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Status and demography of southern sea lions at Sea Lion Island, Falkland Islands

21/07/2020



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Summary

The southern sea lion (*Otaria flavescens;* SSL) is a charismatic South American pinniped that greatly suffered commercial exploitation by sealers. It has a wide geographic distribution and is not immediately threatened, but its status differs in the different parts of its range. In particular, in the Falkland Islands the current population size is much reduced compared to its historical size.

Currently, in the Falklands there is no regular monitoring of southern sea lion colonies, although a whole island census is carried out at five year intervals. We carried out a regular monitoring of southern sea lions at Sea Lion Island, the southernmost inhabited island of the Falklands, during seven breeding seasons (2013-2020). We analyzed our count data to estimate various aspects of the population demography and structure, including sex/age class composition, sex ratio, group size, females/pups per territorial males, and number of pups produced. We modelled pup numbers to estimate parameters related to the timing of the breeding season, and we estimated the population trend. The net productivity of the population showed a large increase from 2013, although there were fluctuations in the last seasons. From a practical point of view, we showed that in different years the accumulation curve of the number of pups had a different shape. This variability, combined with the intraseason variability in counts, cast some doubts about the possibility to accurately estimate the island wide population trends based on a single or few counts of each colony.

Introduction

The southern sea lion (Otaria flavescens; SSL) is a charismatic South American pinniped species that greatly suffered commercial exploitation by sealers (Thompson et al. 2005). Currently, SSL has a wide geographic distribution (Hückstädt et al. 2016), and is not immediately threatened (IUCN Red List: Least concern, Cárdenas-Alayza et al. 2016). On the other hand, the status of SSL in the different parts of its range shows large differences. Most populations of the South American mainland are showing signs of recovery, although the current population size is 40% of the estimated historical population before the beginning of the extensive human commercial exploitation that ended about 50 years ago (Romero et al. 2017). On the other hand, the Falkland Islands population is still much reduced compared to its reported historical size (Baylis et al. 2015a). Surveys carried out in the 1930s (Hamilton 1934, 1939) produced an estimate of net productivity of ~ 80,550 pups and a total population size of ~ 380,000 SSL. A full aerial survey carried out in 1965 produced an estimate of less than 6000 pups, a 93% decrease (Strange 1979). The minimum was reached in 1990 (1.5% of the population of the 1930s) while in recent years the population showed a very slow increase (Thompson et al. 2005; Baylis et al. 2015a), and it is currently at about 6% of the historical size. The reason of this dramatic demographic variation are still unknown, although there are some evidences that a warming of sea surface temperatures between 1930 and 1950, which affected the South Atlantic food chain, may have had an important role (Baylis et al. 2015a). A striking aspect of the SSL population of the Falklands is its scattered distribution. Most colonies are small or very small (mean number of pups = 63.5, median = 49.5, 1-328; data from Baylis et al. 2015a, Appendix A), and they should be, in principle, easy to count. Therefore, the counting error is assumed to be small (~ 5%, Thompson et al. 2005). On the other hand, SSL pups may hide in the tussac grass and under boulders, and colonies are often located in places that are difficult to access. Therefore, counting error can be much greater than 5% (Galimberti and Sanvito 2020b).

Sea Lion Island (SLI hereafter) is the southernmost inhabited island of the Falkland Islands, and shelters a small breeding colony of SSL. There is no information about the historical size of the population, because SLI was not included in the counts carried out in the 1930s (Hamilton 1939). Commercial harvesting of sea lions has been carried out at SLI not only in the far past (1820-1834; Dickinson 1994) but also more recently during the failed sealing operations by the Falkland Islands and Dependencies Sealing Company (1927-1940) and the South Atlantic Sealing Company (1949-1951; Palmer 2004). The first published count belongs to an aerial survey carried out in 1990, when 33 pups were observed (Thompson et al. 2005). The estimation of the status and trend of small populations presents specific problems because of the low power to detect trends, and decrease trends in particular (Galimberti 2002). The capability to detect a decrease trend in a small population depends mostly on the error of the yearly estimates (Gerrodette 1987, Link and Nichols 1994).

In this report, we summarize data collected on SLL of SLI over seven breeding seasons. We carried out regular counts of the sea lion breeding colony. From count data we estimated sex/age class composition, sex ratio, group size and females/pups per territorial male, and pup production. We modelled the accumulation of pups during the breeding season

using various growth functions, and we estimated parameters of the timing of the breeding season like the mean birth day/date. We presented a summary of the available yearly counts and their trend.

Methods

Field work

Field work was carried out at Sea Lion Island (Falkland Islands, $52^{\circ} 26' \text{ S} 59^{\circ} 05' \text{ W}$) during seven southern sea lion breeding seasons (December-April, 2013-2020). At least weekly, we counted the sea lions of the main breeding colony, located on the southern coastline of Sea Lion Island (Figure 1).



Figure 1 - The Sea Lion Island SSL breeding colony from the air.

During counts (Figure 2) we classified sea lions in sex and age classes, we took approximate GPS positions, and we recorded all occurrences of dead pups. Accuracy of counts was checked by having two observers counting at the same time, to estimate inter-counter reliability, and by carrying out repeated counts, to estimate intra-counter reliability. We augmented the manual counts using counts on high resolution aerial photos taken from an unmanned aerial vehicle (details in Galimberti and Sanvito 2020b). UAV counts provide a better estimate of the maximum number of pups compared to ground counts (Galimberti and Sanvito 2020b) and, therefore, we used maximum UAV counts of pups to estimate trend in recent years (from 2016). Some scattered counts of the total number of pups were available

for the period before the beginning of our study, carried out by us or by other surveyors. Although the quality of our counts carried out in the 90s should be comparable with the current study, the quality of counts carried out by other observers is unknown.



Figure 2 - Distribution of the counts of the Sea Lion Island SSL colony. Day of the breeding season: days counted from 1 = 27th of November (day of the first count of the whole dataset). Red dots: the counts; blue dots: the mean counting day, light blue lines: 95% confidence interval of the counting day.

Southern sea lion sex is quite easily recognized using the differences in size, colour and morphology between the two sexes, because the species is strongly dimorphic (Hamilton 1934, 1939). Moreover, males show a gradual development of secondary sexual traits, and of the mane in particular, that help in recognizing male age classes (Hamilton 1934). We classified southern sea lions in the following main classes: pups (P), females (F), yearlings (Y), two-year-olds (YY), juvenile males (J), sub-adult males (S) and adult males (A). We further distinguished juvenile and sub-adult males in three size-based subclasses, small (S), medium (M) and large (L). The main problems in sex/age classification were the discrimination of: 1) yearling vs. two-year-old individuals; 2) small juvenile males vs. breeding females; 3) large sub-adult males vs. adult males. Within each season we tried to identify breeding males by recording their fur colour and external appearance, and we took photos to improve identification. Please note that our sex/age classification was never validated by actual determination of sex/age, and that field observational assessment of age classes is potentially prone to significant errors (e.g., Garel et al. 2006). There is currently no validation study of the reliability of sex/age field determination in any pinniped species.

Demographic statistics

We used custom scripts developed in LiveCode (livecode.com) to extract from the raw counts demographic statistics, sex ratio measures and proportion of individuals in the different sex/age classes. We calculated three different measures of seasonal sex ratio: 1) plain sex ratio (SR = maximum number of pups / maximum number of males); 2) breeding sex ratio (BSR = maximum number of pups / maximum number of territorial males); 3) adult sex ratio (ASR = maximum number of pups / maximum number of adult males). We used the maximum number of pups instead of the number of females as numerator of all sex ratio measures because the maximum number of pups should be a good index of the total number of breeding females, better than the number of females actually counted, that can fluctuate a lot due to the pup attendance pattern of breeding females (Campagna and Le Boeuf 1988a). The number of pups can underestimate the number of breeding females due to the following reasons: 1) some adult females may not be pregnant or may have an abortion or may produce a stillbirth; 2) there is some pup mortality during the breeding season. Both factors probably produce a small negative bias, but there is no current information about female SSL fecundity in the Falklands and at large. Pup mortality of colonial breeding SSL is very low ($\sim 0.7\%$, Campagna et al. 1992), although there is variation between populations and years, and pup mortality can be greatly affected by climatic variation (e.g., El Niño, Soto et al. 2004). At Sea Lion, we always observed a small pup mortality during the breeding season (less than 5%), although we may have missed some dead pups. The territorial males in attendance during the main part of the breeding season were adults or sub-adults of the large class, as observed in other populations (Campagna and Le Boeuf 1988a,b).

To estimate the seasonal sex/age composition of the population during the breeding season we extracted the counts per sex/age class during the census closer to the 15th of January, that is the middle of the breeding season (Hamilton 1934), when the highest count of breeders is usually obtained. To calculate the sex/age class proportions we excluded the pups.

We fit to the distribution of groups various theoretical distributions that proved to be useful to model group size: the exponential distribution (Okubo 1986), the geometric distribution (Okubo 1986), the logarithmic series distribution (Griesser et al. 2011), the lognormal distribution (Niwa 2003), the Pareto distribution (Franks et al. 2010) and the logarithmic distribution (Griesser et al. 2011, Ma et al. 2011). We also fit the Poisson and negative binomial distribution that are frequently used to model ecological counts and had been used in the past to model group size (Caraco 1980). We described the asymmetry of the group size distribution using the sample skewness, and the weight of the right tail using the sample kurtosis (Westfall 2014). To describe the grouping patterns during the breeding season we calculated: 1) the mean and maximum number of individuals in groups; 2) its relative variability (coefficient of variation); 3) the "typical group size", i.e., the group in which the average individual finds itself (Reiczigel et al. 2008). We calculated those statistics including and excluding pups. To describe the number of females/pups associated to territorial males we calculated: 1) the mean and maximum number of females/pups; 2) its relative variability (CV); 3) the Gini index of inequality that is a general index of skewness in the distribution of resources (Galimberti et al. 2002).

Modelling of pup counts

To simplify modelling of pup numbers and to obtain parameters comparable among breeding seasons, we converted dates to days, calculating the number of days from 27th of November that was our first census of all breeding seasons (= day 1). Due to a long gap in 2019 counts we modelled pups only for seasons 2013 to 2018. To model pups accumulation during the breeding season we fitted sigmoid models to pup counts following the approach of Trites (1992). Although Trites (1992) presented both the logistic and the Gompertz functions, he actually used Gompertz only in the Results because of the slightly smaller standard error of parameters estimates for the Gompertz. Following Authors choose by default the Gompertz function without trying any other function (Pitcher et al. 2001; García-Aguilar and Aurioles-Gamboa 2003; Pavés et al. 2016).

Season	Model	Ν	Log-likehood	AICc	BIC
2013/14	Gompertz	17	-35.54	78.93	79.58
	Logistic		-34.22	76.27	76.94
	Von Bertalanffy		-44.54	96.92	97.58
2014/15	Gompertz	9	-27.59	65.98	61.77
	Logistic		-28.52	67.83	63.63
	Von Bertalanffy		-28.18	67.16	62.95
2015/16	Gompertz	23	-74.00	155.27	157.41
	Logistic		-76.18	159.63	161.77
	Von Bertalanffy		-77.44	162.15	164.29
2016/17	Gompertz	24	-67.40	142.00	144.33
	Logistic		-74.56	156.31	158.65
	Von Bertalanffy		-76.56	160.31	162.65
2017/18	Gompertz	12	-38.29	85.58	84.03
	Logistic		-39.28	87.56	86.01
	Von Bertalanffy		-40.36	89.72	88.17
2018/19	Gompertz	21	-46.69	100.78	102.50
	Logistic		-44.74	96.89	98.61
	Von Bertalanffy				

Table 1 - Information criteria of fitted growth models. For all models: y = number of pups, x = day of the breeding season, number of parameters = 3. N: number of counts, AIC_c = Akaike Information Criterion corrected for small samples, BIC = Bayesian Information Criterion, see *Model selection and statistical analysis* below. Von Bertalanffy fit for 2018/19 is empty because convergence was not achieved.

There is nothing special in the usage of the Gompertz function to model pup counts, it is just a convenient function that seems to fit sigmoidal data well (Trites 1992). Therefore, the default usage of the Gompertz function without comparison to other possible sigmoidal models is not justified. In our study we compared the fit of three different models (see below for model selection procedure): the logistic function (LO), the Gompertz function (GO), and the von Bertalanffy function (VB). These models have inflection points at decreasing percentages of the asymptote (LO = 50%, GO = 36.79%, VB = 29.63%) and, therefore, can model processes with different asymmetry between the first and second phase of the growth. A preliminary analysis of the pup counts collected during each season showed that in no case the VB function provided a better fit than the LO or GO functions. Moreover, for 2018/19 we were not able to fit the VB function, so we excluded it in following analyses (Table 1).

The parametrization of both the LO and GO functions proposed by Trites (1992) is not very convenient, because it does not permit to directly estimate the time of the inflection point. An additional problem of the Trites (1992) parametrization in our specific case was the high correlation between the growth coefficient (k) and the constant of integration (c). High correlation between parameters means that coefficients are redundant, and produce instability in the estimation of both the parameters and their standard errors. We used a different parametrization of the ones employed by Trites (1992), that are more useful, because they permit to directly estimate the time of the inflection point of the curves (Tjørve and Tjørve 2017). For the logistic curve we used the following parametrization:

$$P_{t} = \frac{A}{1 + e^{-k_{G}(t - T_{i})}}$$
(1)

where P_t = number of pups at time t, A = upper asymptote, k_G = the growth rate constant, and T_i = time at inflection. For the Gompertz curve we used the following parametrization:

$$P_t = A e^{-e^{-k_G(t-T_i)}} \tag{2}$$

The parametrizations of Trites (1992) and the ones that we used are equivalent, and the parameters of the two parametrizations can be converted using simple equations. Fitting was carried out using the Gauss-Newton algorithm.

An important goal of pup growth modelling is the estimation of the mean/median birth date, and this was also the final goal of Trites (1992). His approach was to estimate the median date (*B*) from the growth rate constant (*k*) and the constant of integration (*c*), and he provided a delta method approximation to estimate the variance of **B**. The variance formula, required to estimate standard error and confidence interval of the birth date, was particularly cumbersome and, in fact, has not been used by following Authors. A much easier approach is to model the mean/median birth date directly. In the case of our parametrization of the logistic function, $B = T_i$, i.e., the mean=median birth date is just the inflection point. In the case of the Gompertz function, the equation can be re-written to directly estimate *B*:

$$P_{t} = Ae^{-e^{-k_{G}(t - \left(B + \frac{\ln(\ln(2))}{k_{G}}\right))}}$$
(3)

where B is the median birth date, and the other parameters are the same of the equations above. The advantage of this approach is that the nonlinear regression fitting procedure produces B standard error and confidence limits directly, and permit to estimate the correlation between B and the other parameters. The maximum growth rate (i.e., the tangent to the Gompertz curve at the inflection point; Zullinger et al. 1984) is related to the growth rate constant and the number of pups at inflection (A/e) by the following equation:

$$K_G = k_G \frac{A}{e} \tag{3}$$

We obtained K_G , its standard error and confidence interval by calculating the first derivative of the number of pups over the first derivative of the day (= marginal effect of day on the number of pups) with respect to the day at the day of inflection. We also calculated the growth rate at the mean/median birth day (k_B), and we graphed the marginal effects at weekly intervals for 14 weeks of the breeding season.

Model selection and statistical analysis

Model selection was carried out using information criteria AIC (Akaike information criterion) and BIC (Bayesian information criterion; Wagenmakers and Farrell 2004). All our yearly models had three parameters and ≤ 24 observations so we used the small samples flavour of AIC, AIC_c. In case of disagreement, we preferred BIC over AIC_c because, in principle, it tends to select more parsimonious models. From AIC_c, we calculated Akaike weights, evidence ratios and normalized probability of all models versus the model with smaller AIC_c. From BIC, we calculated Schwarz weights, evidence ratios and normalized probability of all models versus the model with smaller BIC. An Akaike or Schwarz weight is the probability that the model M_i is the best model given the other models $(M_1 ... M_n)$ and the data. An evidence ratio is the number of times the best model is better than the model M_i. A normalized probability is the same of the evidence ratio but expressed as a probability (i.e., ranging from 0 to 1). To highlight patterns in scatterplots we often superimposed either a local linear smoother or a local polynomial smoother. To describe distribution we used violin plots that are a combination of the boxplot and a kernel density estimator (Hintze and Nelson 1998). Data exploration, nonlinear modelling and Bayesian estimation of change point in pup production were carried out using Stata 14 (www.stata.com). Estimated growth rates and their confidence intervals were calculated from fitted non linear models using the Stata margins command. Fitting of major axis and standard major axis regression was carried out using the *smatr* library of the R language (Warton et al. 2012).

Results

Sex and age classes in the breeding colony

The distribution of sex and age classes at mid breeding season during the seven seasons of the study is presented in Table 2. At this point of the season, we counted an average of 98.7 sea

Season	Date	Total	Adults	Female	Subadults	Juveniles	Yearlings	2-year
2013/14	14/01/2014	85	21.18	75.29	3.53	0.00	0.00	0.00
2014/15	09/01/2015	80	18.75	72.50	3.75	1.25	3.75	0.00
2015/16	16/01/2016	112	12.50	75.00	9.82	0.89	1.79	0.00
2016/17	14/01/2017	119	11.76	68.91	15.13	1.68	2.52	0.00
2017/18	14/01/2018	81	27.16	61.73	6.17	3.70	0.00	1.23
2018/19	15/01/2019	101	27.72	63.37	4.95	0.00	0.99	2.97
2019/20	19/01/2020	113	19.47	69.91	2.65	0.88	0.88	6.19
Mean		98.71	19.79	69.53	6.57	1.20	1.42	1.48
SD		16.58	6.30	5.34	4.46	1.26	1.37	2.35
CV		0.17	0.32	0.08	0.68	1.05	0.97	1.59
Min		80	11.76	61.73	2.65	0.00	0.00	0.00
Max		119	27.72	75.29	15.13	3.70	3.75	6.19

lions (80-119, excluding pups). The colony was occupied almost only by adult males (19.79%) and females (69.53%). All other classes were only 10.68% of the individuals.

Table 2 - Statistics of SSL colony composition at mid breeding season. Adults: adult males, Subadults: subadult males, Juveniles: juvenile males, Yearlings: one-year-old individuals of both sexes, 2-year: two-year-old individuals of both sexes. SD: standard deviation; CV: coefficient of variation.

The distribution of sex and age classes at the end of the breeding season is presented in Table 3. At this stage, adult males were a small percentage of the total (2.70%) and, while females remained almost the same (68.27%), the other classes were the 29.03% of the individuals. Although the percentage of the different sex/age classes changed between the seven breeding seasons of the study, both at mid season and at the end, there was no clear trend in this variation. The percentage of adult males dropped from 2013/14 to 2016/17, then had a large increase in 2017/18 (11.76% to 27.16%; Figure 3).

Season	Date	Total	Adults	Female	Subadults	Juveniles	Yearlings	2-year
2013/14	03/02/2014	87	9.2	81.61	9.2	0	0	0
2014/15	10/02/2015	114	0.88	57.89	6.14	8.77	8.77	17.54
2015/16	08/02/2016	111	1.8	70.27	14.41	7.21	0.9	5.41
2016/17	10/02/2017	112	0	66.96	16.07	1.79	8.04	7.14
2017/18	06/02/2018	93	2.15	63.44	12.9	1.08	6.45	13.98
2018/19	02/02/2019	107	3.74	55.14	7.48	5.61	7.48	20.56
2019/20	17/02/2020	86	1.16	82.56	10.47	2.33	1.16	2.33
Mean		101.43	2.70	68.27	10.95	3.83	4.69	9.57
SD		12.31	3.09	10.73	3.66	3.36	3.82	7.86
CV		0.12	1.14	0.16	0.33	0.88	0.82	0.82
Min		86	0	55.14	6.14	0	0	0
Max		114	9.2	82.56	16.07	8.77	8.77	20.56

Table 3 - Statistics of SSL colony composition at the end of the breeding season. Adults: adult males, Subadults: subadult males, Juveniles: juvenile males, Yearlings: one-year-old individuals of both sexes, 2-year: two-year-old individuals of both sexes. SD: standard deviation; CV: coefficient of variation.



Figure 3 - Percentage of adult and subadult males on the total number of SSL in the colony at mid breeding season. Red: adult males, blue: subadult males.



Figure 4 - Seasonal variation of the proportion of some SSL classes (on the total number of SSL in the colony, excluding pups). The red line is a local linear smoother.

The seasonal variation of the proportion of territorial males and adult males (on the total number of SSL, excluding the pups) showed a clear decrease trend (Figure 4) while the proportion of subadult males showed no clear trend. At the beginning of the season the territorial males, mostly adults, are the main class in the breeding colony, while toward the end of the breeding season they almost completely disappeared. The proportion of females showed a sigmoid variation, but with a lot of dispersion. The seasonal variation of territorial males = $b_1*b_2^{day}$, $R^2 = 0.93$, $b_1 = 1.04$, 95% confidence interval of $b_1 = 0.95-1.12$; $b_2 = 0.973$, 95% confidence interval of $b_1 = 0.971-0.976$). The same was true for adult males, although was marginally worse ($R^2 = 0.90$, $b_1 = 0.81$, 95% confidence interval of $b_1 = 0.73-0.90$; $b_2 = 0.971$, 95% confidence interval of $b_1 = 0.968-0.975$).

Sex ratio variation

The maximum number of total males, territorial males and adult males increased during the study period (Figure 5), although the small sample produced very large confidence intervals for the linear increase.



Figure 5 - Yearly variation of the number of males and sex ratio. Red lines are the linear fit for males and the parabolic fit for sex ratio, gray areas are 95% confidence bands.



Figure 6 - Variation of sex ratio during each breeding season. Sex ratio: number of pups / number of males. Blue line: linear regression line, gray area: 95% confidence bands of the regression.

The maximum number of total males, territorial males and adult males increased during the study period (Figure 5), although the small sample produced very large confidence intervals for the linear increase. Total males increased at a rate of 2.07 males per season (95% CI = 0.85,3.30) and territorial males at 1.64 males per season (95% CI = 0.85,3.30), while the increase of adult males was smaller (1.00) and its confidence interval included 0 (-0.15,2.15). The variation of sex ratio, operational sex ratio and adult sex ratio was concave, although the fitting of a parabolic function has very large confidence bands (Figure 5).

The seasonal variation of sex ratio was almost linear and increasing on the whole dataset and during most seasons, with a R^2 of the linear regression equal to 0.68 for the whole dataset, an yearly mean of 0.78 and a range of 0.57 to 0.87 (Figure 6), although the number of points for each year was small or very small. The same was true for the operational sex ratio (overall $R^2 = 0.59$, mean = 0.71, range = 0.65-0.79), while the adult sex ratio showed no clear seasonal trend (overall $R^2 = 0.25$).

Group size

The distribution of group size showed a strong skewness (2.52-4.17) and a very long right tail (kurtosis = 9.53-24.74; Table 4, Figure 7).



Figure 7 - Distribution of group size during each breeding season. Bars: histogram, curve: kernel density estimator.

All theoretical distribution functions usually used to model group size (see Methods) showed a rather poor fit. In all cases, there was a large difference from the expected in the frequency of the first classes (excess of groups with ≤ 5 individuals) and in the intermediate classes (deficit of groups with 5 > individuals ≤ 20 ; Figure 8). The Poisson distribution and negative binomial distribution, which are often used to model counts, showed a very poor fit to the observed frequencies. The best fitting distribution was a power-law distribution, the Pareto. A very small number of groups had ≥ 20 individuals (overall maximum = 96; seasonal maximum = 41-96). The above patterns were observed in both the whole dataset and in each breeding season.

Season	Ν	Мах	Skewness	Kurtosis
2013/14	279	68	3.00	11.94
2014/15	136	41	2.59	9.53
2015/16	491	79	3.29	15.84
2016/17	404	96	3.37	18.18
2017/18	245	88	4.17	24.74
2018/19	604	69	3.35	17.45
2019/20	132	51	2.52	10.14
All	2291	96	3.45	18.09
Mean			3.19	15.40

 Table 4 - Distribution of group size.
 N: number of groups, Max: maximum group size, Skewness: sample skewness, Kurtosis: sample kurtosis, used as measure of weight of right tail.



Figure 8 - Fit of a sample of theoretical distributions to group size. Red line: theoretical distribution, light blue bars: observed distribution, with bars hanging from the theoretical distribution line (hanging rootogram, Wainer 1974), blue lines with caps: 95% confidence interval of the observed

frequency. The deviation from the zero horizontal line of each bar is the difference between observed and expected frequency.

Summary statistics of group size are shown in Table 5. The mean group size at mid breeding season ranged from 4.62 to 7.31 including pups and from 2.79 to 4.35 excluding pups. The typical group size ranged from 13.02 to 26.80 including pups and from 6.29 to 14.91 excluding pups. The great difference between typical and mean group size showed that the average individual finds itself in a group much larger than the mean. The mean group size showed a decrease from 2015/16 (14.91) to 2018/19 (6.29; Figure 9).

Season	Ν	TGS		Mean	CV	Max	Mean _{NP}	CV_{NP}	Max _{NP}
2013/14	22	20.89	11.07	5.95	1.62	37	3.86	1.40	20
2014/15	20	21.40	13.40	5.50	1.74	41	4.00	1.57	27
2015/16	28	26.80	14.91	6.29	1.84	52	4.00	1.68	30
2016/17	33	19.63	10.85	5.76	1.58	30	3.61	1.44	19
2017/18	29	14.82	6.70	4.62	1.51	37	2.79	1.20	18
2018/19	33	13.02	6.29	5.15	1.26	27	3.06	1.04	13
2019/20	26	17.36	10.73	7.31	1.20	33	4.35	1.24	24

Table 5 - Group size at mid breeding season. N: number of groups, TGS: typical group size, Mean: mean group size, CV: coefficient of variation of group size, Max: maximum group size. NP subscript: no pups, i.e., pups excluded from the group size.



Figure 9 - Variation of the typical group size. TGS calculated including pups.

Number of females and pups in territories

Statistics of females and pups associated to territorial males at mid breeding season are shown in Table 6. The mean number of females and pups associated with territorial males at mid breeding season was rather low (2.99 and 2.47), but the maximum was high (19.57 and 16.57) and the relative variability was also high (1.72 and 1.79), showing that females and pups tended to be clumped in the territories of a few males. The Gini index of inequality was rather large (mean = 0.73 for females and mean = 0.74 for pups), and showed a decrease along the seasons for both females ($R^2 = 0.54$, b = -0.011) and pups ($R^2 = 0.84$, b = -0.023; Figure 10).

	Female	es			Pups			
Season	Mean	CV	Max	Gini	Mean	CV	Max	Gini
2013/14	3.32	1.72	19	0.76	2.37	2.09	17	0.82
2014/15	3.35	1.81	23	0.74	1.76	2.02	14	0.78
2015/16	3.90	1.86	28	0.78	3.05	1.79	22	0.76
2016/17	3.12	1.77	18	0.76	2.73	1.68	14	0.75
2017/18	1.92	1.83	17	0.69	2.04	1.91	19	0.71
2018/19	2.00	1.53	12	0.71	2.16	1.78	18	0.74
2019/20	3.29	1.53	20	0.70	3.21	1.28	12	0.65

 Table 6 - Number of females and pups per territorial male at mid breeding season.
 CV:

 coefficient of variation, Gini: Gini index of inequality.
 Coefficient of variation, Gini: Gini index of inequality.



Figure 10 - Variation of the Gini index of inequality. Index calculated from the number of pups per territorial male.

Models of the number of pups

The accumulation of pups during the breeding season showed a sigmoid shape. The best fitting model changed from one year to the other (Table 7). Although in most cases the difference in AICc and BIC were rather small, the logistic function provided a better fit for 2013/14 and 2018/19, while the Gompertz function provided a better fit for the 2014/15-2017/18 period (see Appendix I for yearly graphics). The only season in which the Gompertz function fitted data much better than the logistic was 2016/17.

Season	Mod.	Ν	AICc	BIC	dAIC _c	dBIC	wAICc	wBIC	eAIC _c	eBIC
2013/14	GO	17	78.93	79.58	2.64	2.64	0.21	0.21	3.75	3.75
	LO	17	76.29	76.94	0.00	0.00	0.79	0.79		
2014/15	GO	9	65.98	61.77	0.00	0.00	0.51	0.51		
	LO	9	67.83	63.63	1.86	1.86	0.20	0.20	2.53	2.53
2015/16	GO	23	155.27	157.41	0.00	0.00	0.87	0.87		
	LO	23	159.63	161.77	4.36	4.36	0.10	0.10	8.85	8.85
2016/17	GO	24	141.99	144.33	0.00	0.00	1.00	1.00		
	LO	24	156.31	158.65	14.32	14.32	0.00	0.00	1287.5	1287.5
2017/18	GO	12	85.58	84.03	0.00	0.00	0.67	0.67		
	LO	12	87.56	86.01	1.98	1.98	0.25	0.25	2.69	2.69
2018/19	GO	21	100.78	102.50	3.89	3.89	0.12	0.12	7.01	7.01
	LO	21	96.89	98.61	0.00	0.00	0.88	0.88		

Table 7 - Information criteria of fitted growth models. For all models: y = number of pups, x = day of the breeding season, number of parameters = 3. GO: Gompertz function, LO: logistic function. N: number of counts, AIC_c = Akaike Information Criterion corrected for small samples, BIC = Bayesian Information Criterion, d: difference in AIC_c or BIC, w: Akaike weights (AICc) or Schwarz weights (BIC), e: evidence ratios, p: normalized probabilities, see *Methods: Model selection and statistical analysis* for description.

Estimates of asymptote and growth coefficient for the best fitting model of the number of pups counted are presented in Table 8. The standard error and confidence intervals of the were large (Figure 11) and large was the overlap of the intervals in consecutive seasons, and the growth coefficient was quite variable among seasons.

Season	Model	RMSE	Res. dev.	Α	LCL(A)	UCL(A)	k _G	LCL(k _G)	UCL(k _G)
2013/14	LO	2.00	68.44	49.49	47.64	51.33	0.24	0.19	0.28
2014/15	GO	6.35	55.18	75.92	56.53	95.31	0.07	0.02	0.12
2015/16	GO	6.48	148.01	86.02	78.24	93.80	0.09	0.06	0.12
2016/17	GO	4.29	134.79	99.35	95.18	103.52	0.09	0.07	0.10
2017/18	GO	6.79	76.58	88.42	75.11	101.74	0.08	0.04	0.13
2018/19	LO	2.20	89.48	74.11	70.62	77.61	0.25	0.22	0.28

Table 8 - Parameters of the best models fitted to the number of pups. For all models: y = number of pups, x = day of the breeding season, number of parameters = 3. GO: Gompertz function, LO: logistic function. RMSE: root-mean-square-error, Res. dev. = deviance of the residuals, A: asymptote of the growth curve, LCL(A) and UCL(A): lower and upper 95% confidence limit of A, k_G : growth constant, LCL(k_G) and UCL(k_G): lower and upper 95% confidence limit of k_G .



Figure 11 - Estimates of the net productivity (= asymptote of the growth curve) of the best fitting model. Gray bar: estimated asymptote A, red lines: 95% confidence interval of A.

The estimated date at inflection ranged from 01/01 to 06/01, while the mean/median birth date ranged from 04/01 to 08/01 (Table 9). For the logistic model fitted in 2013/14 and 2018/19 we estimated the mean birth date = the median birth date, while for the Gompertz model fitted in 2014/15 to 2017/18 what was in fact estimated was the median birth date. Moreover, in the logistic model the mean birth date is equal to the inflection time, while that is not true for the Gompertz model.

Season	Model	Ti	LCL(T _i)	UCL(T _i)	Ti date	Bi	LCL(B _i)	UCL(B _i)	B _i date
2013/14	LO	38.73	37.80	39.67	04/01	38.73	37.80	39.67	04/01
2014/15	GO	38.03	31.46	44.60	03/01	43.37	33.66	53.09	08/01
2015/16	GO	37.18	34.50	39.86	02/01	41.41	38.39	44.42	06/01
2016/17	GO	35.59	34.15	37.02	01/01	39.75	37.91	41.58	05/01
2017/18	GO	38.54	34.04	43.05	04/01	42.96	37.25	48.67	08/01
2018/19	LO	41.06	40.44	41.67	06/01	41.06	40.44	41.67	06/01

Table 9 - Time at inflection and mean/median birth date for the best fitting model (logistic or Gompertz). GO: Gompertz function, LO: logistic function. T_i : time at inflection (day from first day of the breeding season), LCL(T_i) and UCL(T_i): lower and upper 95% confidence limit of T_i , T_i date: date corresponding to the day of inflection, B_i : mean (LO) or median (GO) birth day, LCL(B_i) and UCL(B_i): lower and upper 95% confidence limit of B_i , B_i date: date corresponding to the mean/median birth day.

The maximum growth rate ranged from 1.92 to 4.60 pups/day (mean = 3.01), while the growth rate of the day of mean/median birth ranged from 1.81 to 4.60 pups/day (mean = 2.91; Table 10). The maximum difference between the two growth rates was 0.19 pups/day. Please

Season	Model	K _G	LCL(K _G)	UCL(K _G)	K _B	LCL(K _B)	UCL(K _B)	K _G -K _B
2013/14	LO	2.91	2.45	3.37	2.91	2.45	3.37	0.00
2014/15	GO	1.92	1.01	2.82	1.81	1.14	2.47	0.11
2015/16	GO	2.74	2.03	3.46	2.59	1.95	3.22	0.16
2016/17	GO	3.22	2.74	3.70	3.03	2.65	3.42	0.19
2017/18	GO	2.70	1.65	3.75	2.54	1.69	3.40	0.16
2018/19	LO	4.60	4.17	5.02	4.60	4.17	5.02	0.00

note that for the logistic models $K_G = K_B$ because the time at inflection and the mean birth date are the same.

Table 10 - Maximum growth rate and growth rate at mean/median birth date for the best fitting model (logistic or Gompertz). GO: Gompertz function, LO: logistic function. K_G: maximum growth rate (pups/day), LCL(K_G) and UCL(K_G): lower and upper 95% confidence limit of K_G, K_B: growth rate of mean (LO) or median (GO) birth day, LCL(K_B) and UCL(K_B): lower and upper 95% confidence limit of B_i, K_G-K_B: difference between the maximum growth rate and the growth rate on the mean/median birth day.

The growth rate at weekly intervals for the best fitting models is shown in Figure 12. Weekly growth rate for each year are presented in Appendix II (Gompertz models) and III (logistic models).



Week of the breeding season

Figure 12 - Weekly growth rates of pup number estimated for six consecutive SSL breeding seasons. The points represent the estimate growth at mid week.

Due to the splitting of the seasons in two blocks (2013 and 2018 better fit by the logistic function, and 2014-2017 better fit by the Gompertz function), we produced two unified models to show the difference between the two blocks. We fit a logistic model to the pup

percentage of 2013 and 2018, and a Gompertz model to 2014-2017. The resulting models are shown in Figure 13, and the model parameters are tabulated in Table 11.



Figure 13 - Models of the proportion of pups already born of the maximum number of pups counted for the two blocks of years. Red dots and line: 2013 and 2018 counts and logistic model. Blue dots and line: 2014-2017 counts and Gompertz model.

	18)	Gompertz	(2014-201	7)				
Parameter	Coef.	SE	LCL	UCL	Coef.	SE	LCL	UCL
А	98.8830	1.6735	95.4857	102.2803	96.8282	2.1736	92.4871	101.1692
k _G	0.2478	0.0161	0.2152	0.2805	0.0791	0.0063	0.0666	0.0917
T _i	40.1794	0.2875	39.5957	40.7631	37.1096	0.6664	35.7787	38.4404

Table 11 - Parameters of the models of the proportion of pups already born of the maximum number of pups counted for the two blocks of years. The logistic model was fit on the percentages of 2013 and 2018, the Gompertz model on the percentages of 2014-2017. SE: standard error, LCL and UCL: lower and upper 95% confidence limits.

Trend in pup production

Pup production is the most interesting parameter of sea lion demography. Although the pre-2013 counts should be taken with caution, the number of pups produced definitely had an increase from a mean of 37.2 pups in 1990-2006 to a maximum of 107 in 2016 (148.8% increase from the previous maximum of 43 pups), followed by a decrease in the two following breeding seasons (-32.7%), and a recovery in the last one (19.4%; Figure 14). A Bayesian change point analysis confirmed the presence of a change point in 2013/2014 (cp = 2013.46, 95 % credible interval = 2013.00-2013.97). The mean pup production was estimated at 39.23 (95% CI = 35.12-43.54) in the first period, and 88.93 (95% CI = 81.44-96.72) in the second one. The estimated ratio of pup production between the two periods was 2.27 (95% CI = 1.97-2.63). In recent years, the pup production showed a decrease from the maximum of 2016/2017 followed by an increase during the last breeding season (Figure 14, blue dot).



Figure 14 - Variation of the maximum number of SSL pups counted at Sea Lion Island. Pre-2013 counts were carried out by the ESRG or were from various sources. The other counts are from the current ESRG study. Counts from 2016 are maximum seasonal counts (including UAV counts). Blue dot: the last breeding season.

Practical consideration to improve pup estimates

Although the two blocks of years, 2013+2018 and 2014-2017, were best fit by different growth models (Logistic and Gompertz) and showed quite different pup accumulation curves, a single unified model could be useful for practical reason, to produce correction factors for single counts carried out at a sub-optimal date and to provide guidance about the choice of counting dates. Therefore, we fit various models (the initial three models, plus the U4 model and the Richards model) to the whole dataset of pup percentages. We forced the model asymptote to be = 100%. The best fitting model was again the Gompertz model (Table 12), which parameters are reported in Table 13 (N = 113 counts). This model should be considered tentative due to the large residuals and their irregular distribution (Figure 15).

Model	R ²	RMSE	Res. dev.	Log-likehood	k	AIC	BIC
Gompertz	0.98	8.82	810.64	-405.32	2	814.64	820.09
Logistic	0.98	9.49	827.24	-413.62	2	831.24	836.70
Von Bertalanffy	0.97	12.25	884.99	-442.50	2	888.99	894.45
U4-model	0.98	9.49	827.24	-413.62	2	831.24	836.70
Richards	0.97	11.45	868.68	-434.34	3	874.68	882.86

Table 12 - Fit statistics of the models of the percentage of pups on the full dataset (2013-2018).R2: coefficient of determination, RMSE: root mean square error, Res. dev.: deviance of the residuals,AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion.

Parameter	Coef.	SE	LCL	UCL
k _G	0.1490	0.0094	0.1304	0.1677
T _i	41.1597	0.4531	40.2619	42.0574

Table 13 - Parameters of best fitting model of the proportion of pups already born of the maximum number of pups counted (Gompertz). A = 100. SE: standard error, LCL and UCL: lower and upper 95% confidence limits.



Figure 15 - Best fitting model of the proportion of pups already born of the maximum number of pups counted (Gompertz). Red dots: observed percentages, red line: Gompertz model, blue spikes: residuals. Please note the rather poor distribution of the residuals that definitely not random around the 0 line.

Discussion

From a substantial point of view, our main result was the demonstration that SSL pup production of the Sea Lion Island colony had a clear change point in 2013/2014, with the

mean pup production increasing more than two times. The causes of this striking change are unknown. SSL population dynamics seem to be influenced by sea surface temperatures trough their effect on food availability (Baylis et al. 2015a). Unfortunately, no information about movements at sea, feeding areas and diets is available for the SLI colony. Almost all the tracking data available for the Falkland Islands SSL belong to individuals from breeding colonies quite far from SLI, which are probably not much representative of what may happen to SLI individuals, because SSL tend to forage rather close to their breeding colony (Thompson et al. 1998, Baylis et al. 2015b). The only other pinniped breeding at SLI, the southern elephant seals, had a significant turning point in 2003, when the previously steady population started an increase trend that is currently still ongoing (Galimberti and Sanvito 2020a). On the other hand, the foraging strategies of southern elephant seals are so different from SSL that no coupling of the two population is really not expected. The most notable environmental phenomenon that happened during the study period is the strong El Niño that happened in 2015/16 that was apparently one of the stronger ever recorded (Peak et al. 2017). The impact of this event on pinniped populations was clearly shown in the northern hemisphere (Elorriaga-Verplancken et al. 2016), but its effect on the South Atlantic and the Falklands is still uncertain.

During each season, the variation in the composition of the breeding individuals followed a quite predictable pattern, similar to what observed in other breeding colonies (Campagna 1985). At the beginning of the season the colony was occupied mostly by territorial males and breeding males. The number of territorial males, and adult males in particular, showed a fast decrease, and at the end of the breeding season very few adult and territorial males were still in the colony, and most males were small or medium sized sub-adults. The decrease of territorial males and the increase of sub-adults represent a risk for females and for pups in particular, because of the risk of harassment. Harassment of pups by sub-adult males can be an important cause of pup mortality in SSL (Campagna et al. 1988). Notwithstanding there were cases of male harassment, no clear event of sub-adult induced pup mortality was observed.

We found a notable variation in the number of males and in various measures of sex ratio between the seven breeding seasons of the study. Changes of social composition of the colonies have been observed in other populations subject to fluctuations in size (Milano et al. 2020). At SLI, there was a clear increase of the maximum number of total males, territorial males and adult males. On the contrary, the number of females and pups had a peak in 2015 that was followed by a decrease. Therefore, all measures of sex ratio (including operational and adult) showed a parabolic trend. At the same time, the increase in the number of territorial males produced a gradual reduction in the breeding inequality, as shown by the decrease of the Gini index. All together, over the rather short span of seven breeding seasons, the SLI colony of SSL showed a large variation in its demographic and social composition. Small populations may be subject to intense demographic stochasticity that can produce strong random fluctuations of sex ratio, age class structure and social organization (Lacy 2000). This leads on one side to population instability, which increases the risk of catastrophic outcomes due to environmental variation and human effects, and on the other side increases the problems of determining trends in population size and structure, in

particular when populations are irregularly monitored and the quality of data is scarce (Holmes 2001).

An interesting result of our analysis of the SSL group size was that none of the distributions that are usually applied to group size produced a good fit, due to the excess of individuals in the first class (1 to 5 individuals per group), the lack of individuals in the middle classes (5 to 20 individuals per group) and the presence of a very long right tail due to a few very large groups. There is currently much speculation about the processes that generate the distribution of group size that can be observed in nature (Griesser et al. 2011). The main goal of the ongoing research is to derive mechanistic models of group formation processes that generate simple distribution of group size like the exponential, lognormal or Pareto (Niwa 2003). Often the proposed model is validated simply by fitting the observed distribution of group size to the theoretical distribution that results from the assumed/modelled process. We have shown that, although several of the theoretical distribution, the fit is rather poor and, in particular, no distribution is able to model well the large number of groups with few SSL together with the occurrence of a few much larger groups.

A main result of our study is that the growth curves of the number of pups showed a different shape in different years. While during four of the study seasons (2014/15 to 2017/18) pup number growth was asymmetric, was better modelled using the Gompertz function, and median birth date was later than the inflection date, during two of the seasons (2013/14 and 2018/2019) pup number growth was symmetric and was better modelled by the logistic function, with mean birth date equals to the inflection date. The pup accumulation seemed to be faster in 2013 and 2018, indicating an anticipated breeding combined with a faster pupping rate. The reason of this change is unknown. As we mentioned above, in 2015/16 a very strong El Niño event was recorded. Therefore, the 2013 and 2018 pup number curves may represent the "normal" pattern in the SLI population, while the 2014 to 2017 pattern may be related to unusual oceanographic and/or climatic conditions. Obviously, this statement is fully speculative in absence of any information about foraging patterns of SLI SSL. Moreover, the El Niño Southern Oscillation is a complex phenomenon, that is often linked to ecological, social or health outcomes in a very casual ways (McGregor and Ebi, 2018). Although ENSO has been linked to population trends of wildlife breeding in the Falklands (Baylis et al. 2013), there is currently a rather limited understanding of the effect of ENSO on the South Atlantic.

The main practical goal of our study was to identify a model of pup accumulation in the breeding colony that would permit the estimate of the total number of pups produced even when a single or few counts are carried out at sub-optimal dates (Trites 1992). This can be particularly important when whole islands surveys are carried out, because each colony is usually counted during a single day and, due to the extension of the area on which the colonies are spread, the counting date of each colony can differ by as much as four weeks (Thompson et al. 2005, Baylis et al. 2015a). As described above, the six breeding seasons that we considered showed two different patterns, leading to two different best fitting models and, therefore, the identification of a unified model proved difficult. We decided to propose anyway a single Gompertz model of the pup percentages, to provide a practical solution to the problem of correcting counts, but this model should be considered tentative, because its residuals were large in a part of the curve, and their distribution was far from begin well behaved.

The southern sea lion colony at Sea Lion Island is a small colony, and it is not sure how much representative this colony is of the SSL breeding and haul out in the rest of the Falklands. On the other hand, there is not much regular monitoring of SSL in the Falklands and, therefore, the Sea Lion colony could provide some baseline information that can be useful not only to improve knowledge of SSL breeding biology, but also for more applied matters, e.g., by providing correction factors for irregular counts carried out elsewhere.

Acknowledgments

We would like to thank: Denise Blake, the Environmental Committee and the Environmental Department of the Falkland Islands Government for approving our research licence; the Falkland Islands Development Corporation for permitting us to carry out field work at Sea Lion Island; Wildlife Falklands Ltd. for providing accommodation for the research team at discounted rate and for logistic support; the past Sea Lion Lodge managers, Jenny Luxton and Carol Peck, and the current Sea Lion Lodge owners, Micky Reeves and Sarah Crofts, for their kind help, and their positive attitude towards our research; the Sea Lion Lodge staff for their great friendship.

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Appendix I - Number of pups vs. day of the breeding season

For each season the figure shows the best model (Logistic or Gompertz), the pup counts (red dots), the LOWESS smoother (blue line) and the model fitted values (red line). In all cases, time is expressed as day of the breeding season, i.e., number of days from 27th of November = day 1.







Appendix II - Weekly growth rate of pup number, Gompertz models

Day: centre day of the week (days from first day of the season), with corresponding date, K_d : growth rate (pups/day) of day d, $SE(K_d)$ = standard error of K_d ; $LCL(K_d)$ and $UCL(K_d)$: lower and upper 95% confidence limits of K_d .

2013						
Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0000	0.0000	0.0000	0.0000
2	10.5	09-Dec	0.0000	0.0000	0.0000	0.0000
3	17.5	16-Dec	0.0000	0.0000	0.0000	0.0000
4	24.5	23-Dec	0.0908	0.0842	-0.0742	0.2559
5	31.5	30-Dec	2.0887	0.1472	1.8001	2.3772
6	38.5	06-Jan	2.7794	0.2109	2.3661	3.1927
7	45.5	13-Jan	1.4483	0.1081	1.2364	1.6602
8	52.5	20-Jan	0.5544	0.1008	0.3569	0.7519
9	59.5	27-Jan	0.1917	0.0572	0.0797	0.3037
10	66.5	03-Feb	0.0641	0.0264	0.0123	0.1159
11	73.5	10-Feb	0.0212	0.0111	-0.0006	0.0430
12	80.5	17-Feb	0.0070	0.0044	-0.0017	0.0157
13	87.5	24-Feb	0.0023	0.0017	-0.0011	0.0057
14	94.5	03-Mar	0.0008	0.0006	-0.0005	0.0020

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0013	0.0078	-0.0140	0.0165
2	10.5	09-Dec	0.0462	0.1216	-0.1922	0.2846
3	17.5	16-Dec	0.3563	0.3230	-0.2767	0.9893
4	24.5	23-Dec	1.0494	0.2091	0.6395	1.4592
5	31.5	30-Dec	1.7044	0.3878	0.9443	2.4644
6	38.5	06-Jan	1.9155	0.4561	1.0216	2.8095
7	45.5	13-Jan	1.7144	0.2763	1.1729	2.2559
8	52.5	20-Jan	1.3327	0.1865	0.9672	1.6982
9	59.5	27-Jan	0.9495	0.2522	0.4553	1.4438
10	66.5	03-Feb	0.6410	0.2770	0.0981	1.1839
11	73.5	10-Feb	0.4186	0.2528	-0.0770	0.9141
12	80.5	17-Feb	0.2677	0.2073	-0.1385	0.6739
13	87.5	24-Feb	0.1691	0.1590	-0.1426	0.4808
14	94.5	03-Mar	0.1059	0.1169	-0.1232	0.3351

WeekDayDate K_d SE(K_d)LCL(K_d)UCL(K_d)13.502-Dec0.00000.00000.00000.0000210.509-Dec0.00310.0106-0.01770.0238317.516-Dec0.16610.2047-0.23500.5673424.523-Dec1.11170.34660.43251.7910531.530-Dec2.37640.22881.92792.8249638.506-Jan2.72730.36152.01883.4357745.513-Jan2.23020.23271.77412.6864852.520-Jan1.51620.15941.20381.8286959.527-Jan0.93210.16740.60401.26021066.503-Feb0.54240.15080.24690.8380
1 3.5 02-Dec 0.0000 0.0000 0.0000 2 10.5 09-Dec 0.0031 0.0106 -0.0177 0.0238 3 17.5 16-Dec 0.1661 0.2047 -0.2350 0.5673 4 24.5 23-Dec 1.1117 0.3466 0.4325 1.7910 5 31.5 30-Dec 2.3764 0.2288 1.9279 2.8249 6 38.5 06-Jan 2.7273 0.3615 2.0188 3.4357 7 45.5 13-Jan 2.2302 0.2327 1.7741 2.6864 8 52.5 20-Jan 1.5162 0.1594 1.2038 1.8286 9 59.5 27-Jan 0.9321 0.1674 0.6040 1.2602 10 66.5 03-Feb 0.5424 0.1508 0.2469 0.8380
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531.530-Dec2.37640.22881.92792.8249638.506-Jan2.72730.36152.01883.4357745.513-Jan2.23020.23271.77412.6864852.520-Jan1.51620.15941.20381.8286959.527-Jan0.93210.16740.60401.26021066.503-Feb0.54240.15080.24690.83804473.540 Feb0.20240.44000.27700.5240
638.506-Jan2.72730.36152.01883.4357745.513-Jan2.23020.23271.77412.6864852.520-Jan1.51620.15941.20381.8286959.527-Jan0.93210.16740.60401.26021066.503-Feb0.54240.15080.24690.83804473.540-Feb0.20240.44660.27700.5240
7 45.5 13-Jan 2.2302 0.2327 1.7741 2.6864 8 52.5 20-Jan 1.5162 0.1594 1.2038 1.8286 9 59.5 27-Jan 0.9321 0.1674 0.6040 1.2602 10 66.5 03-Feb 0.5424 0.1508 0.2469 0.8380
8 52.5 20-Jan 1.5162 0.1594 1.2038 1.8286 9 59.5 27-Jan 0.9321 0.1674 0.6040 1.2602 10 66.5 03-Feb 0.5424 0.1508 0.2469 0.8380 14 73.5 10 Feb 0.2024 0.14000 0.2770 0.5210
9 59.5 27-Jan 0.9321 0.1674 0.6040 1.2602 10 66.5 03-Feb 0.5424 0.1508 0.2469 0.8380 14 73.5 40 Feb 0.2004 0.4400 0.2770 0.5040
10 66.5 03-Feb 0.5424 0.1508 0.2469 0.8380
14 70 F 10 Fab 0.0004 0.4400 0.0770 0.5040
11 73.5 10-FED 0.3064 0.1166 0.0779 0.5349
12 80.5 17-Feb 0.1702 0.0822 0.0091 0.3313
13 87.5 24-Feb 0.0938 0.0548 -0.0136 0.2011
14 94.5 03-Mar 0.0514 0.0352 -0.0175 0.1203

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0000	0.0000	0.0000	0.0001
2	10.5	09-Dec	0.0088	0.0124	-0.0155	0.0331
3	17.5	16-Dec	0.3146	0.1417	0.0369	0.5924
4	24.5	23-Dec	1.6333	0.1563	1.3269	1.9397
5	31.5	30-Dec	2.9918	0.2188	2.5630	3.4206
6	38.5	06-Jan	3.1232	0.2146	2.7025	3.5438
7	45.5	13-Jan	2.4068	0.1097	2.1918	2.6218
8	52.5	20-Jan	1.5745	0.1068	1.3651	1.7838
9	59.5	27-Jan	0.9428	0.1142	0.7190	1.1666
10	66.5	03-Feb	0.5382	0.0964	0.3493	0.7272
11	73.5	10-Feb	0.2994	0.0709	0.1604	0.4385
12	80.5	17-Feb	0.1643	0.0482	0.0697	0.2589
13	87.5	24-Feb	0.0895	0.0313	0.0282	0.1507
14	94.5	03-Mar	0.0485	0.0196	0.0101	0.0870

2017						
Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0000	0.0000	0.0000	0.0000
2	10.5	09-Dec	0.0026	0.0130	-0.0228	0.0281
3	17.5	16-Dec	0.1354	0.2436	-0.3420	0.6128
4	24.5	23-Dec	0.9511	0.4538	0.0616	1.8407
5	31.5	30-Dec	2.1895	0.3478	1.5079	2.8711
6	38.5	06-Jan	2.7011	0.5346	1.6534	3.7489
7	45.5	13-Jan	2.3510	0.3463	1.6723	3.0298
8	52.5	20-Jan	1.6837	0.2339	1.2252	2.1422
9	59.5	27-Jan	1.0812	0.2739	0.5443	1.6181
10	66.5	03-Feb	0.6532	0.2634	0.1369	1.1695
11	73.5	10-Feb	0.3814	0.2128	-0.0356	0.7984
12	80.5	17-Feb	0.2185	0.1553	-0.0859	0.5229
13	87.5	24-Feb	0.1238	0.1067	-0.0852	0.3329
14	94.5	03-Mar	0.0698	0.0704	-0.0683	0.2078

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0000	0.0000	0.0000	0.0000
2	10.5	09-Dec	0.0000	0.0000	0.0000	0.0000
3	17.5	16-Dec	0.0000	0.0000	0.0000	0.0000
4	24.5	23-Dec	0.0140	0.0168	-0.0190	0.0470
5	31.5	30-Dec	1.6632	0.1850	1.3007	2.0257
6	38.5	06-Jan	4.4085	0.2488	3.9208	4.8962
7	45.5	13-Jan	3.1108	0.1353	2.8455	3.3761
8	52.5	20-Jan	1.3848	0.1823	1.0275	1.7421
9	59.5	27-Jan	0.5251	0.1206	0.2887	0.7616
10	66.5	03-Feb	0.1883	0.0610	0.0688	0.3078
11	73.5	10-Feb	0.0662	0.0275	0.0124	0.1201
12	80.5	17-Feb	0.0231	0.0117	0.0003	0.0460
13	87.5	24-Feb	0.0081	0.0048	-0.0013	0.0174
14	94.5	03-Mar	0.0028	0.0019	-0.0009	0.0066

Appendix III - Weekly growth rate of pup number, Logistics models

Day: centre day of the week (days from first day of the season), with corresponding date, K_d : growth rate (pups/day) of day d, $SE(K_d)$ = standard error of K_d ; $LCL(K_d)$ and $UCL(K_d)$: lower and upper 95% confidence limits of K_d .

2013						
Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0029	0.0019	-0.0007	0.0065
2	10.5	09-Dec	0.0151	0.0074	0.0006	0.0297
3	17.5	16-Dec	0.0776	0.0268	0.0251	0.1302
4	24.5	23-Dec	0.3815	0.0742	0.2360	0.5270
5	31.5	30-Dec	1.5191	0.0967	1.3296	1.7086
6	38.5	06-Jan	2.9099	0.2343	2.4506	3.3692
7	45.5	13-Jan	1.6354	0.1312	1.3782	1.8926
8	52.5	20-Jan	0.4221	0.0977	0.2306	0.6136
9	59.5	27-Jan	0.0864	0.0333	0.0211	0.1518
10	66.5	03-Feb	0.0168	0.0090	-0.0007	0.0344
11	73.5	10-Feb	0.0033	0.0022	-0.0011	0.0076
12	80.5	17-Feb	0.0006	0.0005	-0.0004	0.0016
13	87.5	24-Feb	0.0001	0.0001	-0.0001	0.0003
14	94.5	03-Mar	0.0001	0.0001	-0.0001	0.0004

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.1017	0.0853	-0.0655	0.2690
2	10.5	09-Dec	0.2122	0.1260	-0.0347	0.4590
3	17.5	16-Dec	0.4282	0.1524	0.1296	0.7268
4	24.5	23-Dec	0.8095	0.1470	0.5214	1.0976
5	31.5	30-Dec	1.3548	0.2962	0.7743	1.9354
6	38.5	06-Jan	1.8566	0.5347	0.8085	2.9047
7	45.5	13-Jan	1.9438	0.4507	1.0605	2.8271
8	52.5	20-Jan	1.5365	0.2639	1.0193	2.0538
9	59.5	27-Jan	0.9696	0.3848	0.2154	1.7238
10	66.5	03-Feb	0.5292	0.3674	-0.1908	1.2493
11	73.5	10-Feb	0.2665	0.2618	-0.2465	0.7796
12	80.5	17-Feb	0.1288	0.1613	-0.1873	0.4449
13	87.5	24-Feb	0.0611	0.0920	-0.1193	0.2414
14	94.5	03-Mar	0.0287	0.0503	-0.0699	0.1272

Week Day Date K _d SE(K _d) LCL(K 1 3.5 02-Dec 0.0872 0.0528 -0.0163	UCL(K_d) 0.1906
1 3.5 02-Dec 0.0872 0.0528 -0.016	0.1906
2 10.5 09-Dec 0.2038 0.0938 0.0199	0.3877
3 17.5 16-Dec 0.4617 0.1439 0.1797	0.7438
4 24.5 23-Dec 0.9749 0.1638 0.6539	1.2960
5 31.5 30-Dec 1.7785 0.1646 1.4559	2.1011
6 38.5 06-Jan 2.5040 0.3298 1.8575	3.1504
7 45.5 13-Jan 2.4698 0.3182 1.8461	3.0935
8 52.5 20-Jan 1.7144 0.2152 1.2925	2.1362
9 59.5 27-Jan 0.9265 0.2199 0.4955	1.3575
10 66.5 03-Feb 0.4357 0.1687 0.1050	0.7663
11 73.5 10-Feb 0.1917 0.1029 -0.010	0.3934
12 80.5 17-Feb 0.0819 0.0558 -0.027	0.1912
13 87.5 24-Feb 0.0345 0.0284 -0.021	0.0902
14 94.5 03-Mar 0.0145 0.0139 -0.012	0.0418

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0727	0.0312	0.0116	0.1338
2	10.5	09-Dec	0.1966	0.0618	0.0755	0.3177
3	17.5	16-Dec	0.5153	0.1033	0.3128	0.7178
4	24.5	23-Dec	1.2458	0.1306	0.9899	1.5017
5	31.5	30-Dec	2.4886	0.2361	2.0259	2.9512
6	38.5	06-Jan	3.4527	0.3788	2.7102	4.1952
7	45.5	13-Jan	2.9359	0.2122	2.5200	3.3518
8	52.5	20-Jan	1.6346	0.2363	1.1715	2.0976
9	59.5	27-Jan	0.7111	0.1979	0.3231	1.0990
10	66.5	03-Feb	0.2768	0.1129	0.0556	0.4980
11	73.5	10-Feb	0.1031	0.0546	-0.0038	0.2101
12	80.5	17-Feb	0.0378	0.0244	-0.0100	0.0856
13	87.5	24-Feb	0.0138	0.0105	-0.0068	0.0343
14	94.5	03-Mar	0.0050	0.0044	-0.0036	0.0136

2017						
Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0695	0.0622	-0.0525	0.1915
2	10.5	09-Dec	0.1647	0.1127	-0.0562	0.3856
3	17.5	16-Dec	0.3808	0.1793	0.0294	0.7321
4	24.5	23-Dec	0.8308	0.2236	0.3926	1.2689
5	31.5	30-Dec	1.6013	0.2552	1.1010	2.1015
6	38.5	06-Jan	2.4458	0.4943	1.4770	3.4147
7	45.5	13-Jan	2.6455	0.5063	1.6532	3.6377
8	52.5	20-Jan	1.9748	0.3251	1.3377	2.6119
9	59.5	27-Jan	1.1106	0.3764	0.3729	1.8483
10	66.5	03-Feb	0.5301	0.3051	-0.0679	1.1280
11	73.5	10-Feb	0.2335	0.1885	-0.1360	0.6031
12	80.5	17-Feb	0.0993	0.1021	-0.1007	0.2993
13	87.5	24-Feb	0.0416	0.0516	-0.0595	0.1427
14	94.5	03-Mar	0.0173	0.0251	-0.0318	0.0664

Week	Day	Date	K _d	SE(K _d)	LCL(K _d)	UCL(K _d)
1	3.5	02-Dec	0.0017	0.0008	0.0001	0.0032
2	10.5	09-Dec	0.0094	0.0035	0.0025	0.0163
3	17.5	16-Dec	0.0530	0.0143	0.0250	0.0810
4	24.5	23-Dec	0.2929	0.0476	0.1997	0.3862
5	31.5	30-Dec	1.4370	0.0810	1.2783	1.5957
6	38.5	06-Jan	4.1640	0.1953	3.7813	4.5467
7	45.5	13-Jan	3.4403	0.1506	3.1452	3.7354
8	52.5	20-Jan	0.9596	0.1520	0.6617	1.2575
9	59.5	27-Jan	0.1855	0.0510	0.0855	0.2855
10	66.5	03-Feb	0.0332	0.0127	0.0083	0.0581
11	73.5	10-Feb	0.0059	0.0029	0.0003	0.0115
12	80.5	17-Feb	0.0010	0.0006	-0.0002	0.0022
13	87.5	24-Feb	0.0002	0.0001	-0.0001	0.0004
14	94.5	03-Mar	0.0002	0.0001	0.0000	0.0004