georgia population. We applied their model to a five year data set for Sea Lion Island (Falkland Islands) southern elephant seals. We tested the assumptions of the model, and found them to be reasonable. We fitted the model to this data set, and obtained an excellent fit in all cases, better than or equal to other models proposed in the literature. The precision of the estimation depended mostly on the duration of females presence on land, which is a constant of the model. A one day variation in stay-length produced a 4% variation in the estimate of the total number of females. When a good model of the haulout process is already available for the population, even a single count close to the peak of the season is enough to estimate the total number of females (± 2%). When such a model is to be estimated directly from data, at least 8 counts distributed along the season are needed to have good results. The model was not only a good description of the haulout process at the population level, but its application to a set of daily counts of single harems demonstrated that it was also useful at sub-population level.

Key words: Haul-out, population size, models, harem size, southern elephant seal, *Mirounga leonina*.

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Introduction

The estimation of population size in pinnipeds is complicated by the fact that, at any time, only part of the population is hauled-out, while the rest is at sea; hence, complete counts of all individuals, of all sex and age classes, are almost impossible to achieve (Eberhardt *et al.*, 1979; Erickson *et al.*, 1993). The estimation of population size is usually carried-out by counting specific age and sex classes of the population at a specific time of the yearly cycle. Then, a correction factor calculated from the sex and age structure of the population is applied to these counts to estimate the whole population size.

Estimation of the total population size in southern elephant seals (*Mirounga leonina*) is usually carried-out starting from counts of females hauled-out during the breeding season (McCann, 1985). Elephant seals show a very regular pattern of breeding events, both at the population and the individual level (Le Boeuf & Laws, 1994). Daily variation in the number of females hauled-out to breed follows a bell-shaped curve with a maximum located in the same, or almost the same, day in different seasons (Barrat & Mougin, 1978). Each female shows a regular sequence of haul-out, parturition, nursing of the pup, copulation and return to sea. This sequence is not only very similar among females during the same breeding season, but it is also very similar from year to year for the same female (Galimberti, unpublished data). The time intervals between breeding events are, hence, quite homogeneous both within and between populations, although there is some variation related to differences in phenotype and breeding effort (Arnbom *et al.*, 1997; Galimberti, unpublished data). The regularity of the breeding pattern shown by counts of hauled-out females is the population-level result of the repeatability in the timing components of individual breeding strategies. This regularity permits simple modelling of the apparently complex pattern of females arriving to land and departuring to sea. This, in turn, permits the estimation of the total number of females using only a few counts, or even a single count, of the number of females hauled-out during specific days of the season. The approximate size of the whole population can be estimated from the total number of females by applying a correction factor calculated from life tables (McCann, 1985).

Different models have been proposed to fit the bell-shaped curve of the number of females hauled-out (Van Aarde, 1980; Pascal, 1979, 1985). All these models are basically empirical models, in that they simply fit to data a simple model that permits a compact and efficient description of the data. Rothery & McCann (1987) proposed a model (RM model hereafter) that is directly rooted in the breeding biology of the species. In their model, the proportion of females hauled-out during each day of the breeding season was the difference between the expected proportion of two cumulative normal curves, defined by the mean and the standard deviation of the distribution of arrivals, and shifted by the mean length of the female presence on land. Hence, the proportion of females hauled-out during each day of the season depends directly on the length of the presence on land, which is in turn a population averaged measure of the individual breeding effort. Rothery & McCann (1987) tested this model on a single data set of daily counts from a single area of the South Georgia population, and then applied it to other areas that had been counted once or a few times during a breeding season (see also Boyd *et al.*, 1996). In this paper, we test the assumptions of the Rothery & McCann model using five year of data from the elephant seals population at Sea Lion Island (Falkland Islands). We applied the model to estimate the total number of females hauled-out during the whole breeding season, and we compared it to other models of the haul-out process. We checked the precision of these estimates with an independent estimate calculated from individual records of marked females. Lastly, we evaluated if the model was effective at the sub-population level, by using daily counts of a large sample of harems.

Materials and Methods

The parameters of the RM model (Equation 1) are: (1) the total number of females hauled-out during the season (N_h); (2) the mean of the distribution of arrivals (μ); (3) the standard deviation of the distribution of arrivals (σ); and (4) the mean length of the presence on land of females (S):

$$n(t) = N_h\left(\Phi\left(\frac{t-\mu}{\sigma}\right) - \Phi\left(\frac{t-S-\mu}{\sigma}\right)\right) \qquad (1)$$

The model was applied by assuming some constant value of the presence on land (e.g., 30 days in Rothery & McCann, 1987 and 27 days in Boyd *et al.*, 1996), and then estimating the remaining three parameters by least-squares fitting to the observed counts.

Field work was carried-out at Sea Lion Island, the main breeding site of elephant seals in the Falkland Islands (Galimberti *et al.*, 2001) from 1995 to 1999. The number of females on land during each day of the 12 weeks of the breeding season was calculated from counts carried-out daily by walking along the whole perimeter of the area used by seals. Each breeding group within the study area was counted repeatedly, using tally counters, until convergence of two consecutive counts was achieved. Breeding groups in the study area were rather small (median at peak haul-out=31 females) and scattered, and, hence, they were easy to count. Around peak haul-out, when groups were bigger, counts were cross-validated by independent counting by two or more people. The counts were conducted from the time of the arrival of the first female until the departure of the last one. The date of each count was expressed as number of days from 1 September inclusive. The pattern of haul-out of the population in different years was almost perfectly synchronized (observed peak haul-out on 19 October in 1995 and 1996, on 20 October in 1997 to 1999).

All females in the population were marked with one or more cattle tags (usually two Jumbo Rototags, Dalton Supplies Ltd.) in the rear flippers; most (70–85%) also were marked with hair dye (up to four marks per female) soon after their arrival on land, to improve recognition during counts and behavioural observations. Information on the reproductive status of females was collected for most individuals, and breeding events were recorded during regular behavioural observations (962–1294 hours per year) and *ad libitum*. Additional information on breeding events was collected by marking every pup in the population, a first time within 24-h from birth and again as soon as the pup was pushed-out from the harem after weaning.

Total number of females breeding during each season was calculated from individual records of marked females. The intensive marking of both females and pups, the small size of the population, and the observational protocol made this estimate accurate and precise for each year of study. The length of the presence on land was calculated from daily serial records of marked females, including only the females for which complete records (i.e., daily observation from arrival to departure inclusive) were available. Additional details on the counting and marking protocols were reported in

Galimberti and Boitani (1999), together with details of estimation of time intervals between breeding events.

We fitted models by least-squares using an iterative procedure (sequential quadratic programming or Levenberg-Marquardt algorithm). Models were easily fitted in most cases, achieving convergence in less than 20 iterations. We estimated standard errors of parameters using both asymptotic approximation and bootstrap (with 500 resamplings). Asymptotic and bootstrap standard errors were very similar in all cases, with bootstrapped errors being only slightly larger. After model fitting, we checked plots of residuals for normality and homogeneity of variances. We tested normality of variables and residuals using the Shapiro–Wilk test.

Model fitting and statistical analysis, including simulations, were carried-out using SPSS 6.1 (SPSS Inc.) and Stata 5.0 (STATA Corporation).

Results

Assumptions of the RM model

The RM model estimates the proportion of females hauled-out daily during the breeding season by assuming that the distribution of arrivals on land occurs according to a normal distribution. We verified this assumption by visual examination of normal plots and by standard tests. The distribution of arrival-day showed a slight positive skew (i.e., the density of arrivals was more concentrated in the right tail of the distribution than expected from the normal distribution), with a skewness index ranging from 0.10 to 0.56 (mean=0.29). The distributions were also leptokurtic (i.e., the distribution of arrivals had a higher peak than expected), with a kurtosis index ranging from 3.21 to 3.80 (mean=3.49). Shapiro–Wilk test demonstrated a large deviation from normality for two years (1995: W=0.9818, z=3.196, *P*=0.0007, and 1998: W=0.9806, z=4.150, *P*<0.0001), a slight deviation for one year (1999: W=0.9921, z=1.874, *P*=0.0305) and no deviation in the remaining two years (1996: W=0.9960, z=0.620, *P*=0.27, and 1997: W=0.9960, z=0.465, *P*=0.32). It should be kept in mind that we tested large samples of arrival days (N ranging from 302 to 481), and that Shapiro–Wilk test is very sensitive to deviations from normality with large samples. Visual inspection of distributions showed that the main difference from a normal distribution were long tails, with most of the deviation from normality occurring due to outliers at the extremes of the spread of the distribution.

In the RM model, the same distribution was used to model both the arrival and the departure process, i.e., the distribution of departures is assumed to have the same shape and spread as the distribution of arrivals. The two distributions are assumed to differ just in the location, with departures distribution shifted by the length of presence on land. To test this assumption, we compared the observed distribution of arrivals and departures for each year (excluding 1995 in which estimates of departures were less reliable). We subtracted the year-specific mean length of presence on land from the departure day, to allow for the shift in location of the two distributions. We tested the difference between distributions using the Kolmogorov–Smirnov test. Distribution of arrivals and departures were not significantly different in 1996 (D=0.0535, *P*=0.495), 1997 (D=0.0529, *P*=0.502) and 1999 (D=0.0598, *P*=0.413), but they were in 1998 (D=0.1205, *P*=0.002). In 1998, the right tail of the departures distribution was shorter than the corresponding tail of the arrivals distribution, with late breeding females spending less time on land. This effect was evident also during the other three years, but much more pronounced in 1998.

The estimation of the RM model requires the specification of the length of presence on land as a model constant. Interannual comparisons should utilize a constant value for the different seasons. This is reasonable if the standard error of the mean on-land time is small, and if this mean value is almost constant across seasons. For the five years of this study, we calculated a pooled mean of 27.2 days (SD=3.36, N=1553). Length of presence was not homogeneous among years (ANOVA: $F_{4,1548}=10.826$, *P*<0.0001) and its mean value ranged from 26.5 to 28.1. This last value was from 1995 data, and was based on a smaller sample (N=148 in 1995 versus N=330–387 in the remaining years). Standard error of the mean was small from 1996 to 1999 (SE ranging from 0.164 to 0.191); it was slightly larger in 1995 (SE=0.284), again due to the smaller sample size. We found various pairwise differences among years. Using Games and Howell *post-hoc* pairwise tests (to account for heteroscedasity), 5 of the 10 comparisons among years were significant at 0.05 level (1995 vs 1996, 1995 vs 1997, 1996 vs 1999, 1997 vs 1998 and 1999).

Fitting of the RM model to population data

We fitted the RM model to daily counts for each breeding season, from 1995 to 1999, using year-specific estimates of the length of presence on land. Fitting was excellent in all cases, with adjusted coefficients of determination above 0.998, and small standard errors for all parameters (Table 1). We repeated the fitting procedure using a common estimate of length (S=27.17 days, mean for five years), and obtained similar fits (R^2 above 0.998 in all cases). Parameters and standard errors obtained with the constant S were very similar to the ones

Table 1. Estimated parameters and standard errors for the Rothery & McCann (1987) model.

Year	S	R^2	μ	$SE(\mu)$	$SE_b(\mu)$	σ	$SE(\sigma)$	$SE_b(\sigma)$	N_h	$SE(N_h)$	$SE_b(N_h)$
1995	28.10	0.9981	32.6879	0.0588	0.0775	8.3579	0.0886	0.1106	504.5811	2.1430	2.5324
1996	26.81	0.9990	33.1971	0.0431	0.0574	8.8836	0.0614	0.0863	541.3108	1.6800	1.9852
1997	26.51	0.9982	35.5091	0.0583	0.0703	9.1647	0.0811	0.1015	569.0143	2.3615	2.8802
1998	27.27	0.9992	36.0065	0.0401	0.0458	9.2754	0.0563	0.0533	559.1288	1.5635	1.6838
1999	27.80	0.9994	36.6496	0.0329	0.0426	9.2390	0.0469	0.0588	542.6573	1.2384	1.5912

S: mean length of presence on land; R^2: adjusted coefficient of determination; μ: mean day of the arrivals distribution, with standard error (SE) and bootstrapped standard errors (SE_b); σ: standard deviation in days of the arrivals distribution; and N_h: number of females hauled-out during the whole season.

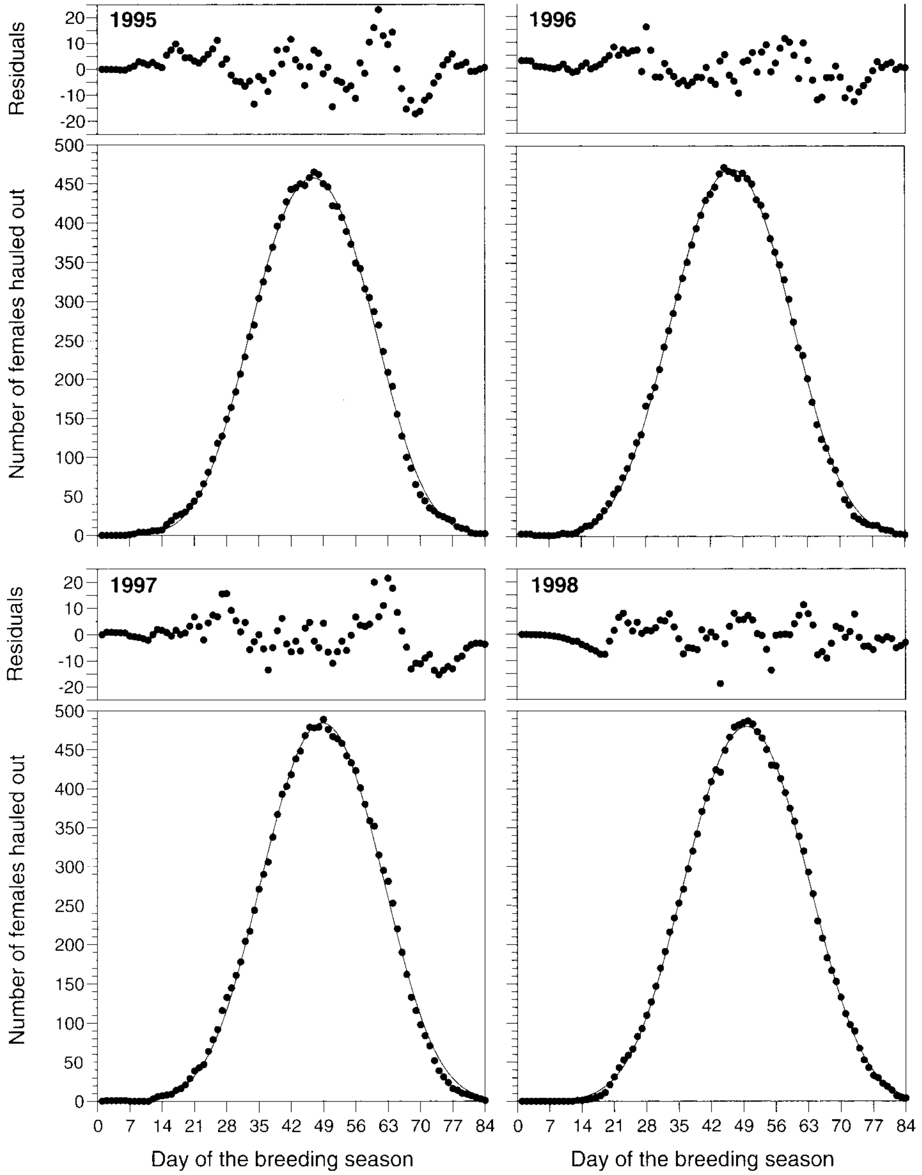

Figure 1. Fit of the Rothery & McCann (1987) model to Sea Lion Island count of southern elephant seals. Each panel, a breeding season from 1995 to 1998, shows the counts and the fitted model in the bottom graph, and the residuals of the fit in the top graph. Date of the season measured in days from 1 September.

obtained with year-specific S. For models with year-specific S, mean value of residuals ranged from − 0.57 to +0.37, with a minimum from − 18.90 to − 9.58 and a maximum from +11.25 to +23.00. Residuals were normally distributed in four of five years (Shapiro-Wilk test: *P* ranging from 0.07 to 0.76), while for 1997 a slight deviation from normality was detected (W=0.9682, z=1.799, *P*=0.036). Visual examination of scatterplots showed no clear deviation from randomness of residuals, at least in the central part of the scatter (Fig. 1).

We fitted our data to some other models of the haul-out process, that were proposed in the literature. Firstly, we fitted a simple quadratic model using least-squares (a parabola curve, Van Aarde

Table 2. Precision of estimates of total number of females hauled-out.

Year	N_{hSc}	N_{hSy}	N_{hObs}	$N_{hSc}-N_{hObs}$	$N_{hSy}-N_{hObs}$	% $N_{hSc}-N_{hObs}$	% $N_{hSy}-N_{hObs}$
1995	523	505	517	+6	−12	1.16	2.32
1996	534	541	527	+7	+14	1.32	2.66
1997	555	569	563	−8	+6	1.42	1.07
1998	561	559	567	+6	−8	1.06	1.41
1999	556	543	533	+23	+10	4.32	1.88

N_{hSc}: number of females hauled-out as estimated by the RM model (Rothery & McCann, 1987) with constant length of presence on land; N_{hSy}: number of females hauled-out as estimated by the RM model with year-specific length of presence on land; and N_{hObs}: number of females hauled-out as calculated from individual records of marked females.

1980). The fit was poor for all years, with much smaller coefficient of determination than for the RM model (R^2 from 0.67 to 0.71). The model severely underestimated the maximum number of females hauled-out (−36.8% to −42.8%). Then, we fitted polynomial models (Pascal, 1979) with orders from 3 to 10. For our counts, cubic models provided poor fits (R^2 ranging from 0.765 to 0.853). Models up to order 5 underestimated the maximum number of females hauled-out, and models up to order 7 produced negative fitted values in the time range of the breeding season. A polynomial of order 8 was needed to produce a fit without unreasonable values. The effectiveness of polynomials of high order was checked by applying an automatic procedure to counts, that fits a large number of models, producing an ordering of them based on fitting quality statistics. The best models were polynomials of order ≥ 7, that, produced an accurate fit for the whole duration of the breeding season. Lastly, we fitted the Gaussian model proposed by Hindell & Burton (1988), which was previously applied to a smaller set of counts of the Sea Lion Island population (Galimberti & Boitani, 1999). This model includes as parameters the maximum number of females hauled-out during the peak day of the season, the mean of the distribution of haul-out, and the standard deviation of this distribution. The distribution of haul-outs is then modelled according to a normal distribution. The fitting of the model was excellent in all cases (R^2 from 0.9962 to 0.9982), standard errors were small, and residuals were normal and homogeneous in the time span of the season.

Estimation of total number of females hauled-out

The final goal of the RM model was to obtain a good estimate of the total number of females hauled-out during the whole season. Hence, we compared the estimates of N_h obtained with the RM model (both with constant and year-specific length of the presence on land) with the observed N_h obtained from individual records of marked females. The mean error of the first estimate was +10 females, while for the second estimate was +2 females (Table 2). The deviation of the estimated value from the observed value had a mean of 1.86% for the single S estimate and a mean of 1.87% for the year-specific S estimate. From the parameters estimated by the RM model, we calculated the year-specific maximum proportion of females hauled-out in a single day (the day of the peak haul-out), which is $2\Phi(S/2\sigma)-1$ (Rothery & McCann, 1987). We then compared these estimates to the observed maximum proportions calculated from daily counts. The estimated proportions had a mean of 0.870, while the mean of observed proportions was 0.886. The RM model slightly underestimated the proportion of females hauled-out at peak in four of five years, with a percent difference (observed-estimated) from −0.87% to 3.11% (mean = 1.75%).

In most practical situations, the total number of females can only be estimated using a single or few counts. The variation of model residuals showed variation of the quality of the fit through the season. Hence, we checked the effect of day of the count on the estimation of total number of females. For each year, using the parameters estimated from the model, we calculated the expected proportion of females on land. From these proportions, and from the corresponding daily counts, we calculated for every day of the season an estimate of the total number of females (N_h). We then analyzed the precision of N_h estimates in different time windows around the peak haul-out. The difference between the estimated number and the actual number (from records of marked females) was large toward the extremes of the season, but was always in the ± 10% range for its central part (Fig. 2).

We used a change-point test (Siegel & Castellan, 1988) to determine if the variation in the trend of differences along the season was significant. For each year, we ran two change-point tests on percent

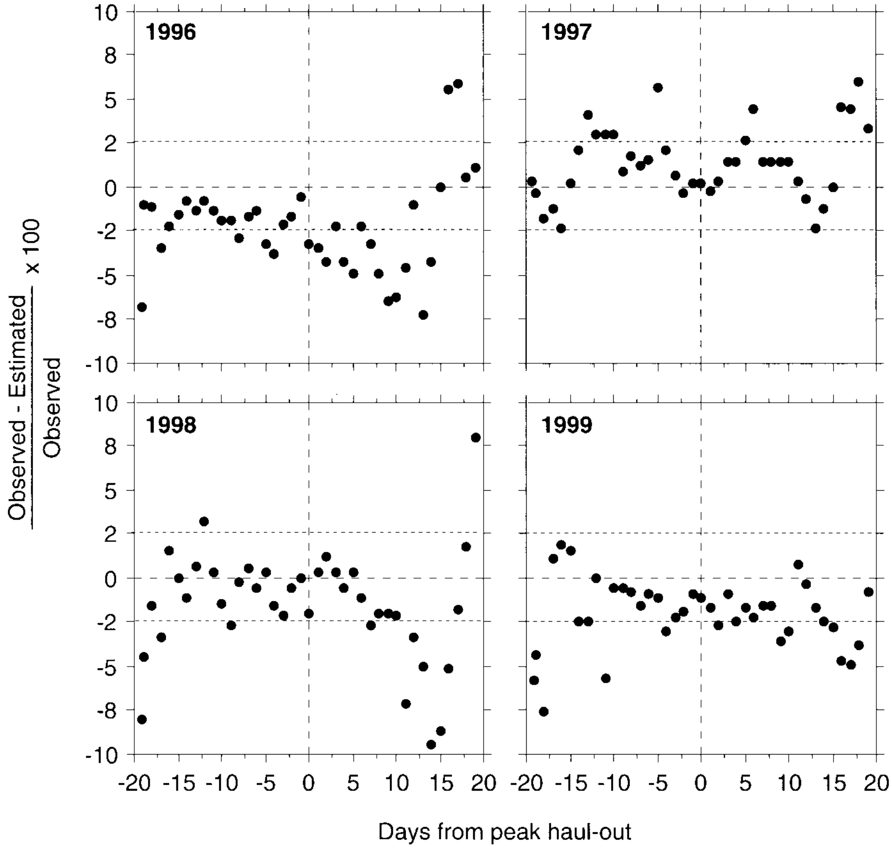

Figure 2. Percent differences between the observed and the estimated (from RM model) number of southern elephant seal females during a 41-day period centered on day of maximum haul-out (peak of the season).

bsolute differences among observed and estimated N_h. The first one was run on the whole series of daily differences, to determine the day of the season on which the trend of differences decreased from the high values of the beginning phase to the low values of the central phase. The second one was run on the days from the first change-point +1 to end of the season, to determine the day on which the trend in differences increases again from the low value of the central phase to the high values of the final phase. We found for each year two highly significant change-points, that represented the limits of the central phase of the season in which the estimation efficiency of the RM model was high. This interval was quite variable among years, had a mean length of 38 days (from 30 to 45), a mean beginning in day 27 (from 21 to 32), and a mean end in day 63 (from 59 to 70).

We calculated statistics of absolute percent differences for three intervals of 7, 15, and 21 days, centred on the day of peak haul-out (Table 3). For the pooled data of the five years, the mean value of the absolute percent differences was 1.63% (max=5.61) for the 7 days period, 1.99% (max=5.64) for the 15 days period, and 2.02% (max=6.45%) for the 21 days period. We pooled absolute percentage differences for the five years, and calculated statistics for twelve, 7-days intervals, starting on September 1, to give a guideline for the choice of the period in which to carry out counts.

Expected peak haul-out on Sea Lion Island was October 19, the end of the 7th interval. The maximum efficiency in estimation of N_h was achieved on the 7th interval (Table 4). From two weeks before the peak day to one week after, the maximum error in the pooled five years data set was within 6%.

Effect of length of presence on land

We fit the RM model with variable S, starting from the baseline of 27 days (see also Boyd *et al.* 1996), to

Table 3. Percent error in estimation of total number of southern elephant seal females hauled-out during the whole season.

Days	1995	1996	1997	1998	1999
7	2.597 ± 1.610 5.609	2.494 ± 1.207 4.175	0.939 ± 0.844 2.131	0.479 ± 0.452 1.411	1.635 ± 0.665 2.627
15	2.876 ± 1.618 5.609	2.808 ± 1.220 4.934	0.947 ± 0.796 2.664	1.587 ± 1.600 5.644	1.726 ± 0.666 3.002
21	2.468 ± 1.574 5.609	3.163 ± 1.574 6.452	1.167 ± 0.868 2.664	1.604 ± 1.386 5.644	1.706 ± 0.864 3.565

Statistics (calculated from absolute values) are presented for three time intervals centered on day of peak haul-out (7, 15, 21 days). First line of each cell is mean ± standard deviation; second line is maximum.

Table 4. Statistics of percentage absolute differences between observed and expected N^h in 7-days intervals.

Interval	Dates	Mean	SD	Min	Max
1	01/09–07/09	392.937	781.935	18.975	3825.996
2	08/09–14/09	76.383	48.223	3.375	236.750
3	15/09–21/09	24.954	22.616	0.375	70.018
4	22/09–28/09	7.282	5.162	0.000	16.696
5	29/09–05/10	2.929	2.219	0.000	7.993
6	06/10–12/10	1.820	1.385	0.000	5.629
7	13/10–19/10	1.691	1.234	0.000	5.644
8	20/10–26/10	2.423	1.555	0.176	5.609
9	27/10–02/11	3.105	2.285	0.353	9.414
10	03/11–09/11	5.698	5.867	0.000	25.532
11	10/11–16/11	15.187	11.841	0.353	44.405
12	17/11–23/11	26.118	18.318	1.741	78.508

evaluate the effect of the variation in the estimate of the length of presence of land. S was increased sequentially by 0.5 day steps in the ± 3 days range. The total number of females varied in a quadratic fashion, with curves from different years being almost parallel to one other, apart from small differences due to rounding errors (Fig. 3). We then calculated the percentage differences from N_h estimated using the baseline length. The percentages for the pooled five years were fit perfectly by a quadratic model (b(S)= − 12.384, b(S^2)=0.158), but also a linear model provided an excellent fit (R^2=0.995; b= − 3.867, SE(b)=0.034). Therefore, we concluded that a 1-day decrease from the baseline S produced approximately a 4% increase in the estimate of N_h, and that a 1-day decrease in S produced an equivalent increase.

To evaluate the effect of the use of a standard value of S, we fit the RM model with S=27 to daily counts from Punta Delgada, a high density area of the Valdés Peninsula (counts were carried-out in 1993 and 1994 using the protocol employed on Sea Lion Island). We compared the fitting with standard S with the fitting obtained using a value (S=28.2) presented in Campagna *et al.* (1993). The quality of the fitting as measured by the coefficient of determination was similar for the two models (R^2=0.993 for 1993 and 0.999 for 1994). However, the model with S=27 underestimated the proportion of females hauled-out at the peak of the season compared to the model with S=28.2 (0.78 vs 0.81 in 1993 and 0.77 vs 0.80 in 1994). These values were different from the 96% reported in Campagna *et al.* (1993). Therefore, the model overestimated the total number of females hauled-out during the whole season (by 4.56% in 1993 and 4.54% in 1994). An independent estimate of the total number of females was not available for 1993, but from individual records of marked females of 1994 we obtained a value of 718, which is in the middle of the two estimates from the RM model (N_h=737 with S=27, N_h=705 with S=28.2). Data on total presence on land for the 1994 sample were not available, but the information we collected on parturition to departure intervals (unpublished data) suggested that the Campagna *et al.* (1993) estimate (which is based on a small sample of females, N=38) could slightly overestimate the true duration.

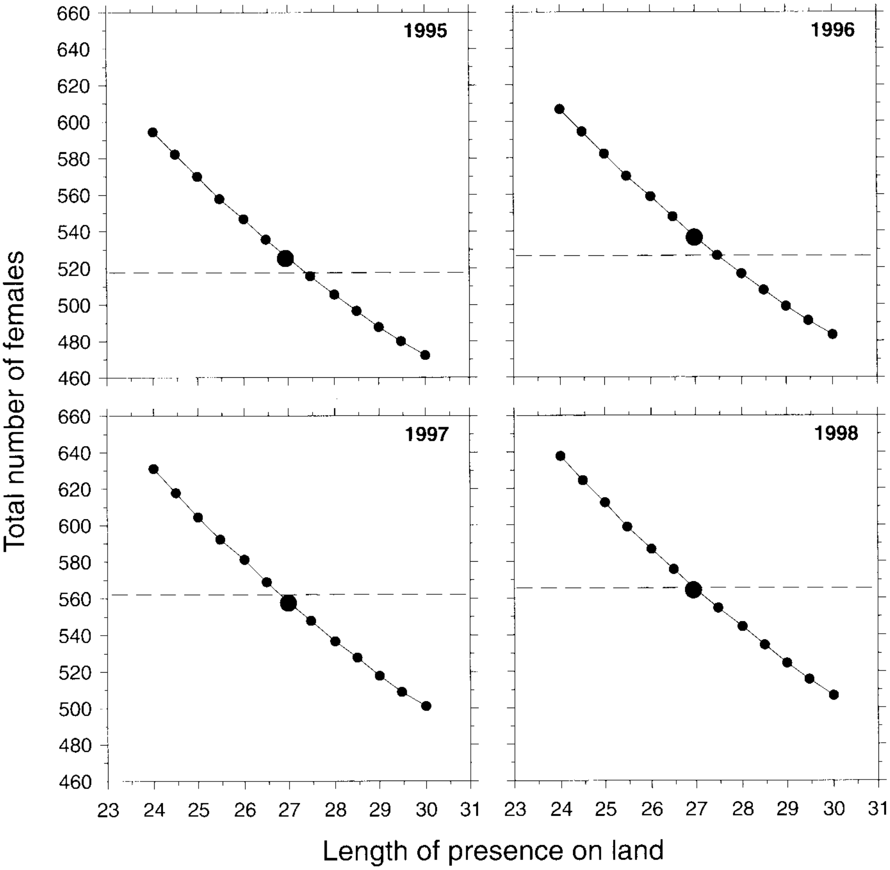

Figure 3. Estimated number of southern elephant seal females at variable lengths of the presence on land, in a ± 3-day range from the baseline (S=27). Dashed line is the observed number, the bigger dot is the number estimated using the baseline length.

Effect of the number of counts

The RM model, being a three parameters model, requires at least three counts to be fitted. We ran a simple simulation to evaluate the effect of the number of counts on the precision of the fitting. We applied the RM model to 4 to 30 counts (3 were unable to get convergence in the fitting for many samples) selected at random (without replacement) from the count series of each of the five years of study (excluding counts from the first week). We repeated 500 times the sampling for each number of counts. We estimated N_h for each sample, and calculated statistics from these distributions of N_h values. For each of the five years, the mean N_h was almost independent from the number of counts, with a variation of 4 to 10 females in different years. The standard deviation of N_h showed a very large variation (Fig. 4), following closely an exponential decrease with increase in the number of counts ($SD_{Nh}=1.847\ e^{15.535/Nc}$; $R^2=0.8635$). It decreased steeply from 4 to 8 counts, and then more slowly up to 15 counts. The increase of the number of counts above 15 had a small effect on the standard deviation of N_h estimates.

Fitting of the RM model to harem data

To evaluate the effectiveness of the RM model at the sub-population level, we fit daily counts of a large set of harems (N=81), with a median size (maximum number of females in the harem) of 38 females (from 6 to 119). We excluded harems originated by fission of existing harems, which had daily variations in the number of females without a regular increase phase. The mean adjusted coefficient of determination of the fitted models was 0.931 (SD=0.114) and the median was 0.971 (MAD=0.0021). Fit was not always good (R^2 ranged from 0.429 to 0.995), but it was very good ($R^2 \geq 0.95$) in 64.2% of cases, and reasonable ($0.90 \leq R^2 < 0.95$) in 17.9%. The quality of the fit as

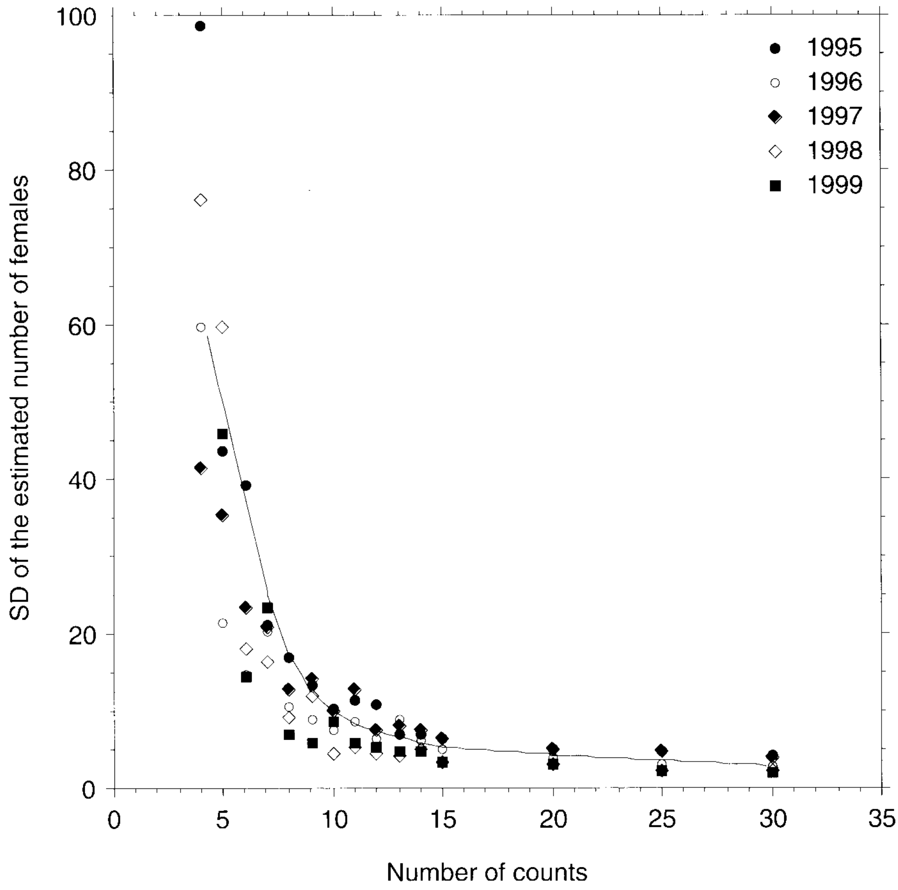

Figure 4. Standard deviation of estimated number of southern elephant seal females, calculated on random samples (N=500) with variable number of counts, extracted from actual counts series (1995–1999). Points are splitted by year, while the line is a LOWESS smoother (Trexler & Travis, 1993) calculated on the pooled years (tension=0.66).

measured by R^2 was linearly related to harem size for harems below the median size (R^2 of the linear regression=0.237), but not for harems above the median, that always had an $R^2 \geq 0.90$. The standard errors of the three parameters of the model were linearly related to harem size for harems below the mean size (SE(M): R^2=0.249, SE(S): R^2=0.270, SE(N_h): R^2=0.221), but not for harems above it.

Discussion

The regularity of haul-out of southern elephant seals permits modeling of arrivals and departures by fairly simply models. Modeling of haul-out behavior has different potential uses. A model can be used to describe, in a compact and efficient manner, the haul-out process itself. The estimated parameters may be used as input for further analysis of the breeding biology of the species, or to compare different populations. Any model that accurately fits the data, and with biologically meaningful parameters, is suitable. Some models of the daily variation of the number of elephant seal females hauled-out are purely empirical, with no formal link to the breeding biology of the species. Their goal was simply to provide a good description of the haul-out process. Pascal (1979) proposed a polynomial model for the Kerguelen population and Van Aarde (1980) a quadratic model for the same population. Although these models may fit the data well, they also produce unreasonable results, in the form of negative estimates of the number of females, because they are not bounded to values ≥ 0. The quadratic model is also a poor description of the number of females hauled-out in the first and last part of the breeding season, when the increase or decrease rate is much smaller than in the central part of the season. Pascal (1985) proposed a Gaussian model fit to the percentage of females hauled-out. Although this model provides a better fit than the previous ones, it has an obvious drawback, because, to calculate percentages, the total number of females needs to be known in advance.

Hindell & Burton (1988) proposed a Gaussian model based on the distribution of haul-outs, and, hence, linked to the actual breeding biology of the species. This model was very effective in modelling the haul-out process. It produces a direct estimate of the day of peak haul-out, that could be useful to compare the timing of breeding in different populations (Galimberti & Boitani, 1999). This model could be applied to other sex and age classes besides breeding females, although it is not as functional for other groups (Hindell & Burton, 1987). It also produces an estimate of the spread of the breeding season, that could be used to compare the level of synchrony in breeding among different areas and populations (Hindell & Burton, 1988), a variable which is valuable in the analysis of life histories and breeding strategies. A second use of the models of the haul-out process is the estimation of the total number of females, and this is the area where the Rotary & McCann (1987) model is superior. This model permits a direct estimation of the number of females hauled-out during the whole breeding season. These estimates could be used to improve the analysis of long-term population trends (Hindell & Burton, 1987; Boyd *et al.*, 1996) or to estimate the whole population size, by building on knowledge of population structure and life tables (McCann, 1985).

Our application of the RM model to the Sea Lion Island population demonstrated that its assumptions regarding the shape of the arrival and departure processes are quite reasonable. Arrivals and departures are effectively modelled by symmetric cumulative normal distributions, although observed tails are longer than expected. The use of a single estimate of the length of presence on land (constant among years) is justifiable because inter-year variations are small. For the Sea Lion Island population, the model produced an excellent fit to the actual daily pattern of haul-out of the females in every year of the study. We found a slight tendency to underestimate the proportion of females hauled-out at peak, and, hence, to overestimate the total number of females. This slight lack of fit is linked to the slight non-normality of the observed haul-out process. The RM model assumes a normal distribution of arrival on lands, while the actual distribution is slightly leptokurtic. Notwithstanding this, the difference between the estimated total number of females hauled-out and the observed number was small.

From a practical point-of-view, the main problem in the application of the RM model is its sensitivity to variation in the estimate of length of presence on land (see also Boyd *et al.*, 1996). A 1-day variation of the estimate of S used in the model produced approximately a 4% variation in the estimate of the total number of females. In the Sea Lion Island population, an on-shore duration of 27 days, as proposed by Boyd *et al.* (1996) for the South Georgia population, provided a good estimation of N_h, because it was very close to the mean length calculated from five breeding seasons (27.17). Estimates of S from other populations are longer (Marion Island: 28.6 days, Condy, 1979; Kerguelen: 28–30, Van Aarde, 1980; Valdés Peninsula: 28.2, Campagna *et al.*, 1993).

The interval from parturition to departure seems to be almost constant in most populations (Marion Island: 22.5, Condy, 1979; Kerguelen: 22.4, Van Aarde, 1980; Crozet and Kerguelen: 21.8, Guinet, 1991; South Georgia: 22.7, Arnbom *et al.*, 1997; Valdés Peninsula: 22.4, Campagna *et al.*, 1992; King George Island: 22.1, Carlini *et al.*, 1997). However, the estimates of the interval between arrival and parturition are more variable, even within the same population (Marion Island: 6.1, Condy, 1979; South Georgia: 6.4, McCann, 1980, and 4.5, Boyd *et al.*, 1996; Valdés Peninsula: 5.7 Campagna *et al.*, 1993), and this variation explains most of the variability in the estimates of total presence on land. Part of this variability was probably related to the lower accuracy in the estimation of the timing of arrivals compared to births and departures, because arrivals are less conspicuous events (Galimberti & Boitani, 1999).

If a good model of the process for the specific population is already available (e.g., because it was estimated on a large series of counts during previous years), even a single count, if carried-out close to peak haul-out, could give an estimate of the number of females in the range ± 2% from the actual number. However, if no previous model is available and just a few counts are carried out the RM model should be used with caution. Ideally, the model should be fitted with $S=27$, when population-specific estimates are not available, using at least 8 counts distributed along the season, with some of them close to the peak. When less counts are available the risk of a poor fit is high. Therefore, in these cases, the total number of females should be estimated from the proportion of females hauled-out in each day of count, calculated using Equation 1, with mean and standard deviation of the arrivals distribution from published sources (e.g., from Table 1). Each count, multiplied by 1/expected proportion, gives an independent estimates of N_h, and the number of females can be calculated as the mean of these estimates. In this

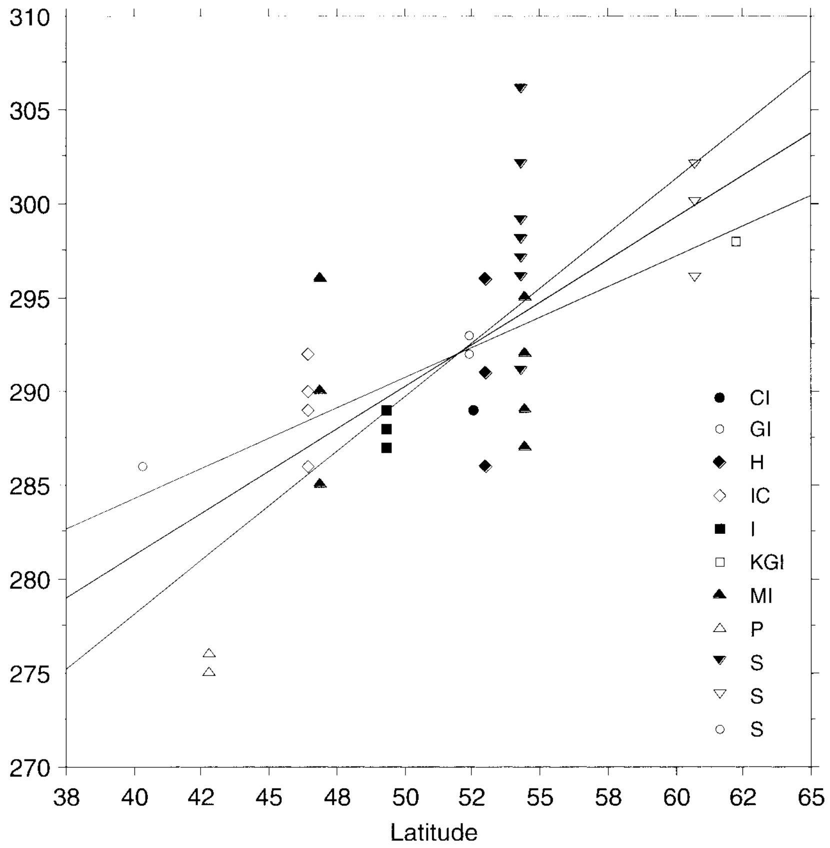

Figure 5. Relationship between latitude (decimal degrees) and the peak day (Julian day). Thick line is a regression line, calculated from multiple yearly values for each population, using an estimation method that accounts for correlation of values within each population and provides robust standard errors (Day of peak=245.16+0.901 Latitude; R^2=0.53, robust SE(b)=0.139). Thin lines are robust 95% confidence limits for the slope. CI: Campbell Is., GI: Gough Is., HI: Heard Island; IC: Iles Crozet, IK: Iles Kerguelen, KGI; King George Is., MI: Macquarie Is., PV: Valdés Peninsula, SG: South Georgia, SI: Signy Is., SLI: Sea Lion Island (Falkland Islands).

cases, counts close to peak haul-out provide better performance. The day of peak, if unknown, can be calculated from the relationship among the day of peak and the latitude (Fig. 5). Although the latitude explains only a part of the variability in the day of peak numbers hauled-out, the relationship is strong enough to provide an estimate to be used to define the schedule of counts.

Apart from being useful for the estimation of population size, the RM model also seems to be a good descriptor of the haul-out process at the sub-population level. Our application of the model to a sample of harems showed that the model was effective in the modeling of the number of females in each harem, at least for harems above the median size. For harems below the median size, the balance between arrivals and departures of females was more irregular, and more influenced by stochastic sampling bias due to the small number of females involved. The size of harems and their daily variation could have an effect on both male mating tactics and female breeding strategies. Harem size interacts with male phenotype, and limits the capability of harem holders to monopolize matings (Modig, 1996). It also affects female behaviour, influencing the density of peripheral males and, therefore, the likelihood of harassment of females (Galimberti *et al.*, 2000).

The capability of modelling harem demography with a small number of parameters provides a useful way to summarize the complex pattern of arrival and departure of females. This may improve our understanding of the components of elephant seals social dynamics that depend on harem size.

Acknowledgments

We thank Carla and Alberto Galimberti for their support of our research on elephant seals; Anna Fabiani, Ilaria Marzetti, Alessia Gallastroni, Alice Camplani, and Daniela Marasco for their help with data collection; the Falkland Islands Government for allowing us to carry-out our research in the Falklands; the Falkland Islands Development Corporation for allowing us to do the field work on Sea Lion Island; David Gray for his help with logistics. Dr Jeanette A. Thomas, Dr. Kit Kovacs, and Dr. Ian Boyd provided very useful comments on a first version of the paper.

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