Age related reproductive variation in a wild marine mammal population

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ABSTRACT

Life history theory predicts a change in reproduction success with age as energy resources are limited and must be allocated effectively to maximise reproduction and survival. In this study we use three reproductive performance measures; maternal expenditure, offspring weaning mass and first year survival to investigate the role maternal age plays in successful reproduction. Long-term uninterrupted life history data available for Marion Island's southern elephant seals and mass change estimates from photogrammetry data allow for assessment of age related reproduction performance and trade-offs. Known-aged adult females were photographed for photogrammetric mass estimation (*n*=29) and their pups weighed at weaning during the 2009 breeding season. Maternal age and proportional mass loss positively influenced pup weaning mass. In turn first year pup return rates (as a proxy for survival) were assessed through the intensive mark-recapture program. Pup survival increased with female age and weaning mass. Pups of young females aged 3 to 6 years have a lower 1st year survival probability compared to pups of older and larger females.

Key words: Southern elephant seals, *Mirounga leonina*, Photogrammetry, Age specific reproduction, pup survival, life history theory

INTRODUCTION

Age specific reproductive parameters are a key life-history trait that affects breeding success (Clutton-Brock 1988). Life history theory predicts a change in age specific reproductive performance as limited resources must be allocated to maximise reproduction not withstanding maternal growth and maintenance (Roff 1992). Three main hypotheses can explain improved performance (1) selection hypothesis, (2) constraint hypothesis and (3) restraint hypothesis (Curios 1983; Bowen et al. 2006). The selection hypothesis (1), states that improved breeding with age is due to the loss of poorer individuals over time, leaving more superior individuals in a cohort causing the appearance of improved survival. The constraint hypothesis (2), postulates that reproduction improves in individuals as they acquire better experience/skill for example improved foraging or breeding experience; and the restraint hypotheses (3) predicts that young individuals postpone reproduction to reduce expenditure and the risk of mortality. These hypotheses provide a platform to explore the influence of maternal age and expenditure and the influence it has on offspring survival with the use of an intensive long-term mark-recapture dataset of Marion Island (MI) southern elephant seals in conjunction with a photogrammetric measuring method (de Bruyn et al. 2009).

Numerous studies have investigated maternal expenditure through offspring size, for example, the relationship between maternal expenditure and offspring survival (Trillmich 1996; McMahon et al. 2004), or female size in relation to offspring growth (Fedak et al. 1996; Arnbom et al. 1997; McMahon et al. 2000). Few studies have incorporated known female age (not merely an estimate of age based on size or cementum layers in extracted teeth - see Fedak et al. 1996; Arnbom et al. 1997). Our continuing long term mark-recapture research (28 years) (de Bruyn & Bester 2012) has provided a unique opportunity to explore known female age in combination with maternal expenditure and pup weaning mass to investigate what pressure it exerts on first year pup survival.

Southern elephant seal pup survival is largely influenced by condition at weaning, both at Macquarie Island (McMahon et al. 1999; 2000) and Marion Island (MI) (McMahon et al. 2003), with larger pups having a greater chance of survival (McMahon et al. 2000). In turn weaning mass is influenced by maternal mass (Carlini et al. 1997), which is influenced by food availability and foraging behaviour, across the Southern Ocean (Biuw et al. 2007). Southern elephant seals only haul out for short periods in the terrestrial environment to breed, moult and over winter (Kirkman et al. 2003; 2004). In the austral spring, adult females haul out for approximately 30 days to give birth and suckle their pups for 22-23 days (Laws et al. 1953b). They are extreme capital breeders; females rely completely on their stored energy reserves for maintenance and lactation throughout the terrestrial breeding phase (Arnbom et al. 1997). In capital breeders, mass has a fundamental influence on reproductive potential (Boyd et al. 1995; Festa-Bianchet et al. 1998), reserves (mass) or the lack thereof appears to be the most important variable influencing reproduction in southern elephant seals (Laws 1956a, b). Consequently there is a large variation in female body size with the largest being three times heavier than the smallest females at parturition (Fedak et al. 1996). This ultimately translates into differential reserves for lactation. There is also large variation in age and subsequent breeding experience among females (McMahon et al. 2004), with older females usually being larger (Arnbom et al. 1994, 1997). Few previous studies have included known female age in assessments of maternal reproductive performance through maternal size and pup survival. In this study we will use three reproductive parameters; 1) maternal expenditure, 2) offspring weaning mass and 3) a proxy for first year pup survival to investigate the role that maternal age plays in successful reproduction.

METHODS

Study site

A sequence of photographs of tagged (known-aged) breeding female southern elephant seals were taken at several breeding colony beaches between Ship's Cove and Archway Beach on the eastern coast of Marion Island from September to October 2009 (Fig 1).

Data collection

Pup tagging

To keep track of mother-pup pairs throughout the breeding season, pups of known mothers were tagged with temporary supersmall® tags (Dalton supplies Ltd, Hendley-on-Thames, U.K; http//www_dalton.co.uk) in the inner inter-digital webbing of the right hind flippers (de Bruyn et al. 2008). At weaning, temporary tags were replaced by long-lasting Dalton Jumbo® tags (Dalton Ltd, UK) (de Bruyn et al. 2008). The weaned pups of photographed females were physically weighed to the nearest 0.5 kg with a calibrated Salter 200 kg scale, using a weighing net and lifting pole.

Mark-recapture program

Almost all weaned pups born on MI since 1983 were double tagged in each of their hind flippers with a uniquely numbered, colour-coded Dalton Jumbo® tag (Pistorius et al. 2011). Since 1983, southern elephant seals were checked for the presence of tags on all popular beaches along the coastline (Fig. 1) every 7 days during the breeding season (mid-August to mid-November) and every 10 days for the remainder of the year. Tagged individuals were documented (tag number and cohort specific colour; sex if known; haulout site) to compile life history data for each individual (de Bruyn et al. 2011).

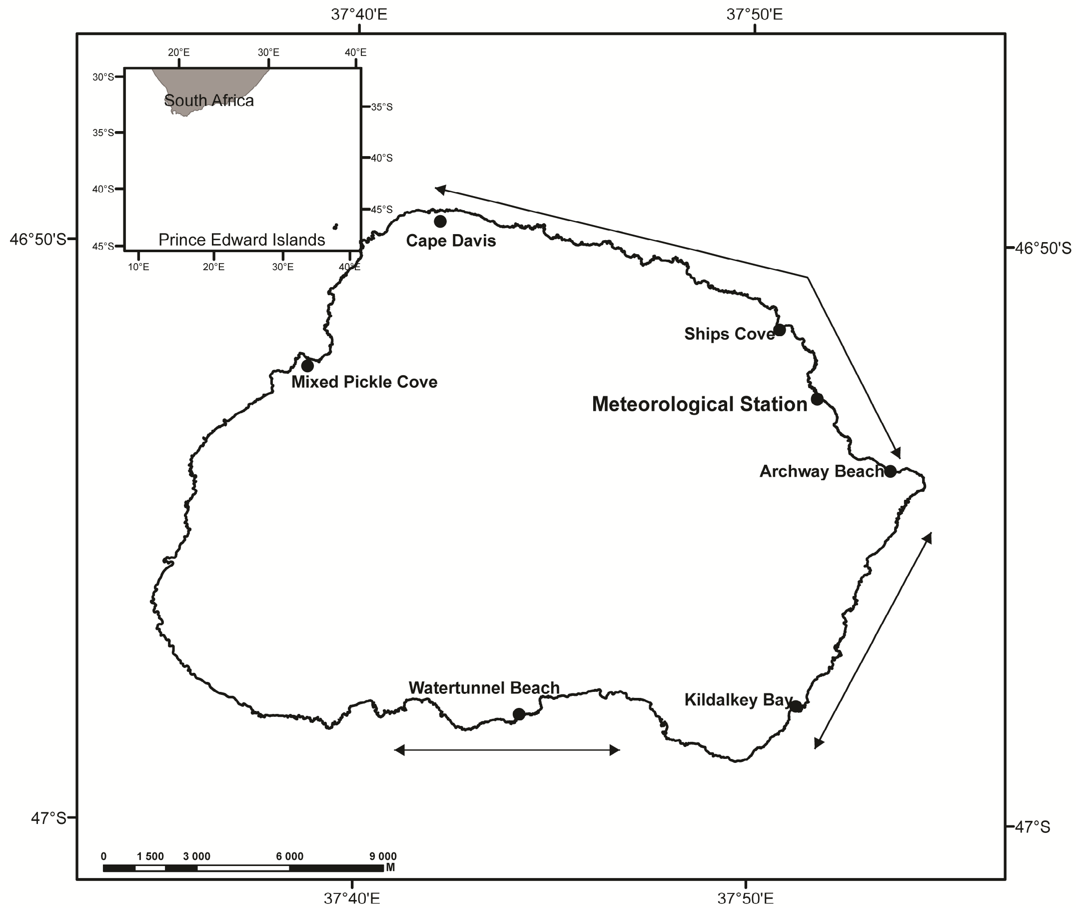

Figure. 1. Marion Island: Photogrammetry was performed between Ships Cove and Archway Beach. We search for tagged seals along the coastline on all the beaches indicated with arrows every 7 days during the breeding season (mid-August to mid-November) and every 10 days from (mid-November to the following mid-August) since 1983.

Pup survival (return)

Pup survival was determined by investigating census data for the pups' first years of life. Pups that survived their first foraging trip and successfully returned to Marion Island were considered. Between 2 and 4 years of extensive mark-recapture data was assessed for pup survival depending on year of birth (2006-2009) to correct for temporary immigration and resight error. As females have a single pup each year and the study includes data from 2006, 2007 and 2009, independence did not hold and a simple linear regression model could not be used. A generalized linear model with a mixed effects approach was implemented.

Photogrammetry

Photographs of unrestrained adult females were taken with calibrated cameras as described in de Bruyn et al. (2009). Photogrammetry was performed with calibrated SLR (single-lens reflex) cameras (Canon 350D, 400D and 450D). Before the first time a camera is used for photogrammetry, each camera and lens combination is calibrated using a calibration grid with coded targets at a set focal length as described in the calibration manual in the Photomodeler Pro® (EOS systems Inc.) software package. Importantly, the calibration procedure is performed for the minimum (in our case = 18mm) or maximum zoom setting to ensure repeatability of this setting in the field. The software requires a structured series of photographs, taking into account yaw (e.g. 90 degree rolls) and repeatable camera settings, to establish the relationship between lens and camera body (in the case of SLR's) or relevant parameters in compact cameras, to ensure that the entire field of view is calibrated. This effectively corrects for orthogonal distortion and conversion for the camera's entire field of view. Auto rotation, image stabiliser and red-eye settings of the camera were switched off for both calibration and field use to reduce unnecessary algorithm calculations/ 'noise' during processing. These precautions allow for optimal accuracy as stipulated in the Photomodeler® calibration procedure.

In independent comparisons between several software packages and traditional calibration procedures, Photomodeler® calibration procedures were shown to be accurate and repeatable for close range photogrammetry applications (Remondino & Fraser 2006). During fieldwork, care was taken to ensure photos were taken at calibrated camera settings. Recalibration is only required if the camera or lens is bumped, otherwise badly damaged or rebuilt. As a matter of course, recalibration of already calibrated cameras is periodically performed to ensure photographic and calibration projects are matched, in the unlikely event that calibration settings are changed.

Eight or more photos were taken from different angles around a seal (subject) to form one project. Twenty-nine female seals ranging from 3 to 19 years of age were repeatedly photographed between September 2009 and November 2009 (Table 1). For each of the animals, photogrammetric (PG) projects were performed (1) upon their arrival for the breeding season, (2) post-partum and (3) immediately pre-departure for their subsequent post breeding pelagic foraging phase. All tagged females in the harems where photographed indiscriminately of their position in the harem. Intensive photogrammetry to estimate female absolute mass loss, percentage mass loss, arrival mass and departure mass (de Bruyn et al. 2009) only commenced in 2009 and thus only one year of pup weaning mass could be incorporated in the analyses. As the 2009 (n =29) sample size was too small to estimate pup survival and a larger dataset was required, the 2006 and 2007 data was included (n = 79), without considering female mass, however all mother – pup pairs and female age were identified and included in the analysis.

Table. 1. Photogrammetry (PG) performed on females during the course of the 2009 breeding season. Females are grouped around partum (P); grey area indicates how long the female hauled out pre-and post-partum (established by concurrent intensive mark-recapture schedule).

Breeding Season 2009																																						
	Pre-partum											P	Post-partum																									
Tag	Days	10	9	8	7	6	5	4	3	2	1	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
LB092												P	PG																									
OB074								PG				P		PG															PG									
BP081												P															PG											
WR093								PG				P	PG																									
PO043						PG						P																						PG				
GG094								PG				P						PG														PG						
WW298												P																						PG				
OO406										PG		P															PG											
BB349											PG	P																			PG							
YY289									PG			P	PG																				PG					
YY237												P			PG			PG												PG								
YY218												P			PG																PG							
YY040												P		PG																PG								
RR468												P	PG							PG															PG			
RR466										PG		P					PG											PG										
RR435			PG									P																PG										
RR347								PG				P																						PG				
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RR024												P	PG																			PG						
PP452		PG										P																									PG	
PP359								PG				P																										
PP196												P																				PG						
PP174												P				PG													PG									
PP042												P				PG																					PG	
GW344										PG		P	PG																					PG				
GW160						PG						P		PG																PG								
GW037											PG	P			PG														PG									

Data analysis

Photogrammetric analysis

Volumetric estimation procedures were executed using the commercially available three-dimensional (3-D) modelling package Photomodeler Pro® version 6.2. Three-dimensional models (based on each of the PG projects), were built and the volumetric mass estimation method employed (de Bruyn et al. 2009). Accuracy of the photogrammetric mass estimation method was assessed in de Bruyn et al. (2009); southern elephant seals (n = 53) were weighed and photographed, physical mass was plotted against estimated photogrammetry mass and the goodness of fit assessed (R^2 = 0.98).

Calculation of date of birth, and pre- and postpartum mass

Daily observations along the coastal study area allowed determination of the exact weaning date for all pups, as well as the concomitant departure date for all mothers, in order to calculate the mean duration of suckling. Repeated observations allowed a linear time model to be created, illustrating the presence of each individual and dates on which PG projects were performed resulting in mass estimates (Table 1). The mean suckling duration, PG projects and census data were used to calculate the date of birth.

Pre- and post-partum PG projects were performed to assess birthing mass loss for all mothers (n = 29). Thirteen females were photographed on arrival. Of these, six females were also photographed immediately pre-partum and pre-departure (i.e. full PG set). The remaining females' arrival mass was estimated by multiplying the calculated mean daily mass loss pre-partum from the 13 females (with arrival PG) with days elapsed between arrival and birth (Table 1). Additionally, daily mass loss between post-partum PG mass estimates and pre-departure PG mass estimates were calculated from 16 females that all had both a post-partum PG and a pre-departure PG mass estimate. Where post-partum PG projects could not be done immediately following parturition, daily post-partum mass loss was multiplied with number of days between postpartum PG and date of birth to obtain estimated mass at the start of lactation (maternal mass at birth = MAB). A mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson et al. 2001) and a placenta mass of 3.5 kg (Arnbom et al. 1997) were added to estimate mass just before birth (MBB). If pup sex was unknown (*n*=4), a mean value of 37.2kg was used. Twelve females were photographed on the day of departure, the remaining females' departure mass was estimated by multiplying the calculated mean mass loss per day (post-partum) with the days elapsed between departure and previous PG.

Breeding haulout equations

Pre-partum mass loss (PEM), lactation mass loss (LML) and absolute mass loss (TM) was calculated for each female using the following equations, where *M* = mass:

$$PEM = M_{arrival} - M_{pre\_partum} \quad (1)$$

$$LML = M_{birth} - M_{departure} \quad (2)$$

$$TM = M_{arrival} - M_{departure} \quad (3)$$

Daily mass loss rates for the pre-partum period were calculated for animals that had arrival PG mass estimates (*n*=13) using the following equation:

$$PEM_{daily} = {M_{arrival} - M_{pre\_partum}} \Big/ {no.days} \quad (4)$$

Daily mass loss rates for the post-partum period were calculated for animals with post partum and departure PG mass estimates (*n*=16) using the following equation:

$$LML_{daily} = {M_{post\_partum} - M_{departure}} \Big/ {no.days} \quad (5)$$

In order to calculate mass loss as a result of parturition, the difference between mass directly before and after parturition was established. Daily mass loss rates were used to calculate the mass of female southern elephant seals directly after parturition using the following equation:

$$Mass_{after\_birth} = M_{post-partum} + (no.days \times LML_{daily}) \qquad (6)$$

Pup mass (Wilkinson et al. 2001) and placenta (Arnbom et al. 1997) was added to mass estimates obtained from equation 6 to obtain mass estimates directly before birth. Birth mass was set as a constant mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson et al. 2001). If no post-partum PG mass estimates were available, mass directly before birth was estimated from arrival PG mass estimates as:

$$Mass_{before\_birth} = M_{arrival} - (no.days \times PEM_{daily}) \qquad (7)$$

If mass before birth was obtained as described in equation 7, pup mass (Wilkinson et al. 2001) and placenta (Arnbom et al. 1997) was subtracted to obtain mass after birth.

Statistical analysis

The program R version 2.13.1 (R Development Core Team 2011) was used for statistical analysis. Linear mixed-effects models were run using S4 classes (lme4) (Bates et al. 2011), Multi-model inference (MuMIn) (Bartoń 2011) and Companion to Applied Regression (car) (Fox et al. 2011). Shapiro-Wilks and Durbin-Watson tests were performed, normality and independence was found to be present. Constant error variance was checked with a Breusch-Pagan test, and was found to be present. Single and multiple linear regression models were used for female age and mass only on the 2009 dataset as intensive breeding photogrammetry only commenced then. General linear model with mixed effects was used to assess pup survival for years: 2006, 2007 and 2009. The year 2008 was excluded as pups were not weighed. Significance was set at $P < 0.05$; and means are reported with standard deviation (SD). To establish which possible variables were significant in influencing pup weaning mass, a multiple linear regression model was performed. Model fit was assessed by plotting the residuals against the fitted values and Akaike Information Criteria (AIC) was used for model selection (Burnham et al. 2002).

RESULTS

Female arrival and departure mass

Female arrival mass greatly influenced her post-breeding departure mass, with heavier females losing proportionately less mass than their smaller counterparts. Arrival mass was significantly influenced by female age, (R^2 = 0.45, df = 27, P < 0, 0001) (Fig 2) as was departure mass (R^2 = 0.63, df = 27, P < 0.0001) (Fig 3), with older females generally being heavier than younger females. Younger females aged 3 to 6 years have a significantly ($t_{(37.07)}$, df = 28, P < 0.001, Table 2) lower arrival mass ranging between 366 kg and 604 kg (mean = 499.86 ± 61.32 kg) compared to older females 7 to 19 years who have a larger arrival mass ranging between 509 and 686 kg (mean = 580.68 ± 58.79 kg).

Absolute and percentage maternal mass loss

Absolute mass loss of a mother during the breeding season haul-out phase equates to maintenance mass loss plus mass transferred to her offspring. Absolute mass loss in the breeding season was not affected by female age (P = 0.3, df = 27, R^2 = 0.008, Table 2). Females lose a mean of 222.06 ± 34.31 kg. A single linear regression model established the relationship between age and percentage mass loss for females during the course of the 2009 breeding season (P = 0.004, df = 27, R^2 = 0.25) (Fig 4). Post partum mass loss per day for Marion Island (mean = 7.5 ± 2.3 $kg.day^{-1}$) is similar to the South Georgia population (post partum mean = 7.9 ± 1.4 $kg.day^{-1}$) (Arnbom et al. 1997). Female age accounted for 25 % of observed variation in relation to percentage mass loss in southern elephant seals.

Table 2. Importance of explanatory variables for each analysis: test statistic (t), coefficients of determination (R^2), degrees of freedom (df), probability (P), linear model (lm), generalized linear model with mixed effects (glmer) are presented.

Response variable	**Influential Variable**	**Data Year**	**Test**	**t**	**R^2**	**df**	**P**
Female mass parameters (Constraint hypothesis testing)							
Female Arrival mass	Female age	09	lm	-	0.45	27	0.0001
Female mass loss	Female age	09	lm	-	0.008	27	0.28
Percentage mass loss	Female age	09	lm	-	0.25	27	0.0035
Female Departure mass	Female age	09	lm	-	0.63	27	0.0001
Pup weanning mass	Female age	09	lm	3.181	-	-	0.0038
	Female mass loss	09	lm	3.073	-	-	0.0049
	Female age + mass loss	09	lm	-	0.45	26	0.0001
Pup survival between age stages							
Female Arrival mass	Female age stage (3-6 years) & (7-19 years)	06/07/09	t test	37.07	-	28	0.0001
Pup survival	Female age stage (3-6 years) & (7-19 years)	06/07/09	glmer	-	0.56	-	0.0070
Restraint hypothesis testing							
Pup weanning mass	Female age class (3, 4 years)	06/07/09	t test	-4.12	-	20.79	0.0001
Pup survival	Female age class (3, 4 years)	06/07/09	t test	-0.4956	-	17.07	0.6265
Female Arrival mass	Female age class (3, 4 years)	09	t test	-5.2749	-	3.336	0.0101

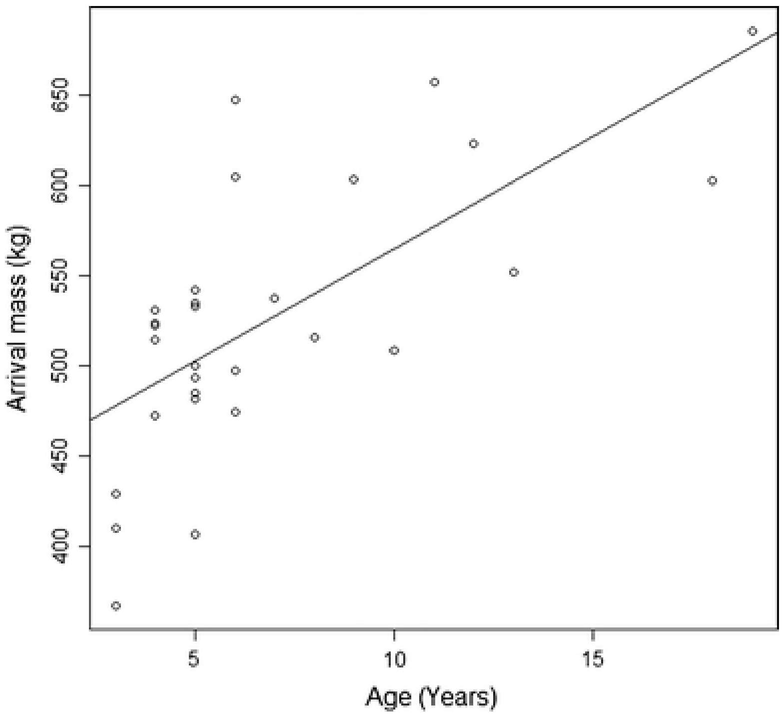

Figure. 2. Female southern elephant seal breeding season arrival mass compared to age, *P* < 0, 0001 (R^2 = 0.4487)

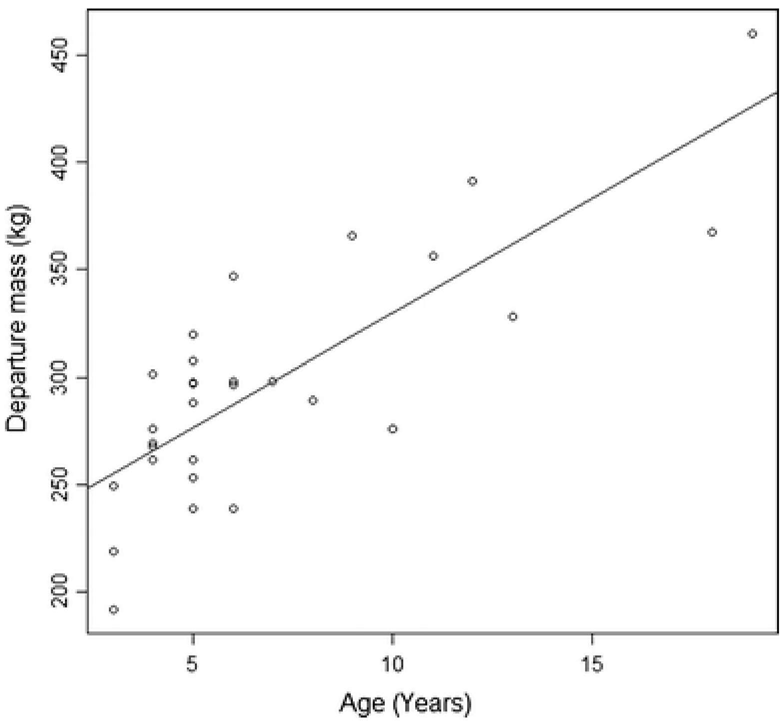

Figure. 3. Female southern elephant seal breeding season departure mass compared to age, *P* < 0.0001 (R^2 = 0.6284)

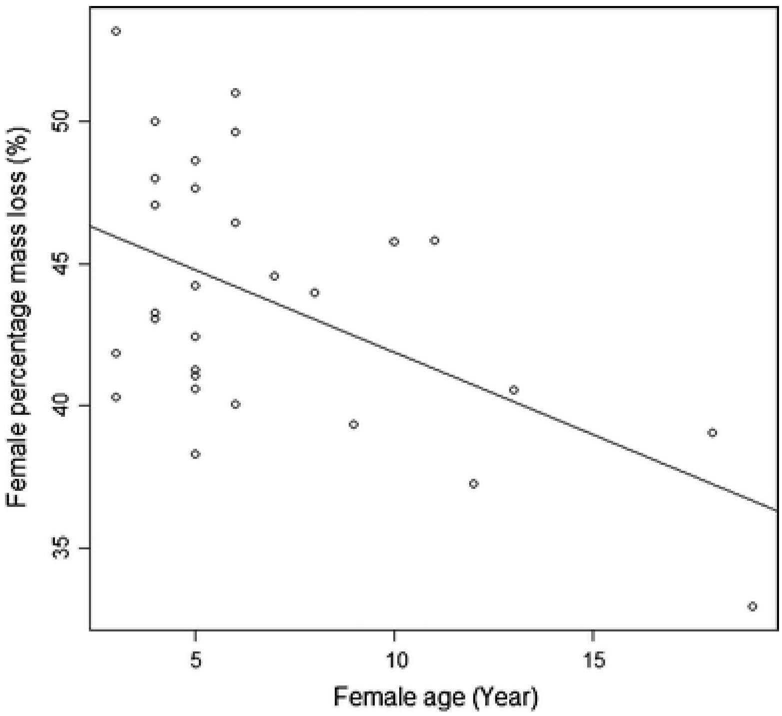

Figure. 4. Female southern elephant seal percentage mass loss compared to female age P = 0.00347 (R^2 = 0.25)

Restraint hypothesis testing

Age compositions of harems at Marion Island usually include a small number of 3 year old females, which could be due to the majority of this female age class gaining insufficient mass to breed (Pistorius et al. 2011). Three year old female arrival mass differed significantly ($t_{(-5.27)}$, df =3.34, P = 0.01, Table 2) from 4 year old females. Pup weaning mass also differed significantly ($t_{(-4.12)}$, df =20.79, P = 0.0001, Table 2) between these maternal age categories, however pup survival did not differ ($t_{(-0.5)}$, df =17.07, P = 0.63) between the two maternal ages.

Pup weaning mass for 2009 breeding haul-out

Female mass loss and age were used as variables and the number of pups a female had produced in her lifetime was eliminated from the final model. It was found to be non-significant and co-linear with female age according to model fit as assessed by Akaike Information Criteria (AIC) and plotting the residuals against the fitted values

(Table 3) (Burnham & Anderson 2002). Female mass loss ($t_{(3.08)}$, $P = 0.005$) and age ($t_{(3.181)}$, $P = 0.004$) was found to significantly influence pup weaning mass ($R^2 = 0.448$, df = 26, $P = 0.0001$, Table 2) (Fig 5). Female age and mass loss variables seem to be linked as determining factors for pup weaning size, as female size increases with age. Furthermore, female age and mass loss combined, explained 45% of variation for relative mass gain in southern elephant seal pups.

Pup survival

Pups were not split into sexes because previous studies indicate no difference in survival between sexes (e.g. McMahon *et al*. 1999; 2004). Adult females ($n = 79$) from 2006, 2007 and 2009 were between 3 to 19 years of age, having given birth to a variable number of pups. Pup weaning masses ranged from 68.42 kg to 160.60 kg (mean = 115.24 ± 20.62 kg). Thirty-six of the pups born in the sample were female and 39 were male, while 4 were of unknown sex. Female age,,number of pups born to each female and pup mass were eliminated from the model based on model fit, assessed by plotting the residuals against the fitted values (Table 4). Pup survival differed significantly ($R^2 = 0.56$, $P = 0.007$, Table 2) based on maternal ages 3–6 years of age or 7-19 years of age. These female age stages (3 – 6; or 7 – 19 year old categories) accounted for 56 % of variation in explaining pup survival (Fig 6).

DISCUSSION

Maternal age and expenditure

Younger female southern elephant seals (aged 3 to 6 years) showed significantly smaller arrival mass for the breeding season, as compared to older prime aged females 7 to 19 years (Reiter et al 1981). The arrival mass of females for the breeding season is vital for successful pup production as maternal expenditure is limited by initial body condition (Laws 1953; Kovacs et al. 1986; Trillmich 1996). Predictable seasonal haul-outs of southern elephant seals could depend on mass

Table. 3. Model selection for multi linear regression. Variables include female age (Age), female mass loss (FMS) and number of pups produced (NPP). Variables were removed and AIC values compared. The first model including age and female mass loss was most parsimonious.

Model selection table

	(Int)	**Age**	**FML**	**NPP**	**k**	**R.Sq**	**Adj.R.sq**	**RSS**	**AIC**	**AICc**	**delta**	**weight**
5	42.51	2.2590	0.2511		4	0.4875	0.4481	6074	245.3	247.0	0.0000	0.469
7	52.25		0.2220	3.692	4	0.4744	0.4340	6230	246.0	247.7	0.7326	0.325
8	45.24	1.6720	0.0241	1.069	5	0.4897	0.4285	6048	247.2	249.8	2.8180	0.115
4	99.71			4.707	3	0.3380	0.3135	7846	250.7	251.7	4.7160	0.044
2	96.90		2.7150		3	0.3014	0.2755	8280	252.3	253.2	6.2780	0.020
3	45.63	0.3055			3	0.2880	0.2616	8439	252.8	253.8	6.8290	0.015
6	99.06	0.3686		4.148	4	0.3388	0.2880	7837	252.7	254.3	7.3880	0.012
1	115.60				2	0.0000	0.0000	11850	260.7	261.1	14.1800	0.000

Table. 4. Model selection (pup survival) for generalized linear model with a mixed effects approach. Variables include female age (Age), Age stage (A.S), Pup mass (Pp.) and number of pups produced (Pp..1.). Variables were removed and AIC values compared. The first model including ‘Age stage’ was most parsimonious.

Model selection table

	(Int)	Age	A.S	Pp.	Pp..1	k	Dev.	AIC	AICc	delta	weight
3	0.02426		1.844			3	95.86	101.9	102.2	0.0000	0.180
9	-2.52700		1.286	0.02393		4	93.99	102.0	102.5	0.3504	0.151
4	-3.52700			0.03858		3	96.75	102.8	103.1	0.8929	0.115
12	-2.36400	-0.15680	2.264	0.02896		5	92.98	103.0	103.8	1.6150	0.080
6	0.45850	-0.09764	2.525			4	95.45	103.5	104.0	1.8100	0.073
11	-3.10000			0.02812	0.16060	4	95.77	103.8	104.3	2.1240	0.062
10	0.11370		2.084		-0.05394	4	95.82	103.8	104.4	2.1820	0.060
15	-2.62100		1.951	0.02742	-0.16690	5	93.66	103.7	104.5	2.3010	0.057
5	-0.32320				0.30220	3	98.37	104.4	104.7	2.5080	0.051
7	-3.50200	0.05994		0.03244		4	96.38	104.4	104.9	2.7390	0.046
2	-0.46570	0.16020				3	99.78	105.8	106.1	3.9170	0.025
16	-2.32000	-0.17590	2.171	0.02850	0.05412	6	92.96	105.0	106.1	3.9400	0.025
13	0.45460	-0.14150	2.305		0.11990	5	95.35	105.3	106.2	3.9850	0.024
14	-3.02300	-0.09098		0.02929	0.29070	5	95.53	105.5	106.4	4.1710	0.022
8	-0.23620	0.04058			0.36250	4	98.32	106.3	106.9	4.6780	0.017
1	0.58800					2	103.60	107.6	107.8	5.6040	0.011

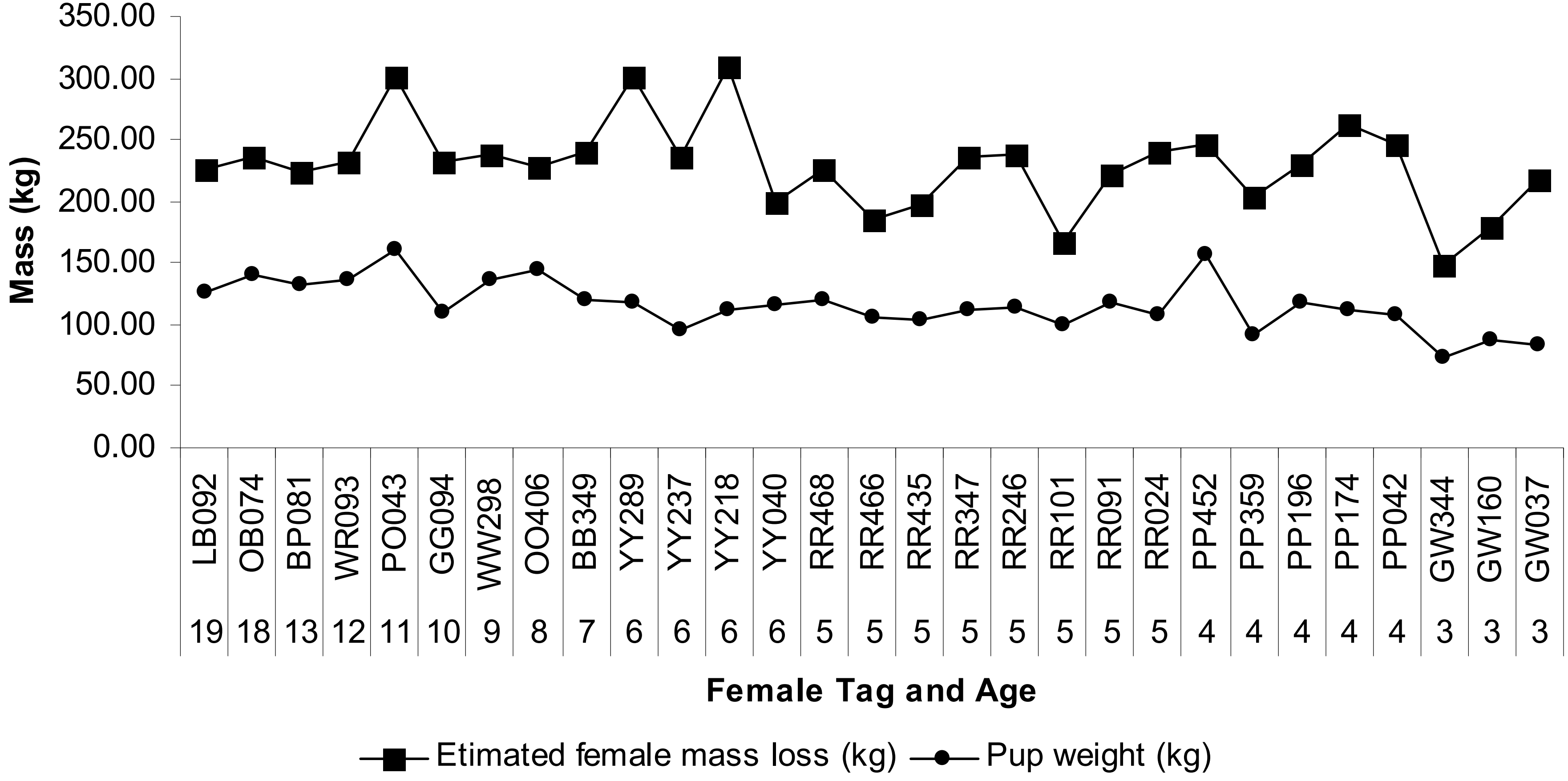

Figure. 5. Comparison of pup weaning mass and female mass loss during the breeding season

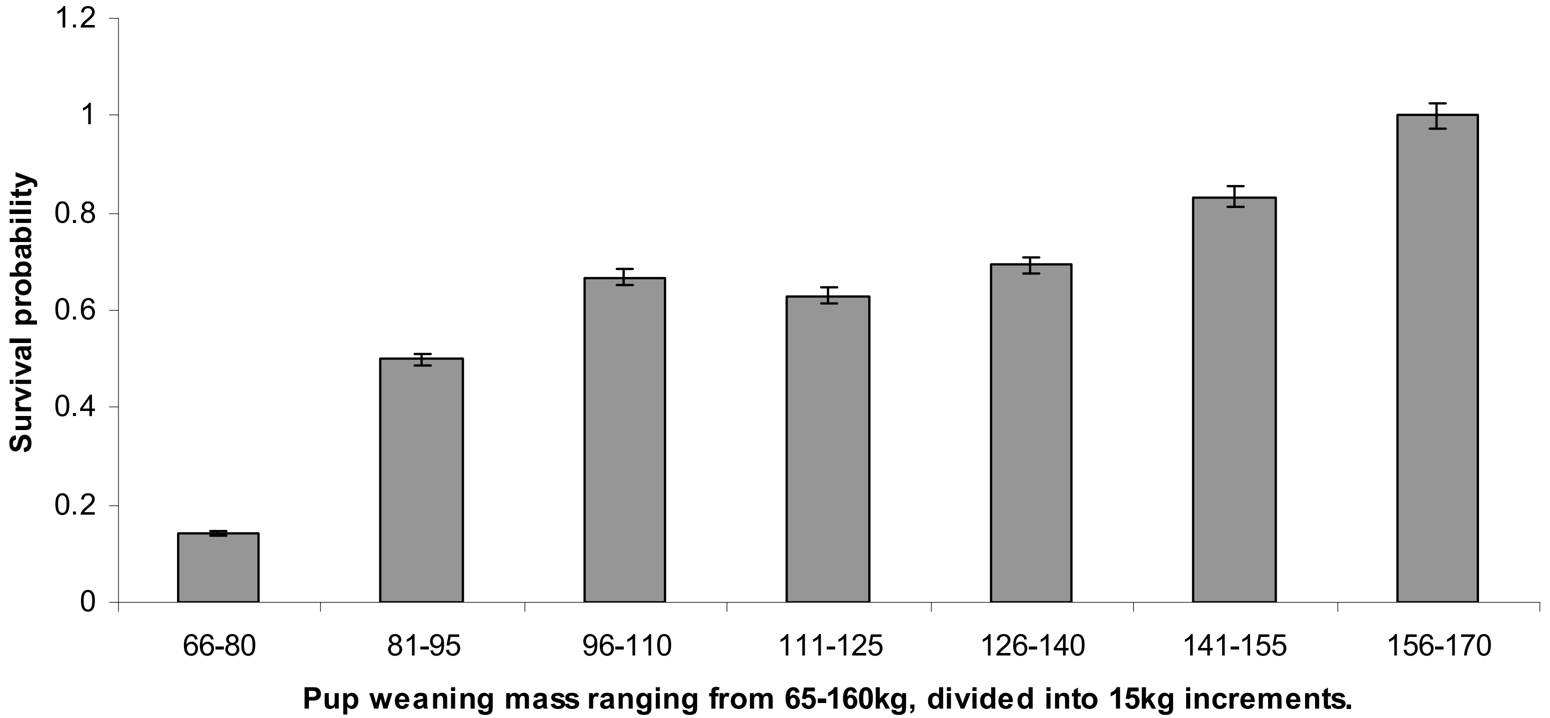

Figure. 6. Pup survival as related to weaning mass ranging from 65 to 169 kg divided into 15kg increments, 95% confidence estimates are indicated.

gain during their pelagic foraging phases. Reserves should be adequate to successfully wean pups and sustain themselves for the duration of the haul-out. Additionally, sufficient reserves should remain to aid post-breeding individuals on their journey back to their pelagic feeding grounds. Many females at MI skip breeding seasons at regular intervals (de Bruyn et al. 2011), raising important questions pertaining to these maternal body condition parameters.

Mean maternal percentage mass loss at MI was 43% over the course of the breeding season (present study), and this was significantly influenced by female age. Younger females (3 to 6 years old; arrival mass between 375 kg and 525 kg (Fig. 2, 3)) lose a larger percentage of mass than older females. Consequently, older females utilize less mass relative to their total body size, retaining more reserves in aid of travel to the post-breeding foraging grounds.

Reduced reserves in younger females can lead to three outcomes, (1) pups gain less mass reducing their survival probability in the first pelagic foraging trips, (2) female reserves reach a critical threshold, where her own survival and future reproduction could be compromised, (3) female abandons the pup to ensure her own survival. Here we focus on the former; pup survival in relation to female age and mass loss.

Offspring survival

An important assumption in assessing pup survival is that tagged individuals rarely permanently emigrate from MI and are therefore not lost for potential future recapture (Pistorius et al 2004). The extensive mark-recapture schedule (de Bruyn et al. 2012) that assessed pup survival for 2-4 years depending on date of birth (by which some are already adults) attributes to high recapture rates (Pistorius et al. 2011). The likelihood of missing an individual in consecutive haulouts if individual is present is small, as haulouts (winter and moult) for this age class last up to a month, which can include 3 census occasions. Furthermore the philopatry of the species at Marion Island; even for this more dispersive age class remains high (Oosthuizen et al. 2009, 2010, 2011). Pup weaning mass increased with female mass loss and age. A larger weaning mass would imply that pups have a larger reserve for development in the post-weaning phase. Large birth size and fast growth of phocid pups during the suckling period is advantageous in obtaining adequate blubber for thermoregulation (Bryden 1969; Kovacs et al. 1986) during the following protracted post weaning phase (Worthy et al. 1983). During their post weaning phase pups grow and simultaneously lose mass, up to 30% of their weaning mass at MI (Wilkinson et al. 1990). In northern elephant seals, *M. angustirostris*, this phase is crucial for the development of their ability to store oxygen and lower their metabolic rates to improve diving abilities (Thorson et al. 1994). During this phase pups have a differential growth order of fat, bone and then muscle (Bell et al. 1997). Muscle growth for pups attains its maximum rate once pups are at sea (Bryden 1969). Sufficient amounts of fat are necessary for development of bone and muscle. Thus, heavier pups could undergo a protracted period before departing their birth sites for the first time and better develop their diving capabilities, but ultimately deplete their reserves more *(*Arnbom et al. 1993). Heavier weaned pups should have adequate blubber as an energy source to rapidly develop swimming and foraging skills in their aquatic environment (Worthy et al. 1983; Thorson et al.1994). This credibly influences pup survival during their first foraging trip. Pups that survived their first foraging bout had a 12% larger weaning mass than those that did not (present study). Smaller pups at weaning have fewer reserves to rely on and depart from breeding sites at an earlier date than pups with a larger weaning mass (Wilkinson et al. 1990). Pups born from females aged 7 to 19 years had a significantly greater survival probability (82%) than pups born from females aged 3 to 6 years (51%) (present study). We attribute the increase in reproductive performance to an increase in maternal body mass with age

Hypotheses accounting for age related reproduction improvement

There are several important findings arising from incorporation of photogrammetry into the long-term mark-recapture program. Collectively, assessing previous life history studies (e.g. Pistorius et al. 2001; 2004; de Bruyn et al. 2011) and our present photogrammetric results enlightened us to different southern elephant seal breeding strategies that might be at work at Marion Island. Firstly, age composition of harems include a relatively smaller number of 3 year old, than 4 year old females which could be due to the majority of this female age class gaining insufficient mass to breed (Pistorius et al. 2011). Three year old female arrival mass significantly differed from that of 4 year old females (present study), corroborating assertions by Pistorius et al. (2011). Weaning mass of pups from 3 year old females (mean = 81.67 ± 7.76 kg) compared to pups from 4 year old mothers (mean = 117.40 ± 24.14 kg) differ greatly and supports the hypothesis that the main contributor to pup mass is female age and size. These findings support the restraint hypothesis, where smaller females may forego reproduction to increase body mass and facilitate future reproduction and increased survival probability (Curios 1983, de Bruyn et al. 2011). Phocid seals must acquire a critical body size to achieve sexual maturity and mass plays an important role in their reproductive potential (Laws et al. 1956; Arnbom et al. 1994). Thus a delay of onset of reproduction results in females being larger and in better condition and able to produce pups that are larger (Pistorius et al. 2004). Delaying the onset of reproduction by a year in order to invest in growth rather than reproduction (Reiter et al. 1991) may therefore increase the probability of survival of the offspring (Pistorius et al. 2004). However no evidence was present for different survival probability between pups born from 3 and 4 year old females. We attribute this to the fact that both these age classes belong to the 3-6 year age stage, for which offspring survival probability is lower (present study).

Secondly, the presence of the same older females throughout the four years of sampling could support the selection hypothesis, where lower quality females are eliminated from cohorts leaving the more skilled/experienced breeding females (Curios 1983). Pre-weaning pup mortality at MI is higher at smaller harems, which contain many smaller and younger inexperienced females giving birth for the first time (Pistorius et al. 2001). Similarly first year mortality rate is 31 % higher for pups that are born from smaller females (aged 3 to 6 years) than from larger females (aged 7 to 19 years) (present study).This increased survival of pups associated with increasing female age, and mass difference between these age stages supports the constraint hypothesis, where older individuals' reproduction should increase either as a result of increased breeding/foraging experience or body size. Older females at Marion Island are larger in mass and are reproductively more successful, presumably then indicating that they are more experienced in breeding and foraging.

In conclusion, female mass loss, size and pup survival could be linked to known age in this study. The first-year survival of pups is positively linked to female age. Older and larger females have larger pups and these have a greater probability of surviving their first foraging trip. Pups that are born from young females or females that do not gain sufficient mass prior to a breeding season do have a lower probability of survival than pups that are born from older and larger females.

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