

Population trends of female Elephant Seals breeding on the Courbet Peninsula, îles Kerguelen

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Abstract Southern Elephant Seals are upper marine predators of the Southern Ocean. As such, their population dynamics and fluctuations reflect environment conditions. Their worldwide populations crashed during the second half of the twentieth century for reasons not yet completely elucidated. Here, we studied the largest population of Southern Elephant Seals within the South Indian Ocean that are breeding on îles Kerguelen. In a previous analysis, Guinet et al. in *Antarct Sci* 11:193–197, 1999 suggested that the decline on îles Kerguelen might be over, as observed elsewhere. Using 10 years of additional data, we updated this analysis using state-of-the-art statistical methods to account for most uncertainties associated with count data. We showed that the population of female Southern Elephant Seals breeding on îles Kerguelen has been stable over the past 20 years. Despite concomitant global changes within the Southern Ocean, we did not find any evidence of a phenological shift in peak haul-out date of breeding females between the 1970s and the 2000s.

Keywords *Mirounga leonina* · Long-term monitoring · Population trend · Bayesian · Southern Ocean

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Introduction

Assessing the status and trends of populations is a necessary prerequisite for effective conservation (Caughley 1994). Indeed, such information is critical to enable a proactive approach to species conservation. Yet, assessing population trends requires sustained and coherent efforts over large time spans to gather sufficient data from which accurate inferences may be drawn. Despite being fundamental to ecologists and conservationists, count data can be tricky to obtain, analyse or both, depending on the focal species. In this regard, marine predators, whose population fluctuations are thought to reliably integrate and reflect environmental conditions (Jenouvrier et al. 2003), are notoriously difficult to monitor.

Seabirds and marine mammals spend most of their life cycle in the marine environment and may be only observable on land, if at all, for a restricted time period. Upon occasions such as breeding or moulting, these animals aggregate in dense, isolated colonies or rookeries where direct counts of individuals may be performed. If performed during the breeding season, such counts will miss the non-breeding fraction of a population, or they may be prone to a large observation error because of the large density of colonies. Such observation error, if ignored, will be confounded with environmental noise and may either eclipse true biological signals or give rise to spurious results (Hovestadt and Nowicki 2008). Further complications may arise when all rookeries cannot be sampled or when animals are not synchronous. In such a case, all animals are never present at any time point over the temporal window when censuses may be logistically feasible (Condit et al. 2007).

With such caveats of count data in mind, we aimed in the present study to re-assess the population status of

Southern Elephant Seals (*Mirounga leonina*) breeding on îles Kerguelen (49°30'S, 69°30'E), Southern Ocean. This species is one of the best-studied phocids, yet the exact causes behind its large decline during the second half of the twentieth century are still debated (McMahon et al. 2005). For example, the population on Marion Island (46°52'S, 37°51'E) went through a 87% decrease since the 1950s, but is now increasing (McMahon et al. 2009). Yet, the Marion population is currently two orders of magnitude smaller than the Kerguelen population (Guinet et al. 1999; McMahon et al. 2009), which represents the main bulk of the South Indian Ocean stock of Southern Elephant Seals (Slade et al. 1998). In the most recent analysis of population trends on Kerguelen, Guinet et al. (1999) asked whether the decline was over, but refrained from making strong statements given their relatively short time series of censuses. Here, we update their analysis with state-of-the-art statistical methods using 10 years of additional data and in the current context of global changes affecting the Southern Ocean (Trathan et al. 2007).

Sources of uncertainty in Elephant Seal counts

Adult Southern Elephant Seals spend most of their time at sea but come ashore for two short bouts each year: to breed during the spring haul-out (September–November) and to moult during the summer haul-out (January–February) (Laws 1993). During the spring haul-out, females aggregate in dense rookeries to give birth to a single pup, wean it in 3 weeks and mate before returning to sea. Female breeding probability quickly rises to unity with age (McMahon et al. 2003). Thus, censuses of breeding females during the spring haul-out are likely to encompass most of the female population. The timing of female return is spread over 2 months, but each female only stays ashore for three to 4 weeks (Van Aarde 1980). Because the population of breeding Southern Elephant Seals is asynchronous, no census can encompass all females that may have come ashore. The latter number must be estimated along with a measure of uncertainty.

Females aggregate in more or less large rookeries, and all rookeries are not formed at the same time during the breeding season; that is, there is some variability associated with breeding sites. All sites cannot be logistically sampled given the large size of îles Kerguelen (approx. 7,200 km² with 2,800 km of coastline). Thus, there is a spatial as well as a temporal variability in counts. A last source of variability stems for field workers who are actually doing the censuses. Our aims here were to use a suitable model to describe the timing of hauling-out and to quantify variability due to sampled sites, to observers and to environmental noise. Because we were particularly concerned

about the different sources of uncertainties intrinsic to our data, we favoured a Bayesian approach. The Bayesian framework emphasizes estimation over null hypothesis testing (Wade 2000; Ellison 2004) and easily allows the flow of uncertainties from one level of analysis to the next. The next two sections detail the different analyses we performed to evaluate the accuracy of our Southern Elephant Seal counts before assessing population trends on îles Kerguelen since the 1950s.

Theory and model building

Several models have been developed to describe the asynchronous behaviour of breeding females Southern Elephant Seals (Van Aarde 1980; Pascal 1981; Rothery and McCann 1987). Among these, that of Rothery and McCann (1987) describing the timing of Southern Elephant Seal haul-out with four parameters that have a straightforward biological interpretation, is particularly attractive. More specifically, the haul-out process is described as the product of a maximum number of breeding females coming ashore (N_{\max}) and a proportion dependent on the day the census was realized. The latter proportion (p), by definition bounded between 0 and 1, is a bell-shaped function of census day (t), centred on a date of maximum presence (μ), of female synchrony (σ) and of the mean time length (pre- and post-partum) females spend ashore (S). For a census performed on day t :

$$N_t = N_{\max} \times p(t, \mu, \sigma, S)$$

All four parameters cannot be estimated simultaneously from the same data (Rothery and McCann 1987; Galimberti and Sanvito 2001; Condit et al. 2007). We used a previous estimate of S in this study. Namely, we assumed the mean time length spent ashore by a female to be 28 days (Van Aarde 1980), with a standard deviation of $\sqrt{5}$ days. This was derived as the sum of a 5 ± 2 day-long pre-partum stay followed by a 23 ± 1 day-long pup-caring period.

Condit et al. (2007) recently highlighted some shortcomings of this model, specifically the assumption of symmetry in the haul-out process, or that females are returning to the sea at the same rate as they hauled-out. This assumption does not hold, a fact already noted by Galimberti and Sanvito (2001), because there is a small, but practically significant, negative correlation between female arrival and departure dates from the rookery (Condit et al. 2007). We nevertheless chose to focus on Rothery and McCann (1987)'s model to analyse our data because we could compare our results to published results using the same model applied to other populations of Southern Elephant Seals.

Materials and methods

Haul-out monitoring

To compute correction factors for census date, six and nine hauling sites were respectively monitored in 2008 and 2009 on a daily basis from the 21 September till 16 November at Cape Ratmanoff, îles Kerguelen. Some eighteen different field workers helped in counting females throughout the study period. We incorporated this variability in a hierarchical model and tested different distributional assumptions for the fraction of variance due to observers and the residual fraction. Specifically we compared a normal versus a Student distribution for the residual variance term. Field workers helping in the field had either some or no prior experience in counting pinnipeds. To assess the impact of such heterogeneity on counts, the variance due to observer was modelled either as following a normal (that is observers were comparably skilled), a Student (that is, a few observers may have been extremely good/bad) or a Skew-normal (that is, observers on average tended to over/underestimate females) distribution. Models thus differed by at most two parameters and were compared with the Bayesian deviance (the smaller the deviance, the better the model fit).

Each site was given a specific set of parameters ($N_{\max}^i, \mu^i, \sigma^i$, where the superscript i denotes the i th site) and the inter-site variability, along with correlations between the different parameters, were explicitly modelled in a hierarchical model. We assumed the $(N_{\max}^i, \mu^i, \sigma^i)$ to follow a multivariate normal distribution. Upon selecting a model, we further checked residuals and draw curves for each sampled site to visually assess any obvious model misfit.

In 2009, we further recorded on the field the total number of pups produced on the study sites. All pups present on the study sites at the end of the breeding season (including dead ones) were recorded. These estimates were then compared to the number of females as predicted by the selected model. Although this estimate of pup production has its own uncertainties, the latter are expected to be smaller than that of females because pups tends to remain on their natal rookery for some time upon weaning (Lenglard and Bester 1982). Weaned pups aggregate outside harem and can be easily approached.

Correction factors

The Bayesian framework easily allows predictions from the posterior distribution. We thus predicted a set of parameters for a “new” site and used this set to compute corrections factors for single-day censuses of females breeding between Cape Digby and Cape Molloy (circa

80 km, hereafter referred to as Courbet Peninsula). As the Bayesian framework allows the incorporation and trickling down of uncertainties across levels, 95% credible intervals were accordingly computed for each census.

Thirty-two censuses, starting from 1952 and spanning 60 years, were available (CEBC CNRS database). They were usually performed within a week around the 15th of October. However, among these censuses, three were incomplete (in 1952, 1970 and 1984). In 1952 and 1984, a large and important part of the Courbet Peninsula was not sampled. These years were thus excluded from further analysis. The 1970 census missed a small part of the Courbet Peninsula that around the permanent field station of Port-Aux-Français. This census is thus incomplete, but was nevertheless retained as the fraction of unrecorded females is proportionally small compared to the total number of females (approx. 5–7%). Moreover, this missing fraction is smaller than the standard error of the corrected estimate. We recently re-found the original field report of the 1970 census in the Kerguelen scientific library while doing fieldwork in 2009. This report revealed a mistake in census dates for 1970 reported in previous works (for example, Guinet et al. 1999) that used data from secondary sources (for example, Pascal 1981). Since correction factors can have a dramatic influence on counts depending on whether the census was performed close to peak haul-out date or not, these mistakes in census dates resulted in a gross over-correction of the 1970 census in previous publications.

Population trends

To assess the population trend in female Southern Elephant Seals breeding on the Courbet Peninsula, we used linear penalized-splines at fixed knot locations (Gurrin et al. 2005) on thirty corrected estimates of the Courbet Peninsula census. This semi-parametric regression does not require any a priori assumption on the trend. We again favoured a Bayesian framework to incorporate the uncertainty associated with corrected estimates.

However, as the posterior distribution of corrected estimates was sometimes heavily skewed, we subsampled 1,000 datasets from the posterior distributions of corrected estimates and analysed them with Bayesian penalized-splines. The 1,000 results were then used to approximate the true posterior distribution. While this procedure actually ignores the uncertainty in estimating the parameters, this source of uncertainty is negligible compared to that due to correction factors. Posterior median and median absolute deviation are reported instead of posterior mean and standard deviation to account for the skewness in these data.

Comparison with published estimates

As we are correcting censuses performed up to 60 years ago, we were interested in whether a phenological shift has taken place or not, as this would have an impact of correction factors. We performed a small literature survey to find estimates of female peak haul-out date (μ) and synchrony (σ). We identified five relevant publications (Rothery and McCann 1987; Hindell and Burton 1988; Boyd et al. 1996; Slip and Burton 1999; Galimberti and Sanvito 2001) that reported iteratively weighted least-square estimates of N_{\max} , μ and σ from five Subantarctic islands, including îles Kerguelen (Table 1), and covering the three currently recognized stocks of Southern Elephant Seals (Slade et al. 1998).

For most estimates, standard errors were not reported, and we therefore could not weight each estimate by its standard error in a small meta-analysis. Because estimates came from different islands, we explicitly took this factor in our analysis to avoid the potentially confounding effect of latitude (Galimberti and Boitani 1999). We were specifically interested in the correlation between μ and σ within each island where females haul-out, to compare it with our own estimate from data collected in 2008 and 2009.

Softwares

All models were fitted with *WinBUGS* (Spiegelhalter et al. 2003) called from *R* (R Development Core Team 2009) with the package *R2WinBUGS* (Sturtz et al. 2005). Weakly informative priors (Half-Cauchy and Cauchy priors for variance and other parameters, respectively) were used (Gelman 2006; Gelman et al. 2008; Fùquene et al. 2009). An Inverse-Wishart prior was used for the variance-covariance matrix for the site effect (see *Haul-Out Monitoring*) or for the island effect (see *Comparisons with Published Estimates*). For each model, three chains were initialized with overdispersed starting values. After appropriate burn-in and thinning of the chains (1 value every 100 or 200 iterations stored) to reduce autocorrelation, convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin 1996) with the *coda* package

Table 1 Populations of Southern Elephant Seals for which published estimates are available

Island	Latitude	Longitude	N	Year
Kerguelen	49°30'S	69°30'E	2	1970–1971
Falkland	52°26'S	59°05'W	5	1995–1999
Heard	53°05'S	73°30'E	7	1949–1992
South Georgia	54°15'S	37°05'W	15	1951–1995
Macquarie	54°30'S	158°57'E	3	1959–1985

These estimates may correspond to different sites on these islands (some sites were monitored many years)

(Plummer et al. 2008). Unless stated otherwise, posterior mean and standard error of the mean ($\theta \pm se$) are reported, along with 95% highest probability density (HPD) credible intervals ([*lower bound*: *upper bound*]).

Results

Haul-out monitoring

The model with the minimal deviance was a model with a Student distributed residual error and a normally distributed observer error (Table 2). Under this model, observer error represented $6 \pm 9\%$ of the total variance.

The estimated curve for the largest surveyed harem in 2009 is illustrated on Fig. 1. The model tended to underestimate the number of females present at the peak haul-out date and to overestimate the number of females present at the closing of the breeding season. Despite these shortcomings, evident on Fig. 1 because it is the largest surveyed harem, model fit was acceptable for smaller surveyed harem (N_{\max} range: 130–340, see Supplementary Fig. 1).

In 2009, the selected model estimated 2,728 ([2584:2873]) females to have hauled-out on the study area. On 1st, 2nd, 3rd and 5th November, we counted an average of 2,958 ([2837:3080]) pups on the study area. Thus, the model underestimated the total number of females that have hauled-out during the breeding season.

On îles Kerguelen, the haul-out peak occurred on 15 October ([13th:17th]) while the synchrony for a rookery was 8.3 ([7.3:9.3]) days. At the site level, N_{\max} was uncorrelated with both μ ($\rho = -0.08$, [−0.57:0.42]) and σ ($\rho = -0.09$, [−0.64:0.51]). On the other hand, μ and σ were negatively correlated ($\rho = -0.59$, [−0.93:−0.11]): precocious harems were less synchronous than late ones.

Correction factors

Correction factors were computed from the selected model by predicting a new, unobserved site. Between-site

Table 2 Model selection

Residual error	Observer error	Deviance
Gaussian	Gaussian	10,080
Gaussian	Skew-Normal	10,090
Gaussian	Student	10,260
Student	Gaussian	10,000
Student	Skew-Normal	10,020
Student	Student	12,230

Different distributional assumptions for residual and observer errors were made and contrasted. The best model had a Student and Gaussian distribution for residual and observer errors, respectively

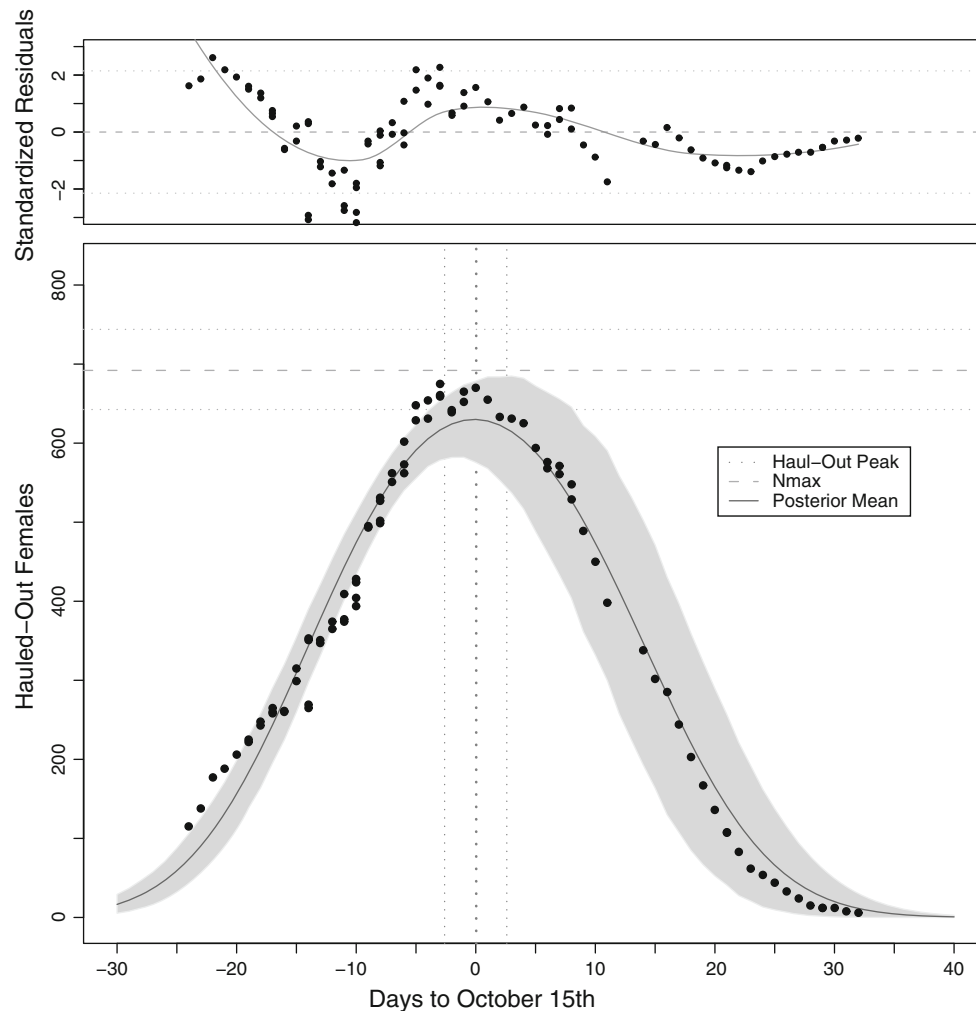


Fig. 1 Haul-out process at the largest rookery surveyed in 2009. Dotted grey lines along with the light grey envelope picture 95% CI. Standardized residuals are depicted on the upper part of the plot. The

variability is thereby taken into account. Correction factors were normally distributed before the peak haul-out date, but became right-skewed after. Thus, a better precision was achieved for censuses conducted before female peak haul-out.

Population trends

Results from the spline analysis are depicted on Fig. 2. The linear penalized-splines accounted for $35 \pm 17\%$ of the variance, and the smoothing parameter, λ , was large ($\lambda = 82 \pm 49$). After a large decrease (approx. one-third) during the 1960–1980s, the population is now stable.

Comparison with published estimates

Results from our small meta-analysis are summarized on Fig. 3. There was no correlation between μ and σ across

wave-like pattern in the residuals indicates model misfit. This misfit can also be seen from the way the fitted curve overestimated the number of hauled-out females at the close of the breeding season

different islands ($\rho = -0.00$, $[-0.35:0.38]$), but there was a trend for a negative correlation within each island ($\rho = -0.50$, $[-0.96:0.32]$), suggesting that harems forming early in the breeding season were less synchronous than harems forming later.

Evident on Fig. 3 is the absence of any shift in the timing of peak haul-out between the late 2000s (this study) and the 1970s (Rothery and McCann 1987).

Discussion

Variability in counts

Using state-of-the-art statistical methods, we partitioned the variation in counts of female Southern Elephant Seals due to observers and to surveyed sites. We further tested the impact of having different field workers performing

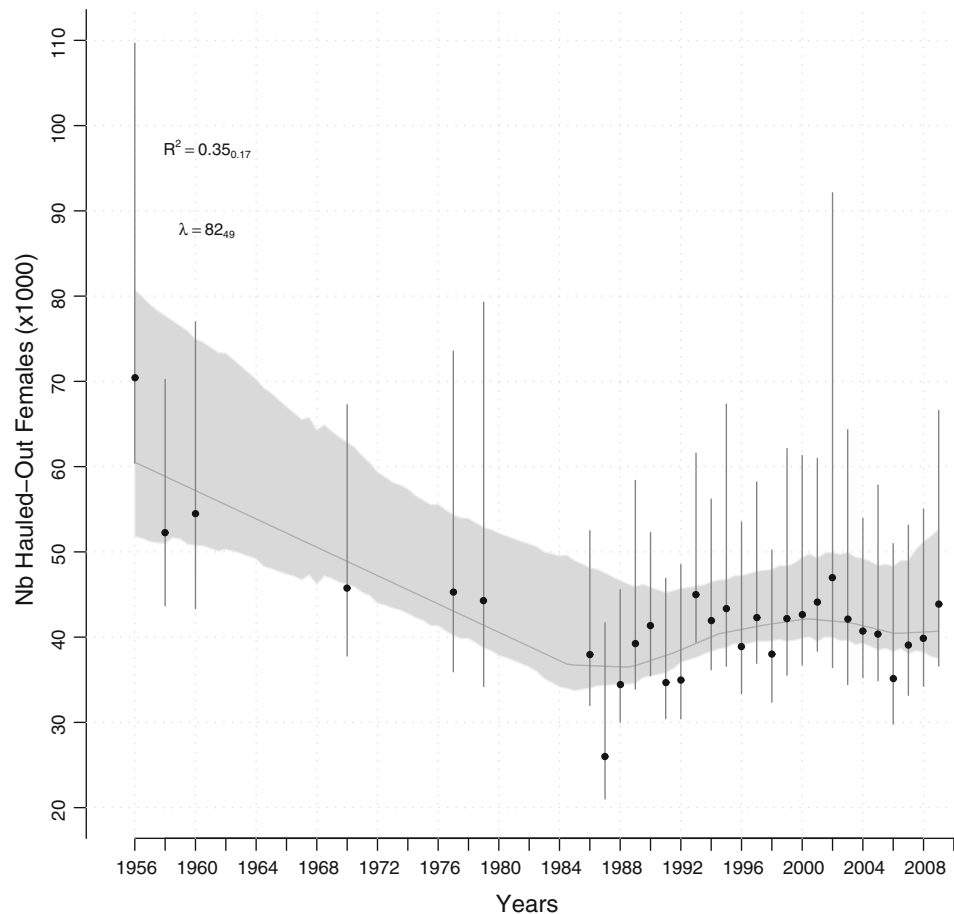


Fig. 2 Population trend of female Southern Elephant Seals breeding on the Courbet Peninsula, Îles Kerguelen since the 1950s. Posterior medians of breeding female counts, corrected for census date, along

with their 95% CI are depicted. The *grey envelope* and the *continuous darker grey line* represent a 95% CI and the posterior median value of the trend, respectively

those counts. In 2008 and 2009, surveyed sites were spread along a 3-km-long strip of gently sloping beach and monitored daily for 2 months. This intensive monitoring was achieved by one (in 2008) or two (in 2009) main fieldworkers, with occasional help from other observers. Because censuses of the Peninsula Courbet are always performed by different fieldworkers from 1 year to the next, quantifying the uncertainty due to observers was essential to assess the reliability of estimates. That this uncertainty is rather small ($6 \pm 9\%$ of the total variance) is testimony to the dedicated work of observers: they are doing their best on a hard job.

The selected model was that with Student error, reflecting the occurrence of some extreme observations. These may have resulted from the frequent inclement conditions during which censuses were performed (strong winds, snow). In addition, the Courbet Peninsula (and Cape Ratmanoff) shows a rather flat landscape, with no promontory points which could help when counting females. That the selected model suggested that counts may be intrinsically hard is thus rather pleasing and in agreement

with the experience of most fieldworkers. Nevertheless, in this analysis, we pooled data from 2008 to 2009, thus ignoring any variability due to year. However, as 2008 and 2009 were very similar (Guinet unpublished data) this variability is, in all likelihood, small.

The variability due to site was also assessed: some harems aggregated early in the breeding season while others appeared later. There is a loose latitudinal gradient in peak haul-out date across Southern Elephant Seal populations (Campagna et al. 1993). Yet, this does not translate in a latitudinal gradient in synchrony. That is, Southern Elephant Seals breeding on Kerguelen, which start breeding earlier, are no less synchronous than those from South Georgia. A significant negative correlation was nevertheless uncovered between peak haul-out date (μ) and synchrony (σ) at the site level, meaning that synchronous harems were those that aggregated late in the breeding season. This correlation was also recovered in our small meta-analysis, with broad agreement in point estimates. Since older females also tend to haul-out later in the season (Arnbom et al. 1994), breeding experience could drive

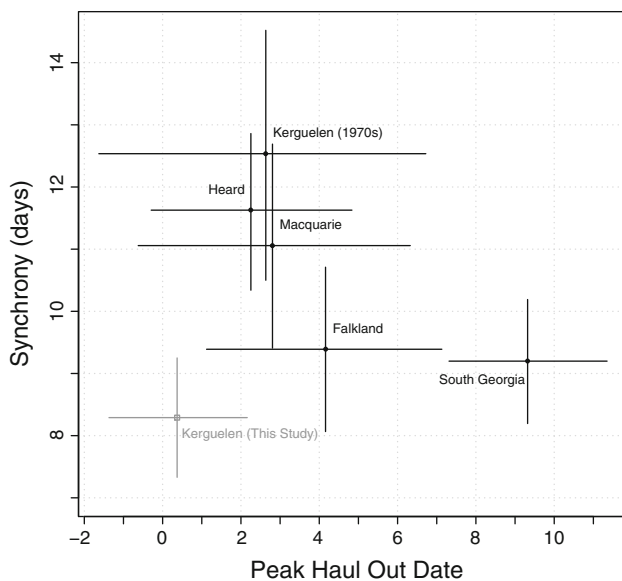


Fig. 3 Relationship between peak haul-out (μ) and synchrony (σ) across Subantarctic islands where female Southern Elephant Seals breed. Zero for peak haul-out corresponds to 15 October. The credibility interval for peak haul-out on îles Kerguelen largely overlaps between the 1970s and the 2000s

such a correlation. Embryo implantation is delayed in Southern Elephant Seals and occurs at the close of the summer moult (Laws 1993). Older, more experienced females may adjust to current environmental conditions at the end of moulting better than primiparous or inexperienced females, thus becoming more synchronized. Such a process could account for this observed correlation.

The number of females to haul-out in a given harem (N_{\max}) was independent of peak haul-out date (μ) and synchrony (σ), that is large number of females could be found in precocious or late, and in synchronous or asynchronous harems. That N_{\max} is uncorrelated to both μ and σ is all the more relevant to the computation of correction factors. Indeed, for a census performed on day t on site i : $N_t^i = N_{\max}^i \times p(t, \mu^i, \sigma^i, S)$.

Correction factors are computed as the inverse of $p(t, \mu^i, \sigma^i, S)$. This could prove problematic if there were any correlation between N_{\max}^i and the other parameters, more so since censuses on the Courbet Peninsula are one or two order of magnitude larger than the largest harem we surveyed in 2008–2009. The absence of such correlations thus justifies the use of these correction factors.

With these factors, we could derive corrected estimates for the numbers of females that came ashore during the breeding season over a 60-year time period. For each estimate, we further computed 95% CI to assess the precision of corrected estimates. These corrected estimates were more precise if censuses were performed prior to 15 October, the peak haul-out date. The optimal strategy to

derive the most precise estimates of the Kerguelen breeding population is therefore to perform censuses prior to, or on the peak haul-out date. Peak haul-out date for breeding Southern Elephant Seals did not appear to have changed between the 1970s and the 2000s (Fig. 3). This absence of any phenological shift is remarkable given the current global changes affecting the Southern Ocean (Trathan et al. 2007). Capital breeding and delayed embryo implantation may help females to buffer against environmental variability, and as a result, to show a stable breeding phenology. As we are comparing two points in time (1970s vs. 2000s), it cannot be excluded that breeding phenology has fluctuated within this 30 years span. Yet, as global changes are currently becoming more and more manifest (Trathan et al. 2007), such a pattern would be surprising.

Population trends

Using Bayesian penalized linear splines, we assessed the population trend of Southern Elephant Seals breeding on the Courbet Peninsula, Kerguelen. This semi-parametric regression revealed that the population has been stable around 40,000 individuals over the last 20 years. However, the spline smoothness penalty was large, betraying oversmoothing. Model fit, as measured by the coefficient of determination, was also modest. This oversmoothing was a consequence of the large uncertainties in corrected estimates. Thus, oversmoothing may not be an issue here as most of the variation results from correction factors per se, and true biological variation, unless very large, may be veiled when correcting censuses. There was in fact a large decrease in Southern Elephant Seal numbers during the 1960–1970s across several Subantarctic islands (Guinet et al. 1999). Our data here suggest a decrease of approximately one-third of breeding females on Kerguelen during the 1960–1970s. Despite oversmoothing, our p-spline model recovered this signal and further suggested that (1) this decrease was over and (2) the Kerguelen population has been stable for the past 20 years (Fig. 2).

Current limitations

Despite its usefulness to shed light on the haul-out process in breeding Southern Elephant Seals, Rothery and McCann (1987)'s model has shortcomings. These are evident on Fig. 1: the model underestimated the number of females ashore at peak haul-out (positive residuals) and overestimates this number at the close of the breeding season (negative residuals). This behaviour results in a wave-like pattern in a plot of residuals against census date, apparent for most surveyed sites but the smallest, and was most pronounced in the largest harem (see Fig. 1). Such a

deficiency stems from the symmetry assumption of the model while there is in fact a small, but practically significant, negative correlation between female arrival and departure dates from the rookery (Condit et al. 2007). This correlation thins the right tail on the bell-shaped curve (see Fig. 1) and results in an underestimation of the proportion of females present at peak haul-out. Thus, correction factors tend to produce overestimates. In addition, these correction factors have a skewed, posterior distribution after the peak haul-out date as a result of model misfit.

Thus, there is room for improving the model, as described in Condit et al. (2007). Most problematic may be the overestimates produced by biased correction factors. Yet, Galimberti and Sanvito (2001) reported this bias to be small: the difference between estimated and observed N_{\max} was less than 5% of observed N_{\max} , which is acceptable in a practical sense. Moreover, the Bayesian point of view adopted here enabled us to compute 95% CI for each corrected counts, thus attenuating the risk of overconfident inferences.

Conclusions

Our objectives in this study were to quantify and partition the different sources of variability in counts of female Southern Elephant Seals breeding on Kerguelen Islands. The hierarchical model we used here could be improved, in particular to account for the correlation between female arrival and departure dates. Such a model would need additional data as Condit et al. (2007)'s model has six parameters and requires additional independent data on mean arrival date and mean departure date of breeding females. Such data are currently lacking for our studied population. Despite these shortcomings of the model, our initial objectives have been reached: we feel confident to assert that the population of Southern Elephant Seals breeding on Kerguelen has not experienced any phenological shift since the 1970s and is currently stable.

The population of female Southern Elephant Seals breeding on South Georgia (54°15'S, 37°05'W) has been stable since the 1950s (Boyd et al. 1996), while that of Macquarie island (54°30'S, 158°57'E) halved between the 1960s and the 1980s but has stabilized since the 2000s (van den Hoff et al. 2007). Thus, population trends in the South Atlantic and South Pacific Oceans are all stable. Concerning the South Indian Ocean stock of Southern Elephant Seals, the number of females breeding on Marion may be increasing (McMahon et al. 2009), is stable on Crozet Archipelago (46°25'S, 51°50'E) (Guinet et al. 1999), Heard island (53°05'S, 73°30'E) (Slip and Burton 1999) and îles Kerguelen (this study). Therefore, the current population trends of the main stocks of Southern Elephant Seals within

the Southern Ocean do not suggest any global threats looming on this species.

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Appendix

WinBUGS code to fit Rothery and McCann (1987)'s model

```
## Data
# N : number of data points
# N.site : number of surveyed rookeries
# N.who : number of different field workers
# t[] : census date (0 = 15th October)
# n[] : number of counted females
# site[] : dummy code for each surveyed rookery
# who[] : dummy code for who made the census
# S : mean length a female stays ashore (in days)
## Parameters of Inferential Interest
# sd : residual error
# nu : number of degrees of freedom of the Student
distribution
# beta : marginal means
# Nmax : maximum number of females present on each
site
# peak.return : date of peak return of females on each
site
# peak.haulout : date of peak presence of females on
each site
# sd.b : site variances
# cor.b : correlation between Nmax, peak.return and
synchrony
# sd.observer : observer error
##
model{
# Likelihood, Student distribution for residual error
for (i in 1 : N) {
n[i] ~ dt(mu[i],tau,nu)
mu[i] <- Nmax[Site[i]]*p[i] + observer[who[i]]
```



```

p[i] <- phi(Arrival[i]) - phi(Departure[i])
Arrival[i] <- (t[i]-peak.return[Site[i]])/synchrony[Site
[i]]
Departure[i] <- (t[i]-S.cut-peak.return[Site[i]])/synchrony
[Site[i]]
}
# Priors
tau <- pow(sd,-2); sd ~ dunif(0,100); nu ~ dunif
(2,50);
for (i in 1 : N.site) {peak.haulout[i] <- peak.
return[i] + S.cut/2}
## the cut() function is to prevent the data from feed-
backing on S
S.cut <- cut(S); S ~ dnorm(28,0.20)
# Half-Cauchy (weakly informative) prior for beta[1]
(Nmax > 0)
beta[1] <- abs(raw.beta[1]); prior.scale[1] <- 1000
raw.beta[1] ~ dnorm(0,tau.beta[1]);
tau.beta[1] <- pow(prior.scale[1,-2]*eta.beta[1];
# Cauchy Prior (weakly informative) for beta[2]
(peak.return)
beta[2] <- raw.beta[2]; prior.scale[2] <- 10
raw.beta[2] ~ dnorm(0,tau.beta[2]);
tau.beta[2] <- pow(prior.scale[2,-2]*eta.beta[2];
# Half-Cauchy (weakly informative) for beta[3]
(synchrony > 0)
beta[3] <- abs(raw.beta[3]); prior.scale[3] <- 10
raw.beta[3] ~ dnorm(0,tau.beta[3]);
tau.beta[3] <- pow(prior.scale[3,-2]*eta.beta[3];
# Inverse-Wishart prior for site variances
for (i in 1 : (N.site + 1)) {
Nmax[i] <- B[i,1]; B.hat[i,1] <- beta[1]
peak.return[i] <- B[i,2]; B.hat[i,2] <- beta[2]
synchrony[i] <- B[i,3]; B.hat[i,3] <- beta[3]
B[i,1:3] ~ dnorm(B.hat[i,],tau.B[,i])
}
tau.B[1:3,1:3] ~ dwish(W[,3]; SD[1:3,1:3] <- inverse
(tau.B[,i]);
W[1,1] <- 150; W[1,2] <- 0; W[1,3] <- 0;
W[2,1] <- 0; W[2,2] <- 4; W[2,3] <- 0;
W[3,1] <- 0; W[3,2] <- 0; W[3,3] <- 2;
for (j in 1 : 3) {
sd.b[j] <- sqrt(SD[j,j]);
eta.beta[j] ~ dgamma(0.5,0.5)
}
cor_b[1] <- SD[1,2]/sqrt(SD[1,1]*SD[2,2])
cor_b[2] <- SD[1,3]/sqrt(SD[1,1]*SD[3,3])
cor_b[3] <- SD[2,3]/sqrt(SD[2,2]*SD[3,3])
# Half-Cauchy Priors for fieldworker variance
for (i in 1:N.who) {
observer[i] <- x*U[i];
U[i] ~ dnorm(0,tau.U)
}

```

```

x ~ dnorm(0,tau.x);
tau.x <- pow(prior.scale.who,-2);
tau.U ~ dgamma(0.5,0.5)
sd.observer <- abs(x)/sqrt(tau.U);
prior.scale.who <- 10
} # end of model

```

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