

The population trend of southern elephant seals (*Mirounga leonina* L.) at Macquarie Island (1952–2004)

John van den Hoff · Harry Burton ·
Ben Raymond

Received: 28 September 2006 / Revised: 5 April 2007 / Accepted: 9 April 2007 / Published online: 14 June 2007
© Springer-Verlag 2007

Abstract Total numbers of adult female southern elephant seals (cows) breeding at Macquarie Island were determined for 19 of the 52 year period between 1952 and 2004. Totals for 1952–1987 (exc. 1959 and 1985) were estimated from the relationship between censuses of the isthmus study area and concurrent censuses for the whole island. Totals for 1987–2004 were obtained by direct census of the entire island in mid-October. Cow numbers decreased from a maximum of about 40,000 in the 1950s to a minimum of 18,300 in 2000, but then increased slightly to 19,200 in 2004. Nonlinear and post-hoc linear analysis of the count data identified 1999 as the year when the exponential rate of change (r) slowed from -1.4% per annum to near zero. The rate of change was not uniform for each census sub-area counted (1987–2004), suggesting that certain terrestrially based density-dependent mechanisms were influencing the annual distribution of cows.

Keywords Long-term study · Rate of increase · GAM · Non-linear · Antarctica · Sub-Antarctic

Introduction

Monitoring population change is an integral part of effective conservation-oriented research and management (Thomas 1996). Population data provide information on population viability (DeSante and Rosenberg 1998), the quality of the environment upon which that population relies for its food, and whether the population is being

influenced by habitat changes (Croxall et al. 1992). For example, the reproductive capacity of a population is negatively affected by reduced food availability because individuals reach sexual maturity later, if at all, and also they may be unable to obtain sufficient body reserves for successful reproduction. Monitoring population change can be also very useful for understanding and predicting the effects of environmental variability and especially where climate change in the Southern Ocean is affecting the resident species (Barbraud and Weimerskirch 2001).

Southern elephant seals (*Mirounga leonina* Linn.) are upper trophic level predators in the Southern Ocean marine food web, preying principally upon fish and squid but also taking some euphausiids should they occur in sufficient densities (van den Hoff et al. 2003). At Macquarie Island, their populations were reduced as a result of being hunted for their oil-rich blubber in the late eighteenth and early nineteenth centuries, and recovery since the closure of the industry appeared to have taken place by the 1950s (Carrick et al. 1962). However, dramatic decreases in southern Indian and Pacific Ocean populations followed (Hindell and Burton 1987; Pistorius et al. 1999). Between 1959 and 1985 the Macquarie Island population decreased by 45–55% at an overall rate of approximately 2.1% per annum (Hindell and Burton 1987), and this negative trend appears to have continued in more recent times (McMahon et al. 2005a, b). Such rapid and dramatic reductions in the number of breeding females in a population can have serious consequences for the future viability of that population. As a result of this continued decrease, the species has been listed as vulnerable under the Australian Environment Protection and Biodiversity Conservation Act 1999.

We have applied a nonlinear regression approach to analysing the long-term (52 years between 1952 and 2004) census data for southern elephant seals at Macquarie

J. van den Hoff (✉) · H. Burton · B. Raymond
Australian Antarctic Division, 203 Channel Highway,
Kingston, TAS 7050, Australia
e-mail: john_van@aad.gov.au

Island. Our aims were (1) to detect significant changes in the population trend over time, (2) to compare intrinsic rates of change (r) between intra-island census areas, and (3) to examine sources of count error and calculate correction factors for any observed biases.

Materials and methods

Data collection

Elephant seals are a highly sexually dimorphic and polygynous species. At Macquarie Island, beach-master males control breeding aggregations (harems) of up to 800 cows. Such large aggregations make direct counts of young elephant seal pups impractical as they are easily hidden amongst the breeding females (hereafter termed “cows”). Therefore we chose cows as our major census unit. Hindell and Burton (1987) have shown that it is possible to obtain robust estimates of cows during census periods and from other studies (McCann 1985; Hindell and Burton 1987) we know that the annual breeding haulout pattern of cows is consistent and predictable (below).

Two monitoring periods occurred over 52 years at Macquarie Island:

1. 1952–1987. Breeding season censuses of cows were undertaken at the isthmus study area (Fig. 1) on known dates in October of most years. Two whole island counts were undertaken between the 6 and 17 October 1959 and the 9 and 15 October 1985.
2. 1988–2004. Near-daily breeding season censuses of cows, dead pups and weaned pups were made annually at the isthmus study area; and a complete island census (including the isthmus area) was conducted as near to October 15 as was practicable. Harem cows were counted at least twice by two or more observers and the mean was used. If individual counts differed by more than 5%, further counts were undertaken until the estimates were within 5% of each other. Usually only a single count by each observer was required.

Sources of count variability and bias

The annual breeding season haulout pattern for cows at Macquarie Island has been shown to follow a Gaussian curve (Press et al. 1988) with the peak haulout day around the 15 of October (Hindell and Burton 1987). This general curve shape has also been shown to describe the haulout pattern for cows at Signy Island (Laws 1956), Marion Island (Condy 1979) and Heard Island (Slip and Burton 1999). Other mathematical distributions can also be fitted to the haul-out data (Rothery and McCann 1987) but they

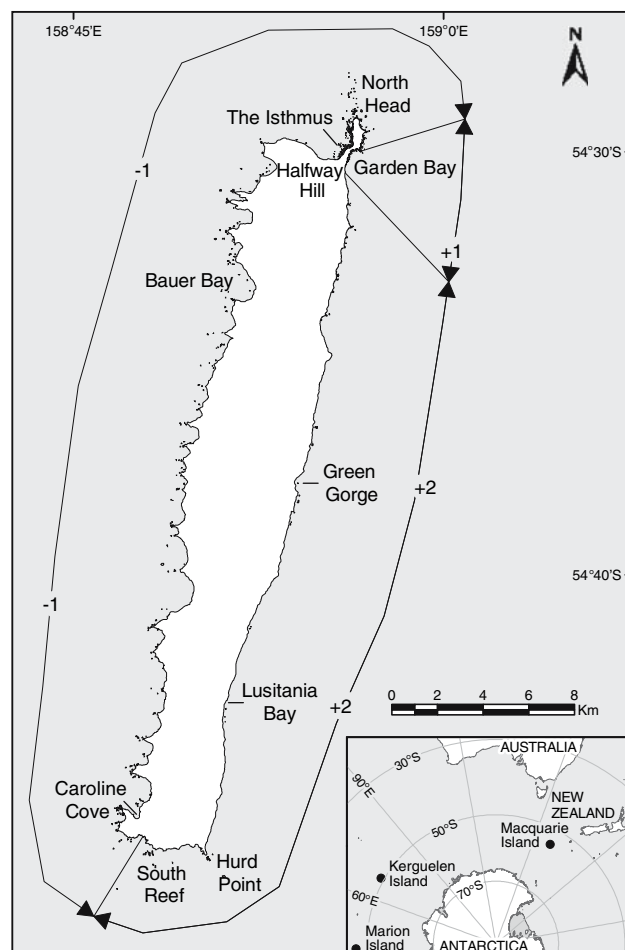


Fig. 1 Map showing the differences in peak haul-out timing (with reference to Oct 15) of adult female southern elephant seal (*Mirounga leonina*) within contiguous zones around Macquarie Island. *Inset* Location of Macquarie Island in the Southern Ocean

offer no advantages over the Gaussian model when count corrections are required (Slip and Burton 1999).

The Gaussian curve provides:

1. A prediction for the maximum number of cows that might be expected to be ashore on any particular day between 1 September and the 30 November.
2. Estimates of count error (the residuals between the observed and the predicted count).
3. A prediction of the peak haulout day.
4. Defined curve widths that can be used as a measure of the length of the breeding season.

We used a Levenberg–Marquardt algorithm (LMA) to determine if the peak haulout day for cows varied around the island. Census sub-areas were centered upon field huts at Green Gorge (1985, 1996, 1997, 1998 and 2000), Bauer Bay (1962, 1964, 1997 and 2000), Hurd Point (1996 and 1997) and Caroline Cove (1985, 1998 and 2000; Fig. 1). The LMA-predicted peak haulout day was used to correct

counts that were undertaken on either side of the peak day within each island sector (Fig. 1).

Maximum cow numbers ashore on the peak day alone do not equate to the total number of cows pupping in a particular breeding season because some cows have abandoned their pups or early arrivals (earlier than the 22 September) have already weaned their pups (McCann 1985). Cows that had either lost or weaned their pup usually left the island within two days (Australian Government Antarctic Division, unpublished data). We estimated the proportion of cows that had departed by counting dead pups and live weaned pups during the annual censuses. Pup mortality in elephant seal harems is difficult to assess with accuracy and our counts are therefore likely to be underestimates as some pups may be either pressed into the beach sand as breeding adults move about, scavenged by giant petrels (*Macronectes* sp.) or skuas (*Catharacta* sp.), washed away in storm conditions, or simply missed during the census. From 1988 to 2004 we made attempts to recover dead pups from the harems so our estimates of pup mortality were not confounded by dead pups being counted more than once. We assumed that each dead or weaned pup we counted represented a single cow that had already departed from the island (McCann 1985) because twinning in southern elephant seals is rare (McMahon and Hindell 2003a). The sum of cows, dead pups and weaned pups approaches an asymptote just after the peak cow haul-out (McCann 1985; Hindell and Burton 1987) and that asymptote represents the total pup production (total cow numbers) for the year.

A complete island census was not conducted in each year of this study. Therefore we developed linear regression models to estimate total island numbers from counts made at the isthmus study area only. Both the isthmus and the complete island were counted on nineteen of the 28 census years. The number of breeding females was multiplied by 3.15 to estimate the total elephant seal population excluding pups of the year (Pistorius et al. 1999).

Rates of population change

The instantaneous rate of population change (r), also known as the intrinsic rate of change, was determined as follows (Caughley 1977):

$$r = (\ln N_t - \ln N_0)/t,$$

where

r intrinsic rate of change
 $\ln N_t$ natural logarithm of the population size at time t
 $\ln N_0$ natural logarithm of the population at starting time
 t time interval between population counts

Assumptions (Gotelli 2001) underlying the model from which r is derived include:

1. The population of female southern elephant seals at Macquarie Island is closed and changes in numbers depend only on variation in birth and death rates. At Macquarie Island immigration and emigration are close to zero (van den Hoff 2001).
2. Resources are unlimited such that birth and death rates are constant. However, climate fluctuations influence ecological processes (Stenseth et al. 2002) such that food resources can be patchy and/or variable in availability.
3. The population has a stable age structure. Age-structure stability for the Macquarie Island population is not known at present (Australian Government Antarctic Division, unpublished data).

The value r can also be determined from the slope of the regression line between the log-transformed counts against time, and is a measure of the per capita rate of population change (the difference between the instantaneous birth and death rates). A positive r -value indicates that births had exceeded deaths.

Our count data were log-transformed to remove heteroscedasticity (variance in the uncertainty of the points). Linear models of log-transformed counts will fit a simple exponential curve to population data but nonlinear analysis has the potential to detect more complex change (Dennis et al. 1995); and therefore we fitted both a linear regression and a generalized additive model to the log-transformed count data. Generalized additive models (GAMs; Hastie and Tibshirani 1990) provide a model response that varies smoothly over time, without imposing any particular shape constraints on that smooth response (as would be the case with, for example, a quadratic model). The smoothness of the curve can be varied by adjusting the parameters of the GAM fitting algorithm, allowing a range of curves of differing smoothness to be fitted to the same data. Linear regression is a special case of the GAM framework, representing the smoothest end of the smoothness continuum. We used the default setting of the GAM fitting routine (as provided by the *mgcv* package for R) that estimates the appropriate smoothness using a generalized cross validation procedure (Hastie and Tibshirani 1990). We also explored the effect of manually setting the smoothness parameters of the GAM curves (by setting the degrees of freedom allocated to the smoothing function), but found that the results were consistent across a range (2–6 degrees of freedom) of smoothness choices. For clarity we present those results obtained by generalized cross validation. We used a Monte Carlo approach to estimate the confidence interval of the GAM regression fit. This approach involved

the use of a number of replicates ($n = 999$) of the original data, each with a random perturbation of up to 5% of the count value, representing the likely errors in the original count data. A GAM was fitted to each of these replicates, giving 1000 estimates of the modelled population counts in each year (including the original fit). The 5 and 95% confidence limits for each year were then calculated from the 5th and 95th percentiles of the fitted values for each year. We estimated the second derivative of the population curve fitted by the GAM and used this to find years in which there were significant changes in the rate of change of abundance (Fewster et al. 2000). Population counts are usually modeled in GAM frameworks using a Poisson distribution and a log link function, as the Poisson distribution is well suited for integer (count) data. For ease of comparison to previous work we used log-transformed data with a Gaussian distribution and identity link function; but we noted that with a Poisson distribution we obtained the same findings as those presented here.

Models were fitted using log-transformed data but fitted values were back-transformed so that the results could be graphically displayed as count data. Analyses were performed with STATISTICA (Statsoft, Oklahoma, USA) and R (Department of Statistics and Mathematics, Wein, Austria). Probability values (P) ≤ 0.05 were considered statistically significant.

Results

Potential sources of count variability

Ground count variability

This error should have a maximum value of five percent (5%) as that was the acceptable pre-determined count difference above which a recount was initiated. Counts ($n = 49$) from varying harem sizes, spread over 3 years and comparing the most extreme counts of two to four people showed no tendency for consistent positive or negative bias (mean = 4.03%, coefficient of variation (CV) = 0.017).

Harem size did not influence the CV between duplicate counts in harems containing <50, 51–100, 101–150, 151–200 and >200 cows ($F_{4, 44} = 0.49$, $P = 0.74$, mean CV = $2.57 \pm 0.46\%$).

Model estimation of cow numbers

(a) *Levenberg-Marquardt algorithm* Percent differences between the observed cow numbers and LMA (predicted) values were at their largest when cow numbers were lowest. The mean difference between the predicted and the

observed peak cow numbers for the years 1988–2004 was 2.74% (95% confidence limits –3.56% and +1.51%).

(b) *Linear regression* Prior to 1988 (apart from 1959 and 1985) the annual cow maxima for the whole island could only be determined from linear regression relationships between the corrected (for peak haulout date) numbers of cows on the isthmus against the corrected number of cows ashore on the whole island (Fig. 2). The regression used 19 years (1959, 1985, and 1988–2004) of concurrent isthmus and whole island data, was highly significant ($P < 0.001$), and had a strong ($R^2 = 0.82$) correlation coefficient (Fig. 2; Equation: Whole island estimate = $-11,478 + 10.7857 \times$ isthmus count; $F_{1,17} = 77.04$, SE of the estimate $\pm 2,222$ cows).

Count bias

From counts of pup mortality and pre-census weaning we estimated the mean annual percentage of cows that had departed the island prior to the cow census was 6.1% (SE $\pm 4.8\%$, range 4.6–8.6; Table 1).

Count corrections

Cow numbers peaked on the island's west coast study areas significantly earlier (2–3 days) than harems on the east coast (all t -test P -values for west vs. east harems < 0.026). The peak dates were: isthmus west side, Bauer Bay and Caroline Cove on the 14 October; isthmus east side 16th October and Green Gorge and Hurd Point 17 October (Fig. 1).

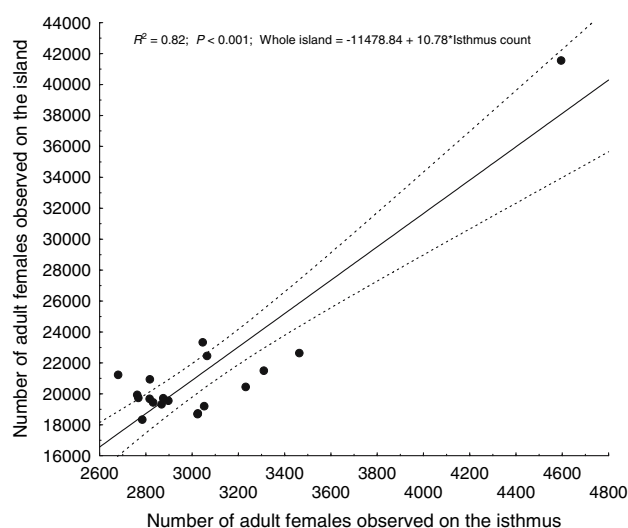


Fig. 2 Relationship between the number of female southern elephant seals ashore on the isthmus and on the whole island. The dotted lines are the 95% confidence limits for the regression

Table 1 Counts and means of adult females (cows), and dead and weaned southern elephant seal (*Mirounga leonina*) pups recorded in harems surveyed at the Macquarie Island isthmus study area (1989–1996)

Year	1989	1990	1991	1992	1993	1994	1995	1996	Mean	SE
Cows	3,080	2,925	2,583	3,178	3,222	2,599	2,822	2,859	2,909	85.80
Pups	113	103	31	59	49	45	47	58	63.13	10.30
Percentage	3.67	3.52	1.20	1.86	1.52	1.73	1.67	2.03	2.15	0.03
Weaners	160	105	100	132	157	100	98	73	115.62	10.92
Percentage	5.19	3.59	3.87	4.15	4.87	3.85	3.47	2.55	3.94	0.29

SE standard error

Thus the island could be divided into three census sub-areas for peak day correction (Fig. 1):

1. The west coast between Garden Bay (inc. North Head) and South Reef.
2. The east isthmus between Garden Bay and Halfway Hill.
3. The east coast between Halfway Hill and South Reef.

Correction factors for counts undertaken on either side of the peak day are shown in Table 2.

There was no significant relationship between the numbers of cows hauled out on the isthmus and variation in the peak haulout date itself ($F_{1,17} = 0.59$, $P > 0.25$); nor was there a relationship between the width of the fitted normal curve and the peak date ($F_{1,17} = 1.01$, $P > 0.25$), i.e. there was no effect of the length of the breeding season on the peak haulout day.

Population number and trend

The estimated maximum number of cows ashore on Macquarie Island decreased from about 46,000 in 1952 to about 19,000 in the late 1990s and early 2000s (Fig. 3). The most recent complete whole island census was conducted in mid-October 2004 when the estimated maximum number of cows was 19,203, which, after accounting for cows that had departed, equates to 20,374 pups born for that breeding season. The total southern elephant seal population at Macquarie Island for 2004 was estimated at 64,180 seals ($20,374 \times 3.15$) in all age classes older than pups of the year.

The intrinsic rate of change (r) in cow numbers was positive on 9 of the 28 census occasions and negative on 17. A linear regression model fitted to the log transformed counts showed a significant ($F_{1,26} = 226.69$, $P < 0.001$) per-annum decrease of -1.95% . If unchecked, such a population can be expected to halve every 35 years ($0.6931/0.0195$, Caughley 1977, p. 52).

The scatter of the plotted data and the linear fit suggested that a nonlinear model may be appropriate, as the data are consistent with an upturn in population since about 2000. A generalized additive model using smoothing splines was found to give a significantly better fit than one

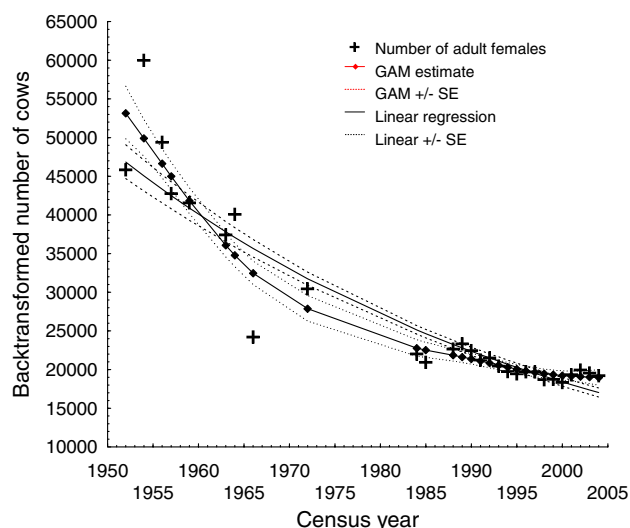


Fig. 3 Numbers of female southern elephant seals ashore on Macquarie Island, 1952–2004. GAM general additive model. SE standard error

restricted to linear, suggesting that the long-term population data do not follow a simple exponential trend (residual deviance test (RDT); $F_{3,23} = 5.77$, $P = 0.0042$; Fig. 3). Analysis of the recent continuous data (1988–2004; Fig. 4) also showed that a nonlinear GAM fitted the count data significantly better than the linear model (RDT; $F_{3,12} = 12.985$, $P < 0.0001$). Bootstrap analysis of the second derivative of the GAM fit (sensu Fewster et al. 2000) indicated that the years 1999 and 2000 showed significant upturns in the rate of change of the population. Post-hoc analysis of the regression slope for the 1988–2004 period showed the average annual r for the years 1988–1999 was -2.1% and for 1999–2004 the trend was barely positive at 0.099% and not significantly different to zero ($F_{1,4} = 2.465$, $P = 0.191$).

Intra-island trend

Cow counts were made between specified geographic land marks from 1985 to 2004 (Fig. 1), thus allowing

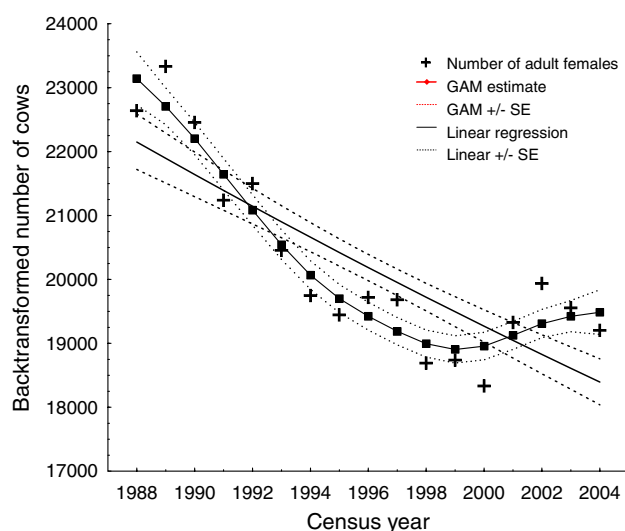


Fig. 4 Numbers of female southern elephant seals ashore on Macquarie Island 1988–2004. *GAM* general additive model. *SE* standard error

intra-island comparisons of r . Intrinsic rates of change (the slope of the regression) were not uniform between island sections. For example, Table 3 shows that the r value for the west coast between Bauer Bay and South Reef was positive ($r = +0.86\%$), but the east coast sector between Hurd Point and Green Gorge was negative ($r = -2.24\%$). The rates of change differed between island sub-areas (Table 3).

Discussion

Gathering sufficient time-series data to undertake accurate analyses of long-term population abundance data for long-lived, annual-breeding organisms is essential when considering the implementation of management and conservation practices. The Macquarie Island elephant seal population has been monitored over a 52 year period, and with the use of a GAM, we found that the population trend has recently changed from a long-term and steep decrease to one of relative stability. This finding suggests that seal numbers at the island are approaching a state where the marine and terrestrial resources promoting population growth can once again take effect. Under these circumstances the southern elephant seal population at Macquarie Island has the capacity for positive intrinsic increase. This was not the case reported by McMahon et al. (2005b), who suggested that the population still had an overall negative capacity for increase.

We also found the overall rate of population change (r) at Macquarie Island (1985–2004) differed significantly between census sub-sectors, a situation also reported at Kerguelen Island (van Aarde 1980; Bester and Lengart

1982). There were years (e.g., 1995, 1999) when the number of cows in one census area decreased as another increased, suggesting that the breeding fidelity of the cows is flexible. Continued monitoring of this population is essential to further understand how the elephant seal population at Macquarie Island may respond to uncertain food availability which could be magnified by global climate variability and future change. Future counts of the population should ideally survey the whole island, and thereby maintain the already established level of accuracy in preference to the decreased accuracy and sensitivity to change that reduced island coverage would introduce.

Data management

As with other studies of southern elephant seal population trends our census units were adult female seals (cows) and the cows hauled out in a consistent and predictable breeding season haulout pattern (McCann 1985; Hindell and Burton 1987; Slip and Burton 1999). During the breeding season at Macquarie Island, cows assembled into harems that contained between 3 and 800 individuals. Such large groupings can make accurate counting very difficult. However, with repeated counting, harem size did not influence count accuracy between harems containing 9–> 200 cows.

The average percentage difference between repeated harem counts was 4.03%. This is higher than that (1.16%) for similar comparisons at Heard Island (Slip and Burton 1999); but there the counts were made by one observer in one year whereas at Macquarie Island the counts were made by a variety of observers over three years. Our comparisons were made between the highest and lowest estimates, when several estimates were available; and so this ~4% error is considered to be a robust upper limit. We also consider this is an upper limit for the error because our counts were on average within 2.74% of that predicted by the Levenberg–Marquardt algorithm fitted to our counts for the years 1988–2004.

A significant source of error we encountered was in the estimation of total cow numbers on the whole island from the isthmus only counts. The relationship had a standard error of $\pm 2,222$ cows (Fig. 2). Model estimates such as these will reduce our sensitivity to detect change over the whole population if estimates of the total numbers of cows on the island are derived from isthmus or other census sub-area counts.

Maximum numbers of cows ashore and recent trends

McCann (1985), Pistorius et al. (1999), Slip and Burton (1999) had established that the proportion of females likely to have departed, due to pup loss or weaning, the island

prior to the peak day census was ca. 0.05–0.06, and our estimates were identical. As Hindell and Burton (1987) and Slip and Burton (1999) had previously done, we used the LMA to calculate the date of maximum haulout. Any counts we made on either side of the peak date were therefore corrected using the LMA model proportion of the maximum number of cows ashore (McCann 1985, this study Table 2). Future counts of cows made outside the peak day at Macquarie Island can be corrected using Table 2.

The total southern elephant seal population at Macquarie Island in 2004 was estimated at 64,180 (excluding pups of the year). We arrived at this figure by multiplying the total number of cows (20,374) by a factor of 3.15 (Pistorius et al. 1999). This is a much lower estimate of the total number of seals at the island than the 76,000 reported by McMahon et al. (2005a). That study used a conversion factor of 3.50 to estimate total population of seals from cow counts (McCann 1985) while we have used a more conservative multiplication factor of 3.15 characteristic of decreasing elephant seal populations (Pistorius et al. 1999).

The last detailed analyses of the population trend at Macquarie Island appeared in the literature in 1987 when Hindell and Burton (1987) reported a net decrease of near 50% between 1949 and 1985. More recently, McMahon et al. (2005a) published population size estimates for southern elephant seals within their circumpolar Southern Ocean distribution, listing the status the elephant seals at Macquarie Island as decreasing. Additionally, McMahon et al. (2005b) briefly discussed the population trend at Macquarie Island, suggesting the rate of decrease had not changed in recent times. Those analyses were in the main done by linear regression which is well suited to populations that are experiencing exponential growth or decay. Our GAM analysis identified 1999 and 2000 as upward inflection points in the trend and a post-hoc linear analysis showed that the rate of population change (r) has now slowed from -1.95% (1952–1998) to near zero ($+0.09\%$) between 1999 and 2004.

Table 2 Correction factors for conversion of adult female southern elephant seals counts on dates either side of the 15 October

Census day	Correction factor
–5	0.9323
–4	0.9570
–3	0.9764
–2	0.9902
–1	0.9981
Peak	1.0000
+1	0.9958
+2	0.9857
+3	0.9697
+4	0.9483
+5	0.9217

Macquarie Island: intra-island variability

Whether the observed population trend at Macquarie Island will continue or reverse is unknown, and thus detailed continuous monitoring of the population is highly recommended. Complete population censuses are rarely if ever feasible (Link and Sauer 1997) but as we have shown over 17 years, the population of adult female southern elephant seals at Macquarie Island can be counted annually and in their entirety. Whole island counts should be encouraged because the rate of population change (r) in certain census sectors may not be an approximation of the population as a whole. For example the r value for the isthmus from 1988–2004 was -0.58 while the whole island was -1.16 (Table 2) over the same period. This finding itself suggests some local island events or characteristics are in some way influencing certain breeding parameters of the cows.

Closer inspection of the census sub-areas for the period 1988–2004 showed there were areas where elephant seal numbers had decreased faster than that recorded for the island as a whole, and some where the change was positive. The most rapid decreases were generally on the east coast, south of the Isthmus, especially in the Hurd Point to Green Gorge section (Table 2). That sector has received relatively little human presence compared to the isthmus study site where scientific and recreational interactions have occurred with regularity. Studies by Wilkinson and Bester (1988), Engelhard et al. (2001), Burton and van den Hoff (2002) and McMahon et al. (2005c) have shown that the southern elephant seal is remarkably unaffected by human interactions. Therefore we ruled out anthropogenic influences as a factor contributing to the observed census area differences in r (Table 3).

Resource (density/space) related factors may be responsible for these observed differences (van Aarde 1980; Bester and Lengart 1982). Those authors suggested the observed differences in rates of population change on

Table 3 Intrinsic rate of population change (r) within census sub-areas at Macquarie Island (1988–2004)

Census region	Annual r	P
North head	-0.52	0.43
Hasselborough corner–Bauer Bay	-1.72	<0.001
Bauer Bay–South Reef	$+0.86$	0.25
Hurd Point–Green Gorge	-2.24	0.005
Green Gorge–Halfway Hill	-1.36	0.01
Isthmus east	$+0.62$	<0.001
Isthmus west	-1.11	0.007
Isthmus total	-0.58	0.06
Whole island	-1.16	0.24

Values in bold type are significantly different to zero

Kerguelen Island may be socially instigated through excessive intraspecies disturbance. Slight increases in harem density where harems are already dense lead to measurable increases in pup mortality. Intraspecific disturbances cannot be confirmed or rejected as a cause for the differences we found at Macquarie Island and we suspect constant interspecies pressures and disturbance may also be a contributing density related factor. Elephant seals prefer gently sloping sand and cobble beaches to raise their pups (Carrick et al. 1962; Campagna and Lewis 1992). King penguins (*Aptenodytes patagonicus*) also prefer gently sloping sandy beaches, often with a source of fresh water nearby, for breeding and raising chicks. After earlier heavy exploitation, king penguins reoccupied Lusitania Bay (situated within the Hurd Point to Green Gorge section; Fig. 1), rapidly filling the available space (Rounsevell and Copson 1982). There are now more than 600,000 king penguins on the island (Wienecke and Robertson 2002), an increase of 350,000 birds since 1980 (Rounsevell and Copson 1982). As the available space at Lusitania Bay filled, new colonies have formed elsewhere on the island's east coast (Rounsevell and Copson 1982) and to the south of Lusitania Bay (Aleks Terauds, personal communication), possibly in direct competition for space with elephant seals. The observed relative increase in seal numbers in the east isthmus area suggests that humans are less of a disturbance to the breeding females than king penguins.

Conclusions

The southern elephant seal at Macquarie Island has been listed as vulnerable under the Australian Environment Protection and Biodiversity Conservation Act 1999 because it has undergone a substantial reduction in numbers, and the species was considered likely to become regionally extinct within 100 years (TSSC 2001). Since then, the rate of decrease has slowed to near zero (this study) and a population viability analysis by McMahon et al. (2005b), using linear regression, found the earliest time to extinction for the Macquarie Island population was over 300 years into the future. The southern elephant seal is unlikely to become regionally extinct unless a very significant change in ocean resources from the present situation is experienced.

We have shown that the population of cows at Macquarie Island has presently ceased to decrease; however the cause/s of this changed population trend requires further investigation. Demographic variables such as female fecundity, fertility, age specific survival, and age at primiparity could be examined against nonlinear changes in population status as they have been examined against linear change at Marion Island (Bester and Wilkinson 1994;

Pistorious et al. 2001; Bradshaw et al. 2002; McMahon et al. 2003b; Pistorious et al. 2004). General additive models could provide the tools for such an analysis because they are not simply smoothing devices, but provide a complete modelling framework such that the timing and extent of population change can be identified (Fewster et al. 2000). Simple linear trend modelling would be relatively inadequate for the identification of these important population attributes.

Acknowledgments This study was carried out with the approval of the Antarctic Animal Care and Ionising Radiation Usage Ethics Committee (Department of the Environment, Commonwealth of Australia) and the Tasmanian Parks and Wildlife Service. We especially thank David Slip for initiating the paper and Clive McMahon for inputs into various earlier versions. We also acknowledge the many members of the 1952–2004 ANARE to Macquarie Island who helped in the counting of seals. Angela Bender drew Fig. 1.

References

- Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. *Nature* 411:183–186
- Bester MN, Lengart P-Y (1982) An analysis of the southern elephant seal *Mirounga leonina* breeding population at Kerguelen. *South Afr J Antarct Res* 12:11–16
- Bester MN, Wilkinson IS (1994) Population ecology of southern elephant seals *Mirounga leonina* at Marion Island. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behaviour and physiology*. University of California Press, California
- Bradshaw CJA, McMahon CR, Hindell MA, Bester MN, Pistorious PA (2002) Do southern elephant seals show density dependence in fecundity? *Polar Biol* 25:650–655
- Burton HR, van den Hoff J (2002) Humans and the southern elephant seal *Mirounga leonina*. *Aust Mammal* 24:127–139
- Carrick R, Csordas SE, Ingham SE, Keith K (1962) Studies on the southern elephant seals *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *CSIRO Wildl Res* 7:119–160
- Campagna C, Lewis M (1992) Growth and distribution of a southern elephant seal colony. *Mar Mammal Sci* 8:387–396
- Caughley G (1977) *Analysis of vertebrate populations*. Wiley, London
- Condy PR (1979) Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South Afr J Zool* 14:95–102
- Croxall JP, Callaghan T, Cervellati R, Walton DWH (1992) Southern Ocean environmental changes: effects on seabird, seal and whale populations [and discussion]. *Philosophical transactions: biological sciences*, vol 338, no. 1285, *Antarctica and Environmental Change* (30 November 1992), pp. 319–328
- DeSante DF, Rosenberg DK (1998) What do we need to monitor in order to manage landbirds? In: Marzluff J, Sallabanks R (eds) *Avian conservation: research and management*. Island Press, Washington, pp. 93–106
- Dennis B, Desharnais RA, Cushing JM, Costantino RF (1995) Nonlinear demographic dynamics: mathematical models, statistical methods and biological experiments. *Ecol Monogr* 65:261–281
- Engelhard GH, van den Hoff J, Broekman M, Baarspul ANJ, Field I, Burton HR, Reijnders PJH (2001) Mass of weaned elephant seal pups in areas of low and high human presence. *Polar Biol* 24:244–251

- Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81:1970–1984
- Gotelli NJ (2001) A primer of ecology, 3rd edn. Sinauer Associates, Inc., Sunderland
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman and Hall, London
- Hindell MA, Burton HR (1987) Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *J Zool Lond* 213:365–380
- Laws RM (1956) The elephant seal (*Mirounga leonina* Linn.) II. General, social and reproductive behaviour. *Falkland Isl Depend Surv Sci Rep* 13:1–88
- Link WA, Sauer JR (1997) Estimation of population trajectories from count data. *Biometrics* 53:488–497
- McCann TS (1985) Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In: Ling JK, Bryden MM (eds) Studies of sea mammals in south latitudes. Proceedings of a symposium of the 52nd ANZAAS congress. South Australian Museum, Adelaide, pp 1–17
- McMahon CR, Hindell MA (2003a) Twinning in southern elephant seals: the implications of resource allocation by mothers. *Wildl Res* 30:35–39
- McMahon CR, Burton HR, Bester MN (2003b) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61–74
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005a) Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Rev* 35:82–100
- McMahon CR, Hindell MA, Burton HR, Bester MN (2005b) Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Mar Ecol Progr Ser* 288:273–283
- McMahon CR, van den Hoff J, Burton HR (2005c) Handling intensity and the short- and long-term survival of elephant seals, addressing and quantifying research effects on wild animals. *AMBIO* 35:420–423
- Pistorius PA, Bester MN, Kirkman SP (1999) Dynamic age-distributions in a declining population of southern elephant seals. *Antarct Sci* 11:445–450
- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biol* 24:343–348
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP (2004) Adult female survival, population trend and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *J Zool Lond* 263:107–119
- Press WH, Flannery BP, Teukolsky SA, Vetterling WT (1988) Numerical recipes: the art of scientific computing. Cambridge University Press, Cambridge, p 818
- Rothery P, McCann TS (1987) Estimating pup production of southern elephant seals at South Georgia. In: Harris S (ed) Mammal population studies. Symposium of the Zoological Society of London 58:211–223
- Rounsevell DE, Copson GR (1982) Growth rate and recovery of a king penguin, *Aptenodytes patagonicus*, population after exploitation. *Aust Wildl Res* 9:519–525
- Slip DJ, Burton HR (1999) Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarct Sci* 11:38–47
- Stenseth NC, Myrseter A, Ottersen G, Hurrell JW, Cahn K-S, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Thomas L (1996) Monitoring long-term population change: why are there so many analysis methods? *Ecology* 77:49–58
- TSSC. (2001) *Mirounga leonina* (southern elephant seal). Advice to the minister for the Environment and Heritage from the Threatened Species Scientific Committee (TSSC) on amendments to the list of threatened species under the Environment Protection and Biodiversity Conservation Act 1999. (<http://www.ea.gov.au/biodiversity/threatened/species/m-leonina.html>)
- van Aarde RJ (1980) Fluctuations in the population of southern elephant seals *Mirounga leonina* at Kerguelen Island. *South Afr J Zool* 15:99–106
- van den Hoff J (2001) Dispersal of southern elephant seals (*Mirounga leonina* L.) marked at Macquarie Island. *Wildl Res* 28:413–418
- van den Hoff J, Burton H, Davies R (2003) Diet of male southern elephant seals (*Mirounga leonina* L.) hauled out at Vincennes Bay, East Antarctica. *Polar Biol* 26:27–31
- Wienecke B, Robertson G (2002) Foraging areas of king penguins from Macquarie Island in relation to a marine protected area. *Environ Manage* 29:662–672
- Wilkinson IS, Bester MN (1988) Is onshore human activity a factor in the decline of the southern elephant seal? *South Afr J Antarct Res* 18:14–18