Top-down and bottom-up influences on demographic rates of Antarctic fur seals *Arctocephalus gazella*

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Summary

1. Two major drivers in population dynamics are bottom-up processes, such as environmental factors that affect foraging success, and the top-down impacts of predation.

2. Many populations of marine mammal and seabird species appear to be declining in response to reductions in prey associated with the bottom-up effects of climate change. However, predation, which usually occurs at sea and is difficult to observe, may also play a key role.

3. We analysed drivers of population dynamics of Antarctic fur seals *Arctocephalus gazella* at Cape Shirreff from 1997 to 2009, including a predator that targets pre-weaned pups and bottom-up environmental effects in an ecosystem particularly sensitive to small changes in temperature.

4. We use Bayesian mark-recapture analysis to demonstrate that although large-scale environmental variability affects annual adult survival and reproduction, first year survival appears to be driving the current decline in this population (as defined by a decline in the annual number of pups born). Although the number of pups increased during the first third of the study, first year survival and recruitment of those pups in later years was very low. Such low survival may be driven by leopard seal *Hydrurga leptonyx* predation, particularly prior to weaning.

5. Our results suggest that without leopard seal predation, this population would most likely increase in size, despite the observed bottom-up effects of climate changes on adult vital rates. More broadly, our results show how age-targeted predation could be a major factor in population decline of K-selected colonial breeders.

Key-words: Antarctic Oscillation, Cormack Jolly Seber, detection probability, El Niño Southern Oscillation, pinniped, Shetland Islands, Southern Annular Mode, tag loss

Introduction

Environmental change can have complex effects on populations, influencing population growth via interactions that impact individual fitness. At the same time, many species are subject to top-down predation. Few studies have attempted to address the two factors simultaneously in large mammals.

A changing environment can produce population-level increases or decreases through changes in available critical habitat (i.e. breeding habitat), alterations in the metabolic requirements of individuals (McDonald *et al.* 2012), and

modifications in prey availability (Costa *et al.* 2010), with the latter defining bottom-up effects. In addition, there may be lags as changes in prey availability work their way through the food web, resulting in different temporal and spatial scales of prey availability across the different age classes (Le Bohec *et al.* 2008).

Although long-lived species, including mammals and seabirds, often have behavioural and physiological mechanisms that buffer them against variations in food resources occurring over large spatial and temporal scales (Costa 1993; Forcada, Trathan & Murphy 2008), some species are exhibiting dramatic declines in survival and reproductive rates attributed to bottom-up forcing over relatively short time periods. For example, vital rates of

several marine bird species are correlated with environmental variability, including El Niño conditions, which may reduce prey availability (Barbraud & Weimerskirch 2001; Le Bohec *et al.* 2008; Rolland, Weimerskirch & Barbraud 2010; Baylis *et al.* 2012). However, none of these studies examined top-down effects, or the relative importance of top-down and bottom-up factors.

With respect to top-down effects, predation is often not random, with predators targeting the most easily caught groups when the energetic costs of prey acquisition are high (Carbone, Teacher & Rowcliffe 2007). If predators prefer younger animals (due to ease of capture, or increased availability) with higher reproductive potential, increases in predation will reduce the prey population growth rate unless the targeted species can compensate by increasing its reproductive rate. However, most long-lived species, and especially large mammals, have limited reproductive flexibility because of restrictions on the number of times a female can reproduce and low offspring-parent ratio per reproductive event. For example, predation has dramatic consequences on early survival of large terrestrial herbivores (Linnell, Aenes & Anderson 1995; Barber-Meyer, Mech & White 2008; Carstensen *et al.* 2009). Additional studies have shown variability in pre-reproductive female survival can be an important component of population growth, particularly when a species exhibits comparatively high and stable adult survival and limited reproductive flexibility (Gaillard, Festa-Bianchet &

Yoccoz 1998; Gaillard *et al.* 2000). Indeed, both empirical data and modelling have shown that, in such cases, prey populations can shift from declining to increasing simply by removing predation during the first year (Banks, Newsome & Dickman 2000; Berger & Conner 2008; Yarkovich, Clark & Murrow 2011).

Antarctic fur seals *Arctocephalus gazella* are emblematic of this life-history strategy, with both bottom-up forcing and predation of young potentially limiting population growth. In South Georgia, where predation of young is low (Forcada *et al.* 2009), both pup production and population growth were associated with El Niño conditions, with variability in breeding female survival as the largest factor in growth rate variability (Forcada *et al.* 2005; Forcada, Trathan & Murphy 2008). In contrast, at a cove on Seal Island, Antarctica, leopard seals *Hydrurga leptonyx* may have taken between 32 and 69% of the annual pup cohort within the first 3 months of a 5 month pupping season (Boveng *et al.* 1998). In addition, by comparing trends in pup counts at sites with and without predation, Boveng *et al.* (1998) suggested leopard seal predation could contribute to declines of some colonies and result in lower population growth in the larger region of the South Shetland Islands.

This research seeks to quantify the relative effects of climate variability and predation on population growth of fur seals at Cape Shirreff, Livingston Island, South Shetland Islands (Fig. 1). Cape Shirreff is the southern-most
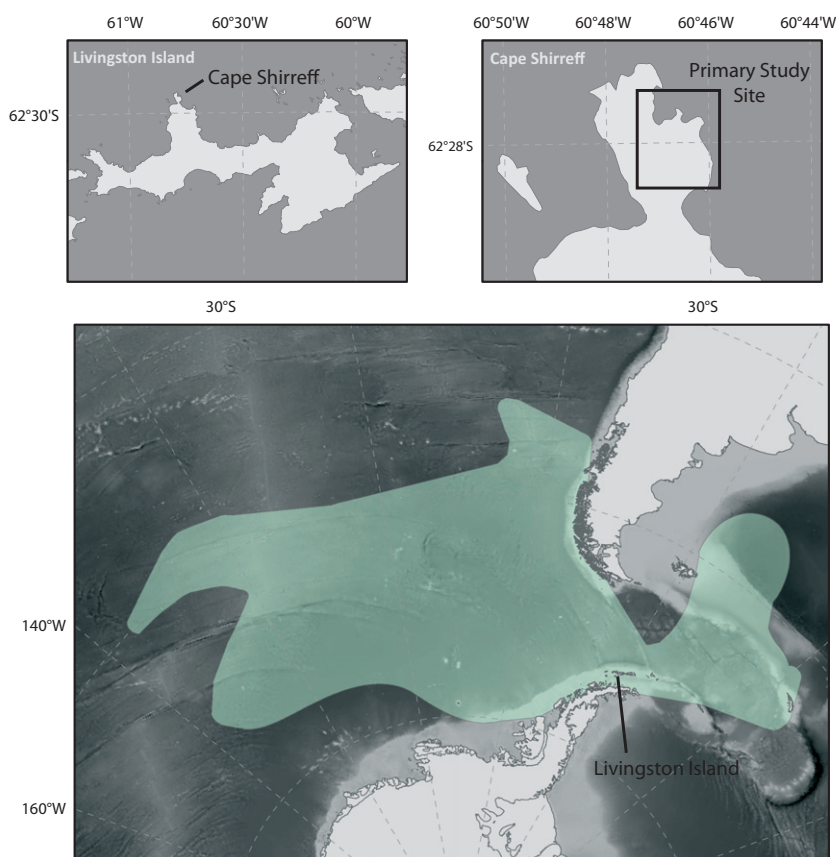

Fig. 1. Location of Cape Shirreff, Livingston Island, Antarctica with primary study area located in the square. General adult female fur seal winter range shaded in green (created by L. Hückstädt, unpublished data from M. L. Lea).

breeding colony for the species, indicating environmental factors may limit population growth. At the same time, leopard seals frequently consume fur seal pups (Goebel *et al.* 2009). Preliminary analysis estimates roughly half of the 87 individual leopard seals identified since 1997 are resident or regular visitors during the breeding season, and leopard seal numbers have increased over the last decade, with a recent maximum count of 30 individuals hauled out at one time (U.S.–AMLR, unpublished data; Vera, Vargas & Torres 2004).

Materials and methods

We use Bayesian mark-recapture techniques to first quantify the effects of environmental variability on adult demographics. Next, on the basis of the findings and methods of Boveng *et al.* (1998), we measure the potential effects of leopard seal predation on early survival by assuming pup survival before entering the water (less than 20 days old) is a measure of non-predatory mortality. Lastly, we combine those results to determine the collective effects of both predation and the environment on Cape Shirreff fur seal population growth, while verifying our results against leopard seal energetic studies.

DATA

We began a dedicated mark-resight programme for Antarctic fur seals at Cape Shirreff, Livingston Island, Antarctica (62°27′32″S, 60°47′19″W) in the austral summer of 1997/1998. Each summer, we individually mark roughly 500 pups and between 30 and 100 lactating females with flipper tags. Annual resight effort coincides with the start of pupping in mid-November and continues to early March, with daily resight effort in the main study area (see Supp. Info.- Tagging and resight methods). Beginning in 2000/2001, we extracted teeth from females tagged as adults to estimate age from cementum layers. A professional tooth ageing laboratory (Matson's Lab, Missoula, MT) counts dentition layers, and we consider age estimates from teeth to be precise and unbiased (see Supp. Info.- Teeth ageing technique and sampling bias).

We used mark-resight data of females from austral summer 1997/1998 through 2006/2007 to estimate annual demographic rates. Because of unintended sampling bias (see Supp. Info.- Teeth ageing technique and sampling bias), adult survival rates by age could only be calculated for years 2002 through 2006. The bias also meant age-structured reproductive rates (the fraction of females giving birth to live young) were calculated for all years, but data were restricted to only animals that survived to 2002/2003. We determined the potential effect of leopard seal predation on pup survival using daily resight data of female pup pairs with known pupping dates for austral summers 2004/2005 through 2007/2008.

ANALYSIS: ANNUAL DEMOGRAPHIC RATES IN RELATION TO ENVIRONMENT

We developed a Bayesian multi-event, multistate method based on the standard Cormack-Jolly-Seber (CJS) mark-recapture model (Poole 2002) that also allowed for mark loss (Reisser *et al.* 2008) and temporary emigration (Dupuis 1995). In our case, we explicitly modelled the probability of an Antarctic fur seal losing one tag and the probability of moving in or out of the main study area (see Supp. Info.- Annual demographic rate analysis). Thus, we estimated five basic probabilities/parameters that define an animal's transition from one state to another state between sample periods: survival rate (s), reproductive rate (r), probability an animal moves in/out of the study area (m), probability of adult female detection (d) and probability of losing one tag (g).

In contrast to fur seals from South Georgia that stay within roughly 500 km of their breeding beaches year-round (Staniland *et al.* 2012), Cape Shirreff seals remain local during breeding season but travel thousands of kilometres offshore to forage in areas off the coast of Chile, north of the Falkland Islands, around South Georgia Island and in Pacific Ocean fronts between 45°S and 65°S during winter (Polito & Goebel 2010; Lea unpublished data) (Fig. 1). We examined the influence of environmental conditions by correlating adult survival and reproduction with an environmental index based on the temporal and spatial scale of the seals' foraging range as the mean of the monthly Antarctic Oscillation (AAO) between April and December of each year (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml). AAO values representing larger and smaller time periods within a year were also evaluated as well as annual lag periods between AAO values and demographic rates. However, the above AAO values with no lag showed the highest correlation and were the most biologically plausible given the seals' temporal and spatial foraging distribution. When estimating reproductive rates, the range and variability in average over-winter AAO during the studied time period were similar to all available years combined (1979–2009), while over-winter AAO values were slightly lower for years when survival rates were estimated (Supp. Info.- Fig. 1). Survival and reproductive rates (x) were estimated as a linear function of the AAO index with categorical age class (AC) as an independent covariate:

$$logit(x) = \beta_0 + \beta_1(AC) + \beta_2(AAO) \qquad \text{eqn 1}$$

The interaction term between AC and AAO was analysed but removed because its posterior distribution centred on zero, and the Deviance Information Criteria (DIC) was higher for a model with this interaction term. Age classes were defined as 5–7, 8–16 and 17 + years old (see Supp. Info.- Annual demographic rate analysis). For comparison, we also estimated annual demographic rates independent of AAO values.

Low juvenile resight probabilities prevented a rigorous analysis of the influence of AAO on survival rates of 1–4 year olds. However, younger survival rates (age classes: 1 and 2–4) were estimated separately by year for years 1998–2005, maintaining between-year posterior correlations to project population counts while acknowledging high within-year uncertainty. In addition, small sample size limited the estimate of reproductive rate for ages three and four to one value across all years which we used in analyses of population growth.

Other transition probabilities were quantified to assess potential differences based on age or reproductive status (see Supp. Info. – Annual demographic rate analysis). However, changes in assumptions about movement, tag loss and tag detection by age, tag number, or reproductive status did not change the overall pattern in demographic rates with respect to AAO. Priors on estimated parameters β_0, β_1 and β_2 were broad, uniform distributions wide enough to prevent truncation of posterior distributions. All other priors were uniform between 0 and 1.

Using a similar multi-event, multistate Bayesian approach, mark-resight analyses were used to estimate pup survival, pup sighting probability and female sighting probability. We used daily re-sights of adult females with and without pups and analysis of mark-recapture data of the pups. Transition probabilities between states were pup survival (s), pup detection (d_p) and female detection (d_f). We made model assumptions based on potential temporal and individual differences in sighting probabilities derived from the animals' natural history (see Supp. Info.- First year pup survival). As the probability of detecting a pup given detection of its mother changes as pups become more independent, pup detection was defined as a cubic-logit function of pup age:

$$logit(d_p) = \beta_0 + \beta_1 Age + \beta_2 Age^2 + \beta_3 Age^3 \qquad \text{eqn 2}$$

Based on DIC values, a cubic function fit better than models with fewer or more parameters. For the other two transition probabilities, we took a hierarchical approach, with pup survival probabilities on the daily scale (s_a) and maternal detection probabilities on the individual scale (d_{fi}). We also allowed for individual variability in the probability of sighting the female given the pup was alive or dead. (Clark *et al.* 2005).

Using daily counts of live pups, Boveng *et al.* (1998) showed that mortality in fur seal pups is constant when leopard seal predation is absent. They then used the non-predatory mortality rate as a control to estimate the proportion of pups taken by leopard seals at a nearby site. Instead of using a nearby site to estimate non-predatory mortality, we used early survival at the same site as a control. So, the analysis was also conducted grouping survival rate into age classes: 1–7, 8–20, and 21 + days old. Because pups do not enter the water until they are approximately 30 days old, we assumed survival from 8 to 20 days represented non-predation mortality, and any additional mortality measured at 96 days old was associated with predation. Ninety-six days was the maximum age at which researchers were present in the area, resighting pups and observing leopard seal predation.

To investigate the potential influence of higher first survival on population growth (as defined by annual pup counts), the proportion of pups alive at 1 year old was also calculated by extending daily survival rate estimates out to 365 days using both the higher daily survival rate (8–20 days) and the lower daily survival rate measured on day 96. The lower rate corresponds to survival if predation were assumed to continue. To determine the feasibility of the assumption that additional mortality was due to predation, we estimated the number of leopard seals required to consume the estimated number of predation mortalities up to 96 days old if all leopard seals were either juvenile females with the lowest consumption rate (0.8 ± 0.15 stdev fur seal pups/day) or adult males with the highest consumption rate (1.3 ± 0.25 fur seals pups/day) (Forcada *et al.* 2009). We then calculated the number of additional days of predation required by the same number of leopard seals to reach the estimated lower first-year survival rate. To compare first year survival based on annual flipper tag resights with estimates from daily pup resights, results are reported as survival from 75 days old (mean age at which pups are generally flipper tagged) to 1 year old.

To determine the effects of both potential top-down and bottom-up factors on this population, we estimated the population age distribution for 1997/1998 derived from pup counts from that year, knowledge of the system, and several assumptions. Using annual mark-recapture estimates of juvenile (age class 2–4) survival rates, reproductive rates ages 3 and 4 pooled for all years, and adult demographic rates as a function of AAO, the population was projected forward, and the number of estimated pups was recorded through 2009/2010. We projected the population using estimates of first year survival based on both higher and lower daily pup survival rates (see Supp. Info. – Age distribution and population projection). In both cases, inter-annual variability in juvenile survival rates is maintained. Model estimates of pup counts were then compared with field counts. In addition, posterior samples of demographic rates were used in a Leslie matrix to calculate growth rate sensitivity with high and low AAO values and high and low first year survival (see Supp. Info.- Sensitivity analysis). To verify our results, we also ran both sensitivity analysis and pup projections doubling the relationship between AAO and adult rates.

Posterior distributions and joint posterior samples of all variables were determined using the program MTG (Metropolis within Gibbs) developed by Daniel Goodman of Montana State University (Schwarz 2008). Standard practices ensured mixing, convergence and stationarity in posterior samples (see Supp. Info – MCMC sampling).

Results

Antarctic fur seals show age variation in demographic rates with prime-age (8–16 years old) females exhibiting the highest reproductive and survival estimates. Oldest females (17 + years old) exhibited the lowest rates, while young animals (5–7 years old) were intermediate (Fig. 2). Uncertainty was higher for the oldest age class due to small sample size (Fig. 2). Annual survival and reproductive rates of animals older than 4 years were slightly positively correlated with AAO (Fig. 2), but the relationship was stronger for survival rates [$\beta_2 = 0.37$ (95% Cred. Int.: -0.09, 0.83)] than that for reproductive rates [$\beta_2 = 0.29$ (-0.05, 0.63)]. Based on annual tag resight data, the mean probability a female survives from time of tagging (roughly 75 days old) to 1 year old is annually variable between 0.04 and 0.26 (Fig. 3). For results on tag loss, tag detection and movement probabilities, see Supp. Info. – Tables 4 and 5.

When grouping pup survival by age class, rates were lower and annually variable for the oldest age class (21 + days old), whereas rates were higher and similar for the younger age classes (1–7 and 8–20 days old) (Table 1). As a result, both the mean proportion of pups surviving to 96 days old and the proportion of pups potentially lost to predation by 96 days old were annually variable (Table 2). When extending daily survival rates out to 365 days old, mean cohort survivorship from 75 days to 1 year old was between 0.18 and 0.28 (Fig. 3). For results
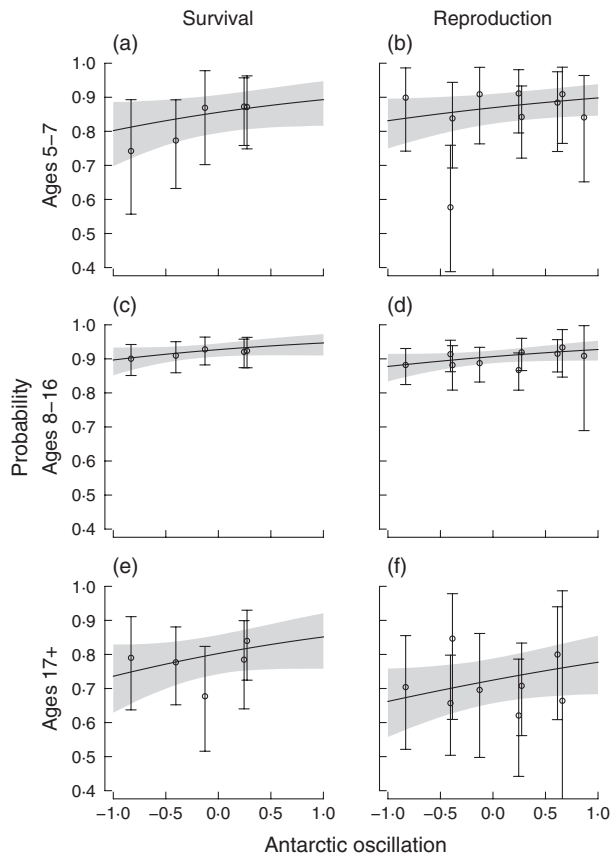
Fig. 2. Posterior distributions of survival and reproductive probabilities as a function of age class and Antarctic Oscillation (AAO). Solid lines are means and grey areas are 95% posterior intervals. Points with bars are posterior mean and 95% credible intervals with years assumed independent from AAO.

on pup and female daily detection probability, see Supp. Info. – Fig. 2 and 3.

Depending on energetic needs and year, the average number of leopard seals needed to consume the estimated number of pups lost to predation at 96 days old was between 6·6 and 15·2 leopard seals per day (Table 2). If the same number of leopard seals continues to consume fur seals at the same rate after 96 days old, they would need an average of 3·0 to 39·7 additional predation days to produce the annual survival rates estimated from daily rates before 96 days old (Table 2).

Pup count estimates using low first-year survival rates closely matched increasing and then declining annual female pup counts [corr = 0·75 (95% Cred. Int.: 0·52, 0·93)] (Fig. 4). Although variability in adult demographic rates did produce some inter-annual variability in pup counts, pup counts were more likely to increase with high first year survival, and such model estimates were negatively correlated with observed pup counts [corr = −0·63 (−0·76, −0·41)]. Correlations are even stronger when limited to years later than 2000 when field pup counts were generally in decline: 0·85 (0·61, 0·97) with low first year survival and −0·85 (−0·95, −0·60) for high first year survival (Fig. 4).

The sensitivity of population growth rate varied with different levels of first year survival and AAO values. Population growth rate is most sensitive to first year survival when it is low, whereas sensitivity is more evenly spread across survival rates of age classes 1 through 16 when first year survival is high (Table 3). In addition, differing AAO values did not change sensitivity estimates by age class when first year survival was high (Table 3). Patterns in pup counts and sensitivity analysis did not change when doubling the relationship between AAO and adult rates.

Discussion

Our goal was to measure both the bottom-up effects of environment and the potential top-down effects of leopard seal predation on Cape Shirreff Antarctic fur seal population growth. Both sensitivity analysis on population growth and projection estimates of pup counts show
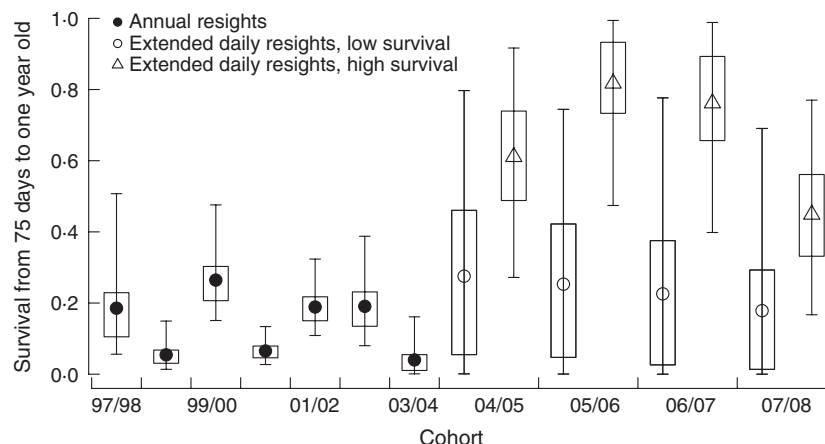

**Fig. 3.** Survival probabilities from 75 days to 1 year old by cohort. Results for cohorts 97/98–03/04 were based on annual resight data for all years and ages (filled circles). Results for cohorts 04/05–07/08 were based on first year survival assuming high daily survival rates (open triangles) and low daily survival rates (open circles). Points are means. Boxes are quartiles, and whiskers are 95% credible intervals.

Table 1. Daily probability of pup survival grouped by age and year Marginal means with 95% credible intervals in parentheses

Breeding season	Age class (days)		
	1–7	8–20	21+
04/05	0·998 (0·994,1·000)	0·998 (0·996,1·000)	0·992 (0·990,0·994)
05/06	0·998 (0·995,1·000)	0·999 (0·997,1·000)	0·991 (0·989,0·993)
06/07	0·999 (0·996,1·000)	0·999 (0·997,1·000)	0·988 (0·985,0·991)
07/08	0·997 (0·993,1·000)	0·997 (0·994,0·999)	0·987 (0·984,0·990)

Table 2. Estimated and measured survival rates from birth to 96 days old based on daily survival rates and sample size (*n*). Also, the estimated proportion of fur seals lost to predation at 96 days old and the number of leopard seals required to produce that estimated loss. Lastly, the additional number of predation days needed for the same number of leopard seals to produce the difference in low and high annual survival rate estimates. Marginal means with 95% posterior intervals in parentheses

Breeding season	*n*	Survival rate (birth to 96 days)		Potential proportion consumed	Number of leopard seals needed		Additional predation days
		Measured	Assumed high		Juvenile females	Adult males	
04/05	174	0.51 (0.43,0.59)	0.80 (0.65,0.90)	0.28 (0.12,0.41)	11.0 (4.3,19.2)	6.8 (2.7,11.9)	27.0 (0.0,101.0)
05/06	173	0.49 (0.40,0.57)	0.87 (0.76,0.93)	0.38 (0.25,0.49)	13.9 (8.0,22.3)	8.6 (4.9,13.9)	39.7 (0.0,112.7)
06/07	166	0.43 (0.33,0.52)	0.85 (0.71,0.93)	0.42 (0.27,0.54)	15.2 (8.5,25.1)	9.4 (5.2,15.5)	26.4 (0.0,84.7)
07/08	143	0.36 (0.27,0.45)	0.71 (0.55,0.83)	0.35 (0.18,0.50)	10.6 (4.9,18.6)	6.6 (3.0,11.2)	3.0 (0.0,28.0)
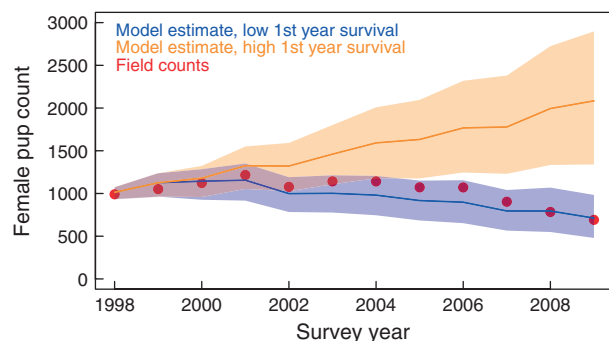
Fig. 4. Estimated annual female pup count based on model estimates with measured low first year survival (blue) and assumed high first year survival (orange) compared to field counts (red points). Lines are means and shaded areas are 95% posterior intervals.

that although adult demographic rates vary as a function of over-winter AAO, first year survival is currently the primary driver of growth for this population. Given the analyses presented here, coupled with preliminary data on leopard seal behaviour, counts and attendance, leopard seal predation prior to weaning could have caused the observed low recruitment of fur seals in this area.

Two studies have hypothesized that summer environmental conditions near the breeding colony influence adult vital rates. Food limitations during a relatively short lactation period may impose fitness costs that reduce maternal survival as well as prevent implantation, the latter resulting in lower pupping rates the following year (Forcada *et al.* 2005; Forcada, Trathan & Murphy 2008). Although that may be the case, over-winter foraging conditions will determine if a female can compensate for

lost energy reserves due to rearing offspring as well as provide nutrients for a developing foetus (Hiruki-Raring *et al*. 2012). Thus, large-scale winter conditions far from the breeding colony may have consequences for adult reproductive and survival rates, similar to what is seen in some colonial seabirds (Le Bohec *et al*. 2008; Baylis *et al*. 2012).

Environmental conditions measured by mean winter AAO values were trending downwards during the period of this study, and adult survival and reproductive rates decreased with decreasing AAO. Many climate models predict the AAO index will decline (IPCC 2007), and our results suggest that this would lead to reduced adult fur seal survival and reproduction and further lower population growth. It follows that survival of younger animals (1–4 years old) would further drive population growth, and as the probability of a female surviving and returning to her birth site after age 4 years is low, it is unlikely this group would recover from consistently poor environmental conditions. However, our analysis is restricted to adult female survival rates as a function of AAO. As juvenile survival rates most likely also respond to environmental perturbation (Beauplet *et al*. 2005), a declining AAO may lead to even further reduction in Cape Shirreff Antarctic fur seal population growth. In addition, the small number of years studied here may not entirely represent the long-term relationship between AAO and fur seal demographic rates or completely capture the periodicity and autocorrelation of AAO. However, effectively doubling the strength of the AAO vs. adult vital rate relationship did not change the pattern seen in sensitivity analysis or pup projections: first year survival is currently driving growth of this population.

Six lines of evidence support the hypothesis that leopard seal predation is the cause of low first year survival

Table 3. Sensitivity analysis with high and low AAO values defining survival and reproduction for ages five and older and high and low first year survival rates. See Supp. Info. – Sensitivity analysis for more details. Marginal means with 95% posterior intervals in parentheses

| | Age class | High 1st year survival[‡] | | Low 1st year survival[¥] | |
		High AAO*	Low AAO[†]	High AAO	Low AAO
Survival	1	0.20 (0.10,0.40)	0.22 (0.12,0.45)	0.83 (0.22,1.67)	0.60 (0.29,0.96)
	2–4	0.34 (0.20,0.42)	0.35 (0.23,0.43)	0.09 (0.04,0.16)	0.20 (0.14,0.25)
	5-7	0.23 (0.14,0.26)	0.25 (0.19,0.27)	0.09 (0.03,0.15)	0.18 (0.13,0.22)
	8–16	0.28 (0.21,0.33)	0.26 (0.19,0.33)	0.20 (0.08,0.31)	0.32 (0.27,0.34)
	17+	0.09 (0.02,0.34)	0.04 (0.01,0.17)	0.56 (0.27,0.85)	0.19 (0.07,0.40)
Reproduction	3–4	0.08 (0.01,0.15)	0.10 (0.02,0.18)	0.00 (0.00,0.01)	0.02 (0.01,0.03)
	5–7	0.08 (0.01,0.14)	0.10 (0.03,0.17)	0.00 (0.00,0.01)	0.02 (0.01,0.04)
	8–16	0.10 (0.04,0.13)	0.12 (0.08,0.14)	0.02 (0.00,0.05)	0.07 (0.03,0.11)
	17+	0.04 (0.02,0.07)	0.03 (0.01,0.07)	0.06 (0.02,0.08)	0.07 (0.06,0.09)

*0.614 in 2001.
†−0.831 in 2002.
‡0.56 (0.15,0.90).
¥0.04 (0.01,0.08) in 2001; 0.10 (0.05,0.19) in 2002.

for Cape Shirreff fur seals. First, in South Georgia where leopard seals are not present during the summer, the majority of pup mortality occurs prior to pups entering the water (Forcada, Trathan & Murphy 2008). Our results show pup mortality is higher after they enter the water in an area where leopard seals are present (Table 1), as previously observed at Elephant Island (Boveng *et al.* 1998). Second, although separated spatially and temporally, Cape Shirreff annual pup count declines from 2002 to 2009 (6·0 ± 7·7%year^{-1}; mean and std) and model predictions (decline 6·0 ± 6·6%year^{-1}) are similar to what was seen at Elephant Island when leopard seals were present (decline 4·2 ± 1·0%year^{-1}) (Boveng *et al.* 1998). Third, the range of annual mean fraction of pups taken by leopard seals at around 75 days old measured at Elephant Island is similar, but slightly higher compared to this study (0·32–0·69 and 0·22–0·35 respectively) (Boveng *et al.* 1998). Fourth, mean cohort survivorship from 75 days to 1 year old extrapolated from high daily pup survival rates (pooled mean: 0·56, mean of annual means: 0·51, range: 0·45–0·82) is comparable to mean survivorship from South Georgia where leopard seal predation is negligible (0·52) (Forcada, Trathan & Murphy 2008). Fifth, although uncertainty was higher when estimating survival from 75 days to 1 year old using daily survival rates, values were comparable to estimates based on annual mark-recapture analysis (Fig. 3).

Lastly, leopard seal estimates fall within a reasonable range of what we know from preliminary leopard seal data. Namely, roughly half of all tagged leopard seals appear to remain in the area for the majority of the breeding season, and the maximum number of hauled out leopard seals has been counted at 30. Regardless of the age structure of the leopard seal population, 15 leopard seals could consume the number of additional pup mortalities estimated at 96 days old (Table 2). Unweaned fur seal pups will remain vulnerable to leopard seals an additional 24 days before they can potentially move out of leopard seal habitat. Depending on the year, the probability the additional mortalities occurred prior to weaning are between 0·34 and 0·97. However, the degree of winter habitat overlap for these two groups is not known, and predation events may occur throughout the year. Leopard seal scat and stable isotope analysis, tracking data, mark-recapture analysis and detailed behavioural studies will allow us to determine temporal and spatial aspects of leopard seal prey type (including prey switching and prey age classes), attendance patterns and consumption rates.

Only a few marine mammal studies have begun to empirically explore population-level effects when predation is targeted on pre-breeders. Horning & Mellish (2012) showed killer whale *Orcinus orca* predation accounted for 10 of 11 documented deaths in juvenile Steller sea lions *Eumetopias jubatus*, and low recruitment prevents some populations from recovering. Based on energetics models, killer whales in the Subantarctic Prince Edward Islands could theoretically consume the entire Antarctic fur seal pup population within a matter of days or potentially reduce the pup population by 10–40% within a year, depending on different prey selection strategies (Reisinger, de Bruyn & Bester 2011). In general, our research, along with the above-mentioned studies, suggest predation on pre-breeders has the potential to create rapid and dramatic changes in marine mammal populations.

Colony breeders may be particularly vulnerable to predation of newborns as the naïve group provides a large and reliable food source for predators. While parental protection and predator saturation can reduce such risk (Ainley *et al.* 2005), some species do not guard their young and require time to physiologically develop effective foraging and fleeing capabilities (flying in birds and diving in marine air breathers) (Noren *et al.* 2001; Fowler *et al.* 2007; Tome & Denac 2012). In addition, physiological and environmental limitations may keep

reproductive rates low that could have otherwise compensated for young lost to predation (Bonin *et al.* 2012). Therefore, future studies investigating the impacts of predation on K-selected species, particularly colonial breeders, need to consider age or size-specific selection by the predator.

Although AAO has an effect, we found that fur seal population growth at Cape Shirreff is more sensitive to top-down processes in the form of leopard seal predation. Most importantly, we have shown that both top-down and bottom-up forces can be important population drivers for Antarctic fur seals, and the way in which the two forces affect population growth can vary from one colony to another. Bottom-up processes appear to be more important at Bird Island, South Georgia (Forcada, Trathan & Murphy 2008; Forcada *et al.* 2009). South Georgia is at the northern extreme of the leopard seals' range, so other conditions may influence the leopard seals' impact on South Georgia fur seals. Or, as seen in Boveng *et al.* (1998), South Georgia leopard seals may consume fur seal pups at nearby, unstudied colonies where hunting conditions are more favourable. In addition, complex interactions may have created a trophic cascade where leopard seals are now more abundant and targeting fur seals at Cape Shirreff, as has been demonstrated in some non-pinniped systems (Anthony *et al.* 2008; Harley 2011). In fact, this research, along with additional leopard seal research, could show environmental changes are potentially driving top-down predation on fur seals. If so, fur seal populations could decline more rapidly than anticipated as a result of environmental change. In general, future studies need to consider entire ecosystem shifts when investigating effects of environmental change, which could have both bottom-up and top-down effects on a species.

Acknowledgements

References

Ainley, D.G., Ballard, G., Karl, B.J. & Dugger, K.M. (2005) Leopard seal predation rates at penguin colonies of different size. *Antarctic Science*, **17**, 335–340.

Anthony, R.G., Estes, J.A., Ricca, M.A., Miles, A.K. & Forsman, E.D. (2008) Bald eagles and sea otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology*, **89**, 2725–2735.

Banks, P.B., Newsome, A.E. & Dickman, C.R. (2000) Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology*, **25**, 283–291.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs*, **169**, 1–30.

Barbraud, C. & Weimerskirch, H. (2001) Emperor penguins and climate change. *Nature*, **411**, 183–186.

Baylis, A.M.M., Zuur, A.F., Brickle, P. & Pistorius, P.A. (2012) Climate as a driver of population variability in breeding gentoo penguins (*Pygoscelis papua*) at the Falkland Islands. *Ibis*, **154**, 30–41.

Beauplet, G., Barbraud, C., Chambellant, M. & Guinet, C. (2005) Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology*, **74**, 1160–1172.

Berger, K.M. & Conner, M.M. (2008) Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. *Ecological Applications*, **18**, 599–612.

Bonin, C.A., Goebel, M.E., O'Corry-Crowe, G.M. & Burton, R.S. (2012) Twins or not? Genetic analysis of putative twins in Antarctic fur seals, *Arctocephalus gazella*, on the South Shetland Islands *Journal of Experimental Marine Biology and Ecology*, **412**, 13–19.

Boveng, P.L., Hiruki, L.M., Schwartz, M.K. & Bengtson, J.L. (1998) Population growth of Antarctic fur seals: limitation by a top predator, the leopard seal? *Ecology*, **79**, 2863–2877.

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007) The costs of carnivory. *Plos Biology*, **5**, 363–368.

Carstensen, M., Delgiudice, G.D., Sampson, B.A. & Kuehn, D.W. (2009) Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *Journal of Wildlife Management*, **73**, 175–183.

Clark, J.S., Ferraz, G.A., Oguge, N., Hays, H. & DiCostanzo, J. (2005) Hierarchical Bayes for structured, variable populations: from recapture data to life-history prediction. *Ecology*, **86**, 2232–2244.

Costa, D.P. (1993) The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposium of the Zoological Society of London*, **66**, 293–314.

Costa, D.P., Crocker, D.E., Goebel, M.E., Fedak, M.A., McDonald, B.I. & Huckstadt, L.A. (2010) Climate change and habitat selection of seals in the Western Antarctic Peninsula. *Integrative and Comparative Biology*, **50**, E34.

Dupuis, J.A. (1995) Bayesian estimation of movement and survival probabilities from capture-recapture data. *Biometrika*, **82**, 761–772.

Forcada, J., Trathan, P.N. & Murphy, E.J. (2008) Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, **14**, 2473–2488.

Forcada, J., Trathan, P.N., Reid, K. & Murphy, E.J. (2005) The effects of global climate variability in pup production of Antarctic fur seals. *Ecology*, **86**, 2408–2417.

Forcada, J., Malone, D., Royle, J.A. & Staniland, I.J. (2009) Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. *Ecological Modelling*, **220**, 1513–1521.

Fowler, S.L., Costa, D.P., Arnould, J.P.Y., Gales, N.J. & Burns, J.M. (2007) Ontogeny of oxygen stores and physiological diving capability in Australian sea lions. *Functional Ecology*, **21**, 922–935.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 170.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Goebel, M.E., Krause, D., Freeman, S., Burner, R., Bonin, C., Mercado, R.V.d, Cise, A.M.V. & Gafney, J. (2009) Pinniped research at Cape Shirreff, Livingston Island, Antarctica, 2008/09. *NOAA-TM-NMFS-SWFSC-445: AMLR 2008/2009 FIELD SEASON REPORT: Objectives, Accomplishments and Tentative Conclusions* (ed. A.M.V. Cise), pp. 38–43. Antarctic Ecosystem Research Group, Southwest Fisheries Science Center, La Jolla, USA.

Harley, C.D.G. (2011) Climate change, keystone predation, and biodiversity loss. *Science*, **334**, 1124–1127.

Hiruki-Raring, L.M., Hoef, J.M.V., Boveng, P.L. & Bengtson, J.L. (2012) A Bayesian hierarchical model of Antarctic fur seal foraging and pup growth related to sea ice and prey abundance. *Ecological Applications*, **22**, 668–684.

Horning, M. & Mellish, J.A.E. (2012) Predation on an upper trophic marine predator, the Steller sea lion: evaluating high juvenile mortality in a density dependent conceptual framework. *PLoS ONE*, **7**, e30173.

IPCC (2007) Climate Change 2007: Synthesis Report.*Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds C.W. Team, R.K. Pachauri & A. Reisinger), pp. 104. IPCC, Geneva, Switzerland.

Le Bohec, C., Durant, J.M., Gauthier-Clerc, M., Stenseth, N.C., Park, Y.-H., Pradel, R., Gremillet, D., Gendner, J.-P. & Le Maho, Y. (2008)

King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 2493–2497.

Linnell, J.D.C., Aenes, R. & Anderson, R. (1995) Who killed Bambi? The role of predation in neonatal mortality of temperate ungulates *Wildlife Biology*, **1**, 209–223.

McDonald, B.I., Goebel, M.E., Crocker, D.E. & Costa, D.P. (2012) Biological and environmental drivers of energy allocation in a dependent mammal, the Antarctic fur seal pup. *Physiological and Biochemical Zoology*, **85**, 134–147.

Noren, S.R., Williams, T.M., Pabst, D.A., McLellan, W.A. & Dearolf, J.L. (2001) The development of diving in marine endotherms: preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **171**, 127–134.

Polito, M.J. & Goebel, M.E. (2010) Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. *Journal of Experimental Marine Biology and Ecology*, **395**, 1–9.

Reisinger, R.R., de Bruyn, P.J.N. & Bester, M.N. (2011) Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward Islands: fact and fiction. *Journal of Zoology*, **285**, 1–10.

Reisser, J., Proietti, M., Kinas, P. & Sazima, I. (2008) Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endangered Species Research*, **5**, 73–82.

Rolland, V., Weimerskirch, H. & Barbraud, C. (2010) Relative influence of fisheries and climate on the demography of four albatross species. *Global Change Biology*, **16**, 1910–1922.

Schwarz, L.K. (2008) Methods and models to determine perinatal status of Florida manatee carcasses. *Marine Mammal Science*, **24**, 881–898.

Staniland, I.J., Robinson, S.L., Silk, J.R.D., Warren, N. & Trathan, P.N. (2012) Winter distribution and haul-out behaviour of female Antarctic fur seals from South Georgia. *Marine Biology*, **159**, 291–301.

Tome, D. & Denac, D. (2012) Survival and development of predator avoidance in the post-fledging period of the Whinchat (*Saxicola rubetra*): consequences for conservation measures. *Journal of Ornithology*, **153**, 131–138.

Vera, C., Vargas, R. & Torres, D. (2004) El impacto de la foca leopardo en la población de cachorros de lobo fino antártico en cabo Shirreff, Antártica, temporada 2003-2004. *Boletín del Instituto Antártico Chileno*, **23**, 19–22.

Yarkovich, J., Clark, J.D. & Murrow, J.L. (2011) Effects of black bear relocation on elk calf recruitment at Great Smoky Mountains National Park. *Journal of Wildlife Management*, **75**, 1145–1154.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Tagging and resight methods, Teeth ageing technique and sampling bias, Annual demographic rate analysis, First year pup survival, Age distribution and population projection, Sensitivity analysis, MCMC sampling

Table S1. Flipper tag deployment count by year.

Table S2. Sighting state transition probabilities.

Table S3. Resight history examples.

Table S4. Tag loss and detection probability.

Table S5. Movement probabilities.

Figure S1. Average over-winter AAO by year.

Figure S2. Pup daily detection probability.

Figure S3. Adult female daily detection probability.

Supplemental Information

Tagging and resight methods

Individually numbered plastic Dalton Jumbo Roto Tags are attached between the fore-flipper digits most proximal to the body. Individuals are initially marked with two tags but sometimes lose those tags over time. To ensure continuity in longitudinal records, every effort is made to add a new tag and replace the existing tag when a seal is observed with one tag. Counts of tagged seals are shown in Table 1.

Within the main study area, observers cover the entire area and record tag numbers at least once a day for 96-110 days (Fig. 1). After pupping begins, daily pup counts (live plus newly-dead) are also recorded. Although their degree of philopatry is unknown, once females begin pupping, their change in pupping location from year to year often varies by only several meters (Lunn & Boyd 1991), and some females pup within several meters of their own birth sites (Hoffman & Forcada 2012). Females and pups are highly visible in the open terrain, and individuals are often resighted on consecutive days (Goebel *et al.* 2001). Young of the year are not marked until late in the study period (late-January through early-March), so individual pup resights are only possible when the mother is present. Resight effort outside the main study area is not as frequent and may occur as seldom as one time per summer for relatively inaccessible colonies on the northwest coast of the Cape.

Teeth aging technique and sampling bias

Tooth age estimation was validated using 23 teeth from animals of known age, with an age range of 2 -21 years old (U.S.–AMLR, unpublished data). One hundred percent of the

validation teeth have been correctly aged from blind readings (i.e. the reader did not know the age of the animal). To ensure accuracy over time and across readers, blind readings from known-age animals are repeated whenever new teeth are processed for aging. Clarity of cementum layers indicated no error in age estimation for 94.4% of all readable processed teeth. The remaining tooth age estimates had some error, but the error was small enough ($\pm$ 1 year) compared to adult age groups, we did not include the error in analyses (U.S.–AMLR, unpublished data). For more information about the technique, see www.matsonslab.com.

Every effort was made to recapture and extract teeth of all adult females that had been tagged prior to the 2000/2001 survey period. However, such methods do not allow age estimation for the animals that were tagged in previous study periods and never seen again. Therefore, when estimating survival rates as a function of age, results prior to 2000/2001 are biased with a mode of 1.0 since there are no animals of known age that disappeared (and represent possible deaths) during that time frame. As of 2001/02, almost all animals had been aged from teeth or were of known age since they were tagged at birth. Overall, cohort year is known for 83% of tagged adult Antarctic fur seal females either through tooth layer counts or from being tagged during the birth year.

Annual demographic rate analysis

At each time step, an individual can fall into several unique categories:

1. Alive or dead (A or X)

2. Parturition or non-parturition (P or NP)

3. In study area or out of study area (I or O)

4. Adult female detected or not detected (D or ND)

5. Number of tags: 0 (tagged but lost), 1, or 2 (T0, T1, T2)

6. Pup detected or not detected (PD or PND)

Overall, the unique categories lead to 96 possible states for a given animal. However, three

simplifications based on data collection procedures for this particular Antarctic fur seal colony

and the specific questions we were interested in answering allow us to reduce the number of

feasible states to 10.

1. Alive, in the study area, detected, two tags, pup (A,I,D,T2,P)

2. Alive, in the study area, detected, two tags, no pup (A,I,D,T2,NP)

3. Alive, outside the study area, detected, two tags (A,O,D,T2)

4. Alive, outside the study area, not detected, two tags (A,O,ND,T2)

5. Alive, in the study area, detected, one tag, pup (A,I,D,T1,P)

6. Alive, in the study area, detected, one tag, no pup (A,I,D,T1,NP)

7. Alive, outside the study area, detected, one tag (A,O,D,T1)

8. Alive, outside the study area, not detected, one tag (A,O,ND,T1)

9. Alive, not detected, lost all tags (A,ND,T0)

10. Dead, not detected (X,ND)

Namely, with high, consistent observer effort and relative ease of reading tags, we assumed all

animals alive and in the main study area are detected. Next, dead animals and animals that have

lost all tags are not detected. Lastly, reproduction outside the main study area is not of concern.

Transition probabilities between states are a multiplicative combination of the

parameters: survival rate (s), reproductive rate (r), probability an animal moves in/out of the

study area (m), probability of adult female detection (d), and probability of losing one tag (g)

(Table 2). From basic probability theory, transition probabilities are multiplied together for each

time step to determine the overall probability of a sighting history. The only states in which an

animal is actually sighted are 1, 2, 3, 5, 6, and 7. When an animal is not detected in a given

season, all potential transition probabilities between unseen states are added together. In such

cases, a transition probability matrix with matrix multiplication can be used to calculate the

sighting history probability (e.g. Table 3). The sighting history probabilities provide the

foundation for a multinomial likelihood in a Bayesian setting.

$$P(\boldsymbol{n}|N, \boldsymbol{g}, \boldsymbol{d}, \boldsymbol{m}, \boldsymbol{s}, \boldsymbol{r}) = \binom{N}{n_1 n_2 \cdots n_\omega} \cdot \prod_{i=1}^{\omega} h_i^{n_i}$$

where

N = total number of tagged animals

n_i = number of tagged animals with sighting history i

h_i = probability of sighting history i (see Table 3 for examples)

ω = index representing total number of all possible sighting histories

We limited our environmental analysis of demographic rates to older age classes because

given low early survival and detection probabilities, sample sizes based on tagged pups were too

small to effectively measure annual differences in early reproductive rates. However, by age 5,

80% of reproducing females had been seen with a pup. Still, we wanted to calculate population

growth rate when older-age demographics are a function of annual environmental variability.

Females can reproduce as young as three years old, so reproductive rates were estimated for ages

three and four without interannual variability.

Tag loss and tag detection outside the study area were estimated separately for younger

and older age groups (0-4 years old vs 5+ years old). Additionally, tag detection outside the main

study area was estimated separately by the number of tags. Movement probabilities after age four

were estimated separately for the periods before and after the first observed reproductive event

and in relation to the location of that event.

First year pup survival

A pup is only identified in relation to its mother, so each sighting of a female is an opportunity to sight or resight her pup. Therefore, female-pup pairs fell in to three unique categories:

1. Pup alive or dead

2. Pup seen or not seen

3. Female seen or not seen

Dead pups are not detected, and live pups are only detected when their mothers are seen, reducing the eight theoretical female-pup states to five:

1. Pup alive, pup seen, female seen

2. Pup alive, pup not seen, female seen

3. Pup alive, pup not seen, female not seen

4. Pup dead, pup not seen, female seen

5. Pup dead, pup not seen, female not seen

Transition probabilities between states are pup survival (s), pup detection (d_p), and female detection (d_f). The probabilities are represented as vectors because they can be analyzed separately based on many different factors such as age and individual.

Females arrive at the rookery 1-2 days before parturition, and after an initial period of about seven days with their newborn pups on land, they begin to make foraging trips to sea (Goebel *et al.* 2003). The duration of those trips is variable depending on feeding conditions, with trips lasting about 3 days during favorable years and up to 7 days during poor years (Goebel *et al.* 2008). Each period back on land to nurse the pup lasts about 1.5 days, with longer nursing periods during good years (Goebel *et al.* 2008). Even if a pup dies, the mother will continue to

forage and periodically return to the rookery (Goebel *et al.* 2008). Pup mortality may consist of

two peaks associated with (1) females first returning to sea when young pups are more

vulnerable to weather conditions and (2) soon after pups start entering the water at about one

month of age when they are naïve to leopard seal predation (Goebel *et al.* 2008).

Individual sighting probabilities allowed for individual differences in foraging strategies

and other behaviors that may affect detection probability, including a difficult-to-access pupping

location. Estimating sighting probabilities separately by pup status (dead or alive) allowed for

differences in female foraging and sighting probabilities under those two conditions.

Hyperparameters were two parameters of a beta distribution.

$$p(\pmb{x}|\alpha_x, \beta_x) = \prod_{i=1}^{I} \frac{\Gamma(\alpha_x + \beta_x)}{\Gamma(\alpha_x)\Gamma(\beta_x)} x_i^{\alpha_x - 1}(1 - x_i)^{\beta_x - 1}$$

where

$\pmb{x} = s_a$, d_{fi}|pup dead, or d_{fi}|pup alive

i = age or individual

I = maximum age or total number of individuals

For all hierarchical analyses we chose a diffuse hyperprior joint density of $p(\alpha, \beta) =$

$(\alpha + \beta)^{-5/2}$ (Gelman *et al.* 2004). The hierarchical approach produced daily survival rate

estimates closer to the hyperdistribution mean estimate which reduced uncertainty for ages with

smaller sample sizes i.e. later in the season. The hierarchical approach on individual detection

accounts for individual variation in detection while still reducing uncertainty for individuals that

were first detected later in the season and thus have fewer days from which to sample detection.

Analyses were conducted separately for each summer study period to account for differences in

annual foraging success that would affect the female's proportion of time on land and, thus, her detection probability.

Age distribution and population projection

Assuming a 50:50 ratio, annual pup counts were divided by two to determine annual female pup counts. Given annual pup counts, we assumed the population was relatively stable from 1986/1987 to 1997/1998 and increasing at 8.5 % per year (Hucke-Gaete *et al.* 2004). Lastly, we assumed the relationship between AAO and adult rates held from 1997/1998 to 2009/2010, and leopard seal predation was not prevalent until 1998/1999. Therefore, starting age distribution in 1997/1998 was based on the 1997/1998 pup count, the highest estimated first year survival rate from 2006 (0.73 (0.38, 0.92)), survival rate ages 2-4 pooled for all years, and all other rates estimated using the 1997 AAO (-0.17).

For future years, annual first year survival estimates were randomly drawn from posterior samples of high survival rates based on daily survival rates, pooled for all four years. Low survival rates were either posterior samples of rates measured from annual mark-recapture analysis adjusted to account for the first 75 days (1998-2003) or annual estimates from daily rates (2004-2008), or first year survival pooled for all years (2009). Adjustments to first year survival based on annual mark-recapture models were made by multiplying mark-recapture survival estimates (75 days to one year) with a random sample of survival estimates from birth to 75 days old based on daily resight analysis pooled for all years. In the case of low first year survival, the first few cohorts who become first time breeders in the first few years have higher recruitment than cohort 1998/1999 and later. Annual adult (> 4 years old) survival and reproductive rate estimates were calculated as a function of AAO. To isolate the effects of low and high first year survival from uncertainty in juvenile survival, rates for age classes two

through four were set constant at the modal value of those estimates for that year. If annual

juvenile rates were not available, they were held constant at 0.93, the modal value when pooling

all years. Variability in all other rates was included in the projections. However, reproductive

rates for age classes three and four were estimated by pooling all years and did not vary annually.

Counts in each age class were multiplied by the appropriate annual survival and reproductive

rates to estimate annual pup counts and age distributions for the next year. I.e., individual

stochasticity was not accounted for. The process was repeated through 2009/2010.

Sensitivity analysis

To investigate differences in the sensitivity of population growth rate to different values

of AAO and first year survival, two years with relatively high and low values of AAO were

chosen (2002: -0.831 and 2001: 0.614) where all demographic rates were either measured or

estimated from AAO values. Survival rates ages two through four were measured from annual

resights. High first year survival is from pooled high estimates based on daily survival rates (0.56

(0.15,0.90)). Low first year survival was measured from annual mark recapture analyses in 2001

for high AAO and 2002 for low AAO (Fig. 3) with adjustments to account for pups lost prior to

75 days old. Adjustments were made by multiplying mark-recapture survival estimates (75 days

to one year) with a random sample of survival estimates from birth to 75 days old based on daily

resight analysis pooled for all years. Reproductive rates for age classes three and four were

measured from annual mark-recapture pooling all years and did not vary between sensitivity

cases. Uncertainty in all demographic rates was incorporated in to the analysis.

MCMC sampling

Simulations were set for a rejection rate near 0.7, a subsampling (thinning) of 1 in 150,

and a burn-in period of 150, continuing for a subsample size of 15,000 (Cowles & Carlin 1995).

The resulting lag-1 autocorrelations were < 0.1, and independent chains with different parameter starting values gave indistinguishable results. To verify convergence and stationarity within the final chains, we used the Heidelberger and Welch convergence diagnostic available from the CODA package in R using standard 10% increments and $p \leq 0.05$ (Heidelberger & Welch 1983; Plummer *et al.* 2006).

References

Cowles, M.K. & Carlin, B.P. (1995) Markov Chain Monte Carlo diagnostics: A comparative review. *Journal of the American Statistical Society,* **91,** 883-904.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis, 2nd Edition,* 2nd edn. Chapman and Hall/CRC, New York, NY.

Goebel, M.E., McDonald, B.I., Freeman, S., Haner, R.G., Spear, N.B. & Sexton, S.N. (2008) Pinniped research at Cape Shirreff , Livingston Island, Antarctica, 2007/08. *NOAA-TM-NMFS-SWFSC-427: AMLR 2007/2008 FIELD SEASON REPORT: Objectives, Accomplishments and Tentative Conclusions* (ed. A.M.V. Cise), pp. 120-132. Antarctic Ecosystem Research Group, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California, USA 92037.

Goebel, M.E., Rutishauser, M.R., Parker, B., Banks, A., Costa, D.P., Gales, N. & Holt, R.S. (2001) Pinniped research at Cape Shirreff, Livingston Island, Antarctica, 1999/2000. *NOAA-TM-NMFS-SWFSC-302: AMLR 1999/2000 FIELD SEASON REPORT: Objectives, Accomplishments and Tentative Conclusions* (ed. J.D. Lipsky), pp. 118-136. Antarctic Ecosystem Research Group, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California, USA 92037.

Goebel, M.E., Vallejos, V.I., Trivelpiece, W.Z., Holt, R.S. & Acevedo, J. (2003) Antarctic fur seal pup production in the South Shetland Islands. *NOAA-TM-NMFS-SWFSC-350: AMLR 2001/2002 FIELD SEASON REPORT: Objectives, Accomplishments and Tentative Conclusions* (ed. J.D. Lipsky), pp. 139-152. Antarctic Ecosystem Research Group, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California, USA 92037.

Heidelberger, P. & Welch, P.D. (1983) Simulation run length control in the presence of an initial transient. *Operations Research (INFORMS),* **31,** 1109-1144.

Hoffman, J.I. & Forcada, J. (2012) Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazella*). *Mammalian Biology,* **77,** 71-73.

Hucke-Gaete, R., Osman, L.P., Moreno, C.A. & Torres, D. (2004) Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica. *Polar Biology,* **27,** 304-311.

Lunn, N.J. & Boyd, I.L. (1991) Pupping site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy,* **72,** 202-206.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News,* **6,** 7-11.

Table S1. Number of newly tagged (not

retagged) Antarctic fur seals by age and

survey season.

Survey season	Adult females	Pups (fem, mal, unk)
1997/98	36	504 (232,248,20)
1998/99	52	500 (244,256,0)
1999/00	100	500 (251,246,2)
2000/01	34	499 (266,232,1)
2001/02	40	499 (262,237,0)
2002/03	40	499 (267,232,0)
2003/04	33	499 (245,254,0)
2004/05	31	497 (265,231,1)
2005/06	12	495 (251,244,0)
2006/07	12	500 (238,261,1)

Table S2. Transition probabilities between sighting states (p_{ij}, where i = state at time t, and j = state at time $t + 1$). See text for definitions of states and probabilities.

From (i)	To (j)									
	1	2	3	4	5	6	7	8	9	10
1	$a(1\text{-}m)r$	$a(1\text{-}m)(1\text{-}r)$	amd_0	$am(1\text{-}d_0)$	$b(1\text{-}m)r$	$b(1\text{-}m)(1\text{-}r)$	bmd_0	$bm(1\text{-}d_0)$	sg^2	$1\text{-}s$
2	$a(1\text{-}m)r$	$a(1\text{-}m)(1\text{-}r)$	amd_0	$am(1\text{-}d_0)$	$b(1\text{-}m)r$	$b(1\text{-}m)(1\text{-}r)$	bmd_0	$bm(1\text{-}d_0)$	sg^2	$1\text{-}s$
3	amr	$am(1\text{-}r)$	$a(1\text{-}m)d_0$	$a(1\text{-}m)(1\text{-}d_0)$	bmr	$bm(1\text{-}r)$	$b(1\text{-}m)d_0$	$b(1\text{-}m)(1\text{-}d_0)$	sg^2	$1\text{-}s$
4	amr	$am(1\text{-}r)$	$a(1\text{-}m)d_0$	$a(1\text{-}m)(1\text{-}d_0)$	bmr	$bm(1\text{-}r)$	$b(1\text{-}m)d_0$	$b(1\text{-}m)(1\text{-}d_0)$	sg^2	$1\text{-}s$
5					$c(1\text{-}m)r$	$c(1\text{-}m)(1\text{-}r)$	cmd_0	$cm(1\text{-}d_0)$	sg	$1\text{-}s$
6					$c(1\text{-}m)r$	$c(1\text{-}m)(1\text{-}r)$	cmd_0	$cm(1\text{-}d_0)$	sg	$1\text{-}s$
7					cmr	$cm(1\text{-}r)$	$c(1\text{-}m)d_0$	$c(1\text{-}m)(1\text{-}d_0)$	sg	$1\text{-}s$
8					cmr	$cm(1\text{-}r)$	$c(1\text{-}m)d_0$	$c(1\text{-}m)(1\text{-}d_0)$	sg	$1\text{-}s$
9									s	$1\text{-}s$
10										1

$a = s(1\text{-}g)^2$
$b = 2sg(1\text{-}g)$
$c = s(1\text{-}g)$

$p_{11} = s(1\text{-}g)^2(1\text{-}m)r$

Table S3. Examples of sighting histories and their

respective probabilities given five study

periods. See text for state definitions.

Sighting history	Probability
125_r21^*	$p_{12}p_{25}p_{12}p_{21}$
12021	$p_{12}p_{24}p_{42}p_{21}$
11000	$\sum p_{11}\boldsymbol{V}_{148910}\boldsymbol{M}_{48910}\,\boldsymbol{M}_{48910}$
16000	$\sum p_{16}\boldsymbol{V}_{68910}\boldsymbol{M}_{8910}\,\boldsymbol{M}_{8910}$

*: 5_r is an animal that was retagged with two
tags after a sighting with one tag.

Where

$$\boldsymbol{V}_{148910} = \begin{bmatrix} p_{14} & p_{18} & p_{19} & p_{110} \end{bmatrix}$$

$$\boldsymbol{M}_{48910} = \begin{bmatrix} p_{44} & p_{48} & p_{49} & p_{410} \\ 0 & p_{88} & p_{89} & p_{810} \\ 0 & 0 & p_{99} & p_{910} \\ 0 & 0 & 0 & p_{1010} \end{bmatrix}$$

$$\boldsymbol{V}_{68910} = \begin{bmatrix} p_{68} & p_{69} & p_{610} \end{bmatrix}$$

$$\boldsymbol{M}_{8910} = \begin{bmatrix} p_{88} & p_{89} & p_{810} \\ 0 & p_{99} & p_{910} \\ 0 & 0 & p_{1010} \end{bmatrix}$$

Table S4. Statistics of marginal posterior distributions of annual probability of

one tag loss and detection probability outside the main study area for

juvenile and adult females. Values are means with 95% credible intervals

in parentheses.

Probabilities	Juvenile (1-4 yo)	Adult (5+ yo)
Tag loss	0.092 (0.069,0.118)	0.027 (0.021,0.033)
Detection outside main study area		
One tag	0.044 (0.017,0.085)	0.495 (0.323, 0.670)
Two tags	0.029 (0.014,0.049)	0.737 (0.622,0.841)

Table S5. Annual movement probabilities in and out of the area where a female is first

observed pupping before and after the 1st observed reproductive event.

Numbers are means with 95% credible intervals in parentheses.

Probabilities	Unknown reproductive status (5+ years old)	After 1st observed pup
Move out of pupping area	0.162 (0.055,0.318)	0.025 (0.017,0.035)
Move into pupping area	0.695 (0.537,0.832)	0.256 (0.144,0.386)
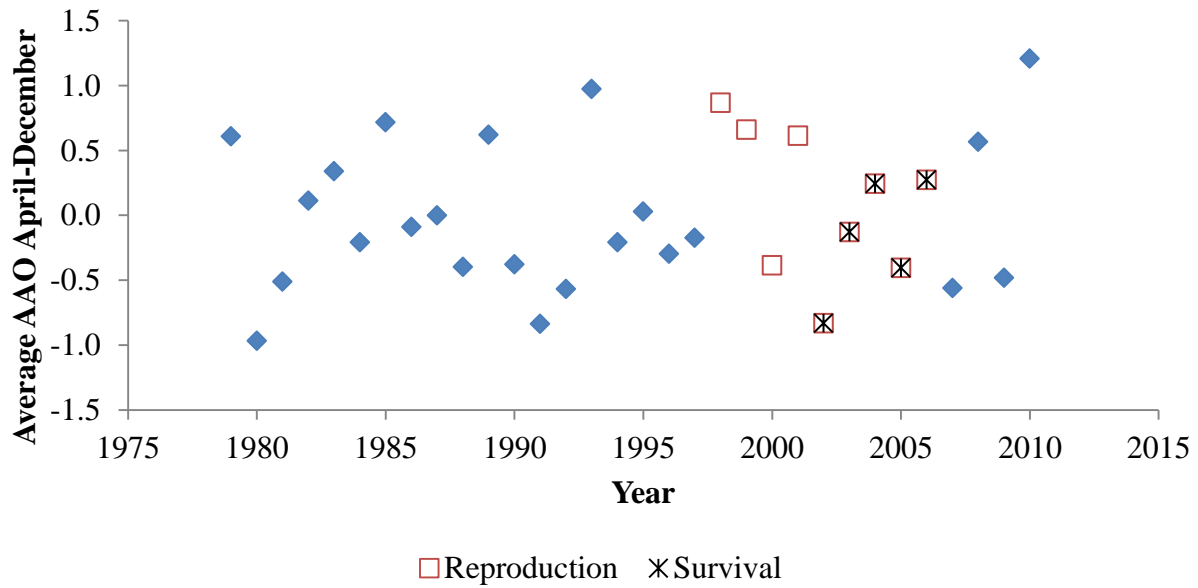
Figure S1. Average over-winter AAO by year. Mark-recapture reproductive rates were measured in years 1998 – 2006 (red boxes) and survival rates were measured in years 2002 – 2006 (black stars).
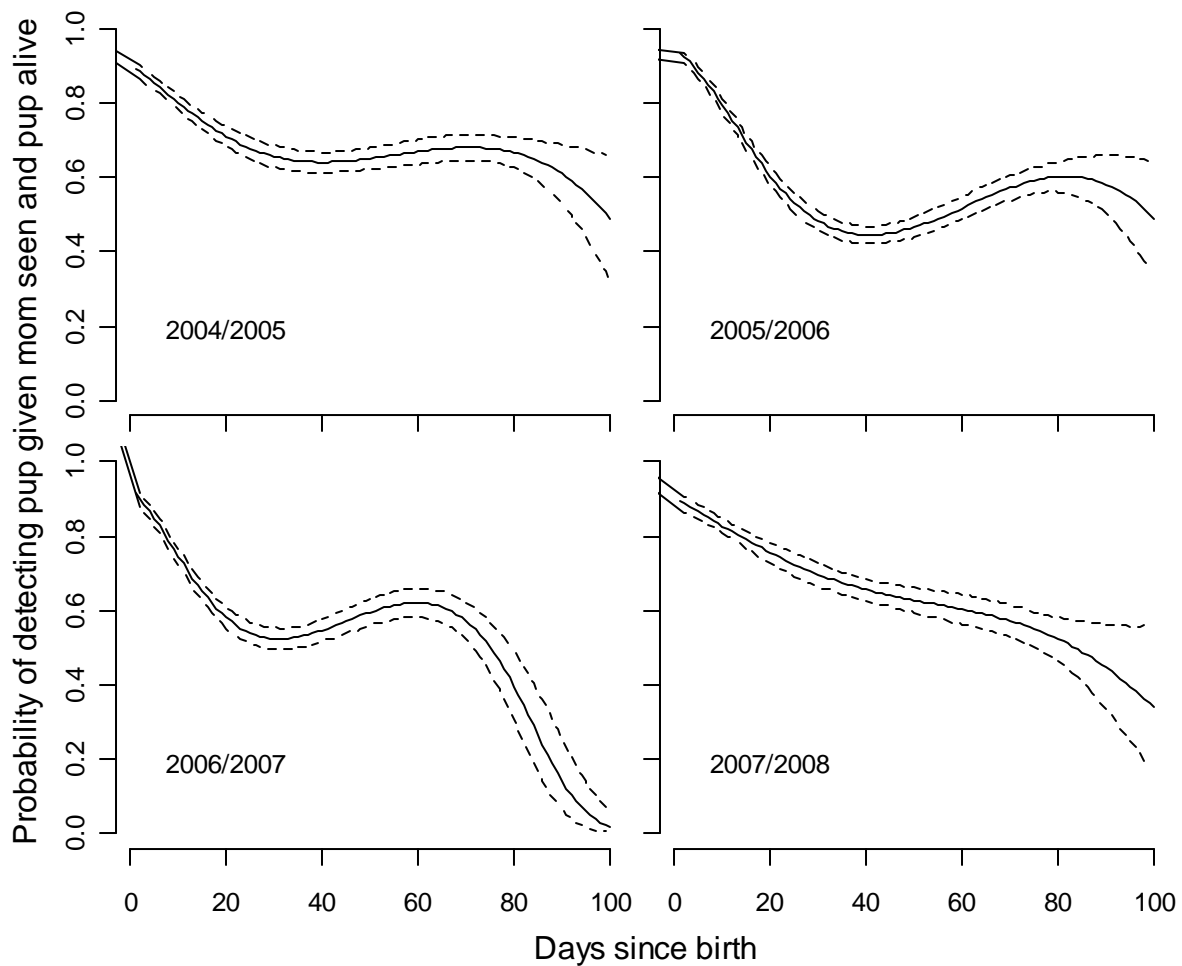
Figure S2. Detection probability of a pup given the mother was seen and given the pup was alive by pup

age and survey year. Solid lines are means and dashed lines are 95% posterior intervals calculated

from posterior samples of a cubic-logit function of pup age. During all survey seasons except

2007/2008, pup detection was highest just after birth, declined with pup age until about

30 days old, and then increased and peaked again between 60 and 80 days old before
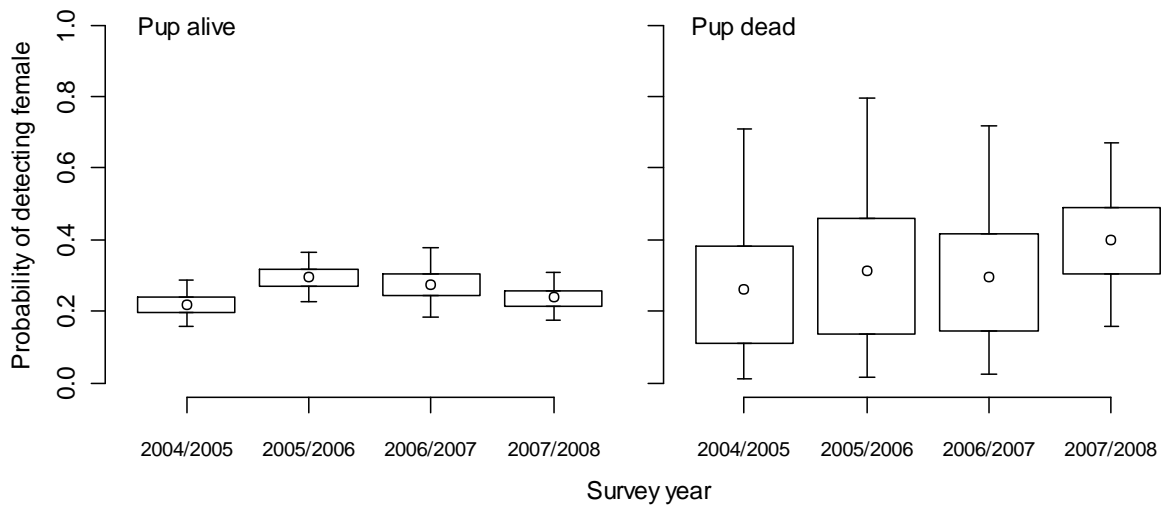
once more declining.

Figure S3. Probability of detecting a female conditional on pup status (alive or dead) by survey year. Points are means. Boxes are quartiles, and whiskers are 95% posterior intervals from posterior samples of the parameters of a hierarchical beta distribution. Detection of females was more variable after their pups had died, but variability in female detection probability between years was not high.