Behav Ecol Sociobiol
DOI 10.1007/s00265-007-0450-y

ORIGINAL PAPER

The cost of success: reproductive effort in male southern elephant seals (*Mirounga leonina*)

Filippo Galimberti · Simona Sanvito · Chiara Braschi · Luigi Boitani

Received: 15 August 2006 / Revised: 7 May 2007 / Accepted: 4 July 2007

Abstract Reproductive effort is a key parameter of life history because it measures the resources allocated to reproduction at the expense of growth and maintenance. Male reproductive effort always had a minor role with respect to female effort both in the development of theories and in field research. Elephant seals are an ideal subject for reproductive effort studies because they fast during the breeding season, splitting the phase of energy acquisition from the phase of energy use for breeding. In this paper, we present results on male reproductive effort (weight loss estimated by photogrammetry) in southern elephant seals (*Mirounga leonina*), the most dimorphic and polygynous of all mammal species. We show that total reproductive effort increases with age, with no sign of late decrease or senescence. Male reproductive effort in this species depends mostly on behavioral factors, i.e., the success in competition with other males, and the intensity of interaction with females. A large effort results in large gains in both mating success and fertilizations. The large reproductive success that a few males are able to achieve come at a big cost in terms of energy expenditure, but this cost does not seem to affect the likelihood of survival to the following breeding season.

Keywords Reproductive effort · Body size · Male competition · Reproductive success · Southern elephant seal · *Mirounga leonina* · Falkland Islands

Introduction

The classic approach in the development of life history theories is to define a criterion of optimality (e.g., lifetime reproductive success) and then identify the pattern of reproduction that produces an optimal life history given a set of constraints (Gadgil and Bossert 1970). Although there are now alternatives, this optimization approach still has a very important role in the study of life histories (Stearns 2000). Reproductive effort, i.e., an organism's investment in any current act of reproduction as opposed to growth and maintenance or survival (Fisher 1930), is central in the optimization of life histories (Pianka 1988; Charlesworth 1994). Assuming that reproduction involves a cost, there should be, for any age class, a level of reproductive effort that optimizes the trade-offs between current and future reproduction (Gadgil and Bossert 1970; Pianka and Parker 1975). Unfortunately, reproductive effort and cost of reproduction are somehow blurred concepts, with different authors using different, sometimes incompatible, definitions (Tuomi et al. 1983). Moreover, the actual

Communicated by V. Janik

F. Galimberti · S. Sanvito
Elephant Seal Research Group,
Sea Lion Island, Falklands Islands

S. Sanvito
Department of Biology, Memorial University of Newfoundland,
St. John's NF A1B 3X9, Canada

C. Braschi · L. Boitani
Department of Animal Biology,
University of Rome "La Sapienza",
Viale dell' Università 32,
00185 Rome, Italy

F. Galimberti (✉)
Laboratorio de Ecología Molecular, Facultad de Ciencias Marinas,
Universidad Autónoma de Baja California,
Km 103 Carretera Tijuana–Ensenada,
Ensenada 22860 Baja California, Mexico
e-mail: fil_esrg@prodigy.net.mx

measurement of reproductive effort is difficult, especially for field studies (Reznick 1985).

A main problem of the study of breeding effort is that, in most species, energy use is not separated from energy acquisition, and individuals carry on feeding during the breeding period. The estimation of reproductive effort is much easier in capital breeders, i.e., in species in which feeding is reduced or null during the breeding. In these species, reproductive effort can be estimated directly from weight lost during the breeding season (Yoccoz et al. 2002; McElligott et al. 2003; Mysterud et al. 2004; Mysterud et al. 2005). Although weight loss is particularly effective in capital breeders, it is also the best index of male reproductive effort in mammals at large (e.g., Isaac 2005) because it is more directly linked to true effort than the more common behavioral indices (e.g., Huber et al. 2002). Many seal species are excellent examples of capital breeders because they fast completely during the breeding season, and there is a clear separation between an aquatic phase of energy acquisition and a terrestrial breeding phase of energy consumption. Therefore, seals are an ideal subject for the study of reproductive effort and are becoming modal species for the study of the energetics of reproduction at large (Fedak and Anderson 1987; Boyd 2002). Most studies of seal reproductive effort concentrated on females (e.g., Schulz and Bowen 2004), and much less information is available for males (*Cystophora cristata*: Kovacs et al. 1996; *Halichoerus grypus*: Anderson and Fedak 1985; Tinker et al. 1995; *Mirounga angustirostris*: Deutsch et al. 1990; *Phoca vitulina*: Walker and Bowen 1993). This bias is due in part to the complexity of measuring breeding effort in males compared to females (Deutsch 1990). Moreover, females occupy a central role in demography and life history modelling because the rate of population growth is limited by female, and not by male, fecundity (Stearns 1992; Wilkinson and Van Aarde 1999). Only recently the males role begins to be recognized (Mysterud et al. 2002). In many mammal species, the evolution of female reproductive effort was probably driven by ecological factors, while male reproductive effort was probably driven by sexual selection (Trivers 1972), although ecological constraints surely played a limiting role. Therefore, it is not easy to compare the reproductive effort between the sexes, and this is, in turn, a crucial step to understand the large differences that the sexes show in almost all phenotypic traits, including morphology, behavior, and life history.

The elephant seal (genus *Mirounga*) mating system is probably the most extreme example of polygyny observed in mammals and vertebrates at large (Clutton-Brock 1989). Females haul out and gather in large groups to give birth, males establish dominance relationships that regulate access to females, and the resulting distribution of reproductive success is exceptionally skewed (Galimberti et al. 2002). Variance in lifetime reproductive success is much higher in males than in females (Le Boeuf and Reiter 1988), and most life history traits are different between the two sexes (Clinton 1994). Male elephant seals show no parental care, and, therefore, all their reproductive effort is mating effort. They are possibly the best example of capital breeders because they fast during the whole breeding season, which can last for more than a hundred days (Le Boeuf and Laws 1994). Their weight loss, therefore, is an excellent measure of reproductive effort (Deutsch et al. 1990).

The main problem in estimation of reproductive effort in male elephant seals is their large size (Le Boeuf and Laws 1994). We used a photogrammetric method to measure weight loss in a large sample of southern elephant seal (*Mirounga leonina*) males during two consecutive breeding seasons at Sea Lion Island (Falkland Islands). In this paper, we describe male body length, weight, and weight loss; we estimate population-average and individual weight loss rates; we examine the age-specific variation of weight loss; we analyze the relationship between weight loss and structural size (i.e., size as determined by the skeleton), breeding status, tenure, and behavior. Moreover, we test the hypothesis that there should be a positive correlation between reproductive effort and competition success, and we examine the effect of current reproductive effort on seasonal reproductive success and survival to the following breeding season.

Materials and methods

Data were collected during two breeding seasons (September–November, 2002 and 2003) at Sea Lion Island (Falkland Islands; SLI hereafter), where there is a small and almost isolated population of southern elephant seals, comprising about 550 females and about 60 breeding males (Galimberti et al. 2001). We defined “breeding males” as all that were observed in areas where one or more females were present (Galimberti and Boitani 1999). All breeding males were marked with hair dye upon arrival, and all had cattle tags placed during previous breeding seasons. Details of the marking protocol may be found in Galimberti and Boitani (1999).

Estimation of length, weight, and weight loss

We calculated body length and estimated weight using a photogrammetric method (Haley et al. 1991; Bell et al. 1997). High-resolution digital pictures of males were taken opportunistically along the whole span of each breeding season (12 weeks). An assistant kept a calibrated surveying pole (4 m long) above the male back. The body length (beginning of trunk to beginning of tail) and the side area were measured from the pictures using the Object Image software (http://simon.bio.uva.nl/object-image.html). The side area is the single best photogrammetric estimator of weight in southern elephant seals (Bell et al. 1997). Side areas were converted to weight using the formula presented in Table 1 of Haley et al. 1991 for northern elephant seals: Weight$=507.738\times$Area$^{1.544}$. Southern and northern elephant seal males have the same shape and morphology, the only notable difference being the proboscis (more developed in the northern species, Le Boeuf and Laws 1994), which is not involved in the photogrammetric estimation.

We obtained a total of 336 weight estimates (141 in 2002 and 195 in 2003) for 110 individuals (54 in 2002, with a mean of 2.6 estimates per individual, range 1–7; 56 in 2003, with a mean of 3.5 estimates per individual, range 1–10). The sampled males represent the vast majority of the breeding males ($n=59$ in 2002, with 91.5% coverage, and 62 in 2003, 90.3%). Repeated pictures were taken at intervals ranging from 4 to 71 days (mean=39.0±19.2). Twenty-six males were present in both seasons, and the total number of individual males in one or both seasons was 84. The measures of the same male in different seasons are correlated, and this increases the risk of pseudo-replication (Machlis et al. 1985), although the duplicated measures were only 24% of the dataset. To assess the effect of this longitudinal data structure, we ran, for each hypothesis, a mixed regression using the male identities as random effect, and then we calculated the significance of this effect with the Breusch–Pagan Lagrange multiplier test (Breusch and Pagan 1980). The random effect was nonsignificant in all cases, and the probabilities of the test statistics were large (always >0.20). Therefore, we used ordinary least squares regressions, ignoring the random effect.

To check the validity of the photogrammetric method, we estimated the repeatability of measurements of length and side area (Lessells and Boag 1987; Bailey and Byrnes 1990). We calculated confidence limits of repeatability using bootstrap (1,000 samples), and we tested the significance of its difference from zero by randomization (10,000 resamplings; Manly 1997). Only males with three or more independent pictures (i.e., pictures taken during the same day but at different times, after the male moved to a different location) were included in the repeatability analysis. Repeatability of length measures was excellent (2002: 364 measures, $R=0.981$, 95% confidence interval= 0.971−0.991, $p=0.0001$; 2003: 346 measures, $R=0.982$, 95% ci=0.974–0.991, $p=0.0001$). Repeatability of side area was also high (2002: 295 measures, $R=0.946$, 95% ci=0.926–0.966, $p=0.0001$; 2003: 170 measures, $R=0.959$, 95% ci=0.942–0.976, $p=0.0001$).

From photogrammetric measures we calculated various total and relative measures of reproductive effort. The latter measures are better to compare males reproductive effort among males of different size, but the former are useful to evaluate the consequences of this effort. For males with three or more measures we calculated: (1) the initial weight at arrival and the final weight at the end of the breeding season (kilogram), calculated from the individual rate of weight loss (see “Results” for estimation details) and the observed dates of arrival and departure; (2) the total weight loss (=initial weight − final weight, kilogram); (3) the percentage weight loss (weight loss/initial weight×100); (4) the daily loss rate (weight loss/number of days on land, kilogram); (5) the daily loss rate per unit weight (weight loss per kilogram of body weight per day, gram). Ratios, proportions, and percentages are useful for description, but they have undesirable statistical properties (Atchley 1978). Our results should be robust because distributions showed no 0 or 100% values, skewness was not pronounced, and we analyzed these variables using randomization tests (Manly 1997).

Body size affects the absolute energetic requirement of maintenance metabolism and, therefore, weight loss should depend on size (Schmidt-Nielson 1984), although this has been shown to not always be true in male pinnipeds (Kovacs et al. 1996). To obtain a measure of weight loss independent from size, we calculated the residuals of the linear regression of total weight loss vs length (size-independent loss; see “Results” for regression details). We used length as measure of size because it does not change during the breeding season, and, therefore, is more representative of the true structural size of each male.

Age determination

Age was known for males up to age 7 (in 2002) and 8 (in 2003) because they were marked as pups (see Galimberti and Boitani 1999 for details). The other males of the sample were tagged as juveniles, and, therefore, their age was estimated using external morphology (development of the proboscis, rugosity of the neck shield), which permits classification of elephant seals in yearly age classes with good accuracy (Deutsch et al. 1990; Galimberti et al. 2000a). Male ages ranged from 6 to 12, but just four males (5.1%) were older than 10 years. We classified males of age 9 and above as *mature* and the others as *young*. The rationale of this classification is that most harem holder were 9 years old or older. Our young males are equivalent to the “subadult” males in the northern elephant seals literature (e.g., Deutsch et al. 1990).

Estimation of behavioral factors

We estimated the duration of presence on land of each male from the individual serial records collected during daily censuses. We collected behavioral data during 514 2-h observation periods in 2002 and 838 in 2003. We used all occurrences sampling and continuous recording (Altmann 1974). Full details of the observation protocol are available elsewhere (Galimberti et al. 2000a). From these data we calculated: (1) an index of general activity, given by the proportion of observation periods in which a male had social interactions with males or females; (2) an index of interaction with males, given by the mean number per observation period of male vs male interactions in which the male was involved as actor or reactor; (3) an index of aggression, given by the mean number of male vs male interactions that the male started per observation period; (4) an index of interaction with females, given by the mean number of male interactions with females per observation period.

We assembled yearly dominance matrices of wins and losses using the results of male vs male interactions recorded during observation periods. From these matrices, we calculated an index of success in competition with other males based on the David's score (Gammell et al. 2003). We corrected the proportions of wins and losses for random effects with the method of De Vries (1998). Almost the same number of breeding males was included in the estimation of the competition index in the 2 years, and, therefore, its absolute values were comparable between the years without any transformation.

Estimation of breeding performance

At Sea Lion Island, there was a harem-based female defense mating system, with a single male able to monopolize access to females of each harem (Fabiani et al. 2004). We define as *harem holder* the male within the female group as observed during the daily census. We define as *main breeding males* the males who were holders of the same harem for at least 2 consecutive days when there were females in oestrus. We define all other males as *peripheral males*. The number of females held by each male was not stable through the breeding season because of the pattern of arrival and departure of females (Galimberti and Boitani 1999). Therefore, we calculated a *females days index* (Clutton-Brock et al. 1982) by summing the number of females held by a male in each day of the breeding season for all days of its presence on land. We estimated the mating success of each male by calculating the number of copulations observed and standardizing it for 100 h of observation (Campagna and Le Boeuf 1988). We estimated the male reproductive success using the *estimated number of females inseminated* (ENFI, Le Boeuf 1974), calculated by summing, for each male and for each harem in which it was observed to copulate, the product of the proportion of copulations achieved and the number of females that bred in the harem. At SLI, ENFI showed a very high correlation with true genetic success, as estimated by microsatellite paternity analysis (Fabiani et al. 2004).

Statistical analysis

Body size variables had a symmetric normal distribution (Shapiro–Wilk tests—length: $W=0.989$, $n=110$, $z=0.047$, $p=0.48$; initial weight: $W=0.973$, $n=78$, $z=1.313$, $p=0.09$; final weight: $W=0.985$, $n=78$, $z=0.056$, $p=0.48$). Some variables were very skewed and not normally distributed (total weight loss: $W=0.920$, $n=78$, $z=3.69$, $p=0.0001$; percentage weight loss: $W=0.954$, $n=78$, $z=2.49$, $p=0.0064$; mating success: $W=0.684$, $n=78$, $z=7.45$, $p<0.0001$; ENFI: $W=0.664$, $n=78$, $z=7.58$, $p<0.0001$). Mating success and ENFI distributions showed a very long positive tail. Not being able to specify expected error distributions for these variables, we tested models involving them using randomization tests, which make no assumption about the distribution of the variables and of their errors (Manly 1997). The number of random permutations used in each test was 10,000 except where noted. Most analyses were carried out using ordinary least squares regression. We compared regression coefficients between two groups (e.g., adult vs subadults) using the Chow (1960) test. We included in regression results the standardized coefficients (*betas*) to permit an approximate comparison of the magnitude of effects of the different regressors. Multiple regression validation included the calculation of multi-collinearity diagnostics. To check the homogeneity of regression residuals, we visually inspected residual vs fitted scatterplots, and we applied the White (1980) test of heteroscedasticity. To verify the presence of nonlinear effects, we inspected scatterplots with fitted LOWESS (Trexler and Travis 1993), and we ran a robust version of the Ramsey RESET tests for omitted variables (Ramsey 1969). Statistics are presented as mean±standard deviation. Data analysis was carried out in STATA version 7 (Stata Corporation).

Results

Body size

The mean photogrammetric length (about 91% of the standard body length, Haley et al. 1991) was 364±23.5 cm ($n=110$; Fig. 1). Length was not different between the 2 years of study (*t* test: mean diff.=4.0 cm, se=4.5, $t=0.90$, $df=108$, $p=0.37$). The mean weight at first measurement was 1,809±458 kg. The mean weight at arrival date was 2,092±445 kg ($n=78$), ranging from 1,316 to 3,182 (Fig. 1). The mean weight at the end of the breeding season was 1,541±323 kg. In 2003, males were significantly

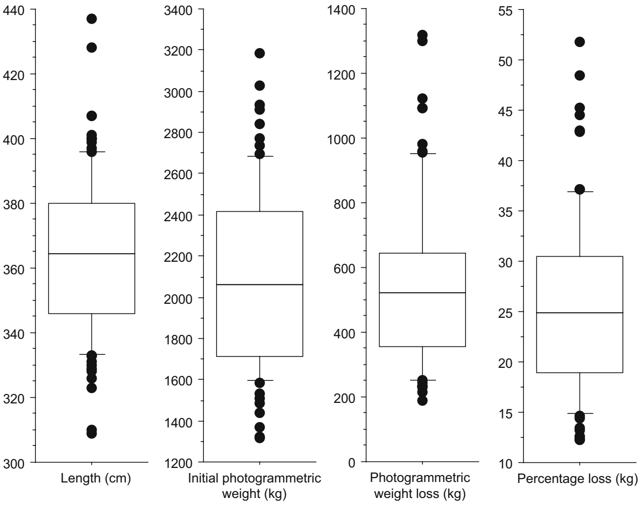

Fig. 1 Boxplots of the distribution of the morphometric variables. Length in centimeters; weight and photogrammetric weight loss in kilograms. The *box* represents the range between the 25th and 75th percentile, and the *horizontal line* within the box is the median; the *two lines* outside the box represent the 10th and 90th percentile; the *black points* are the observation <10th or >90th percentile

heavier at arrival (*t* test: mean diff.=219 kg, se=98, t=2.23, *df*=76, p=0.0289) and at the end of the breeding season (mean diff.=208 kg, se=70, t=2.99, *df*=76, p=0.038). Body weight at arrival increased with body length at a rate of 16.8 kg/cm (Linear regression: se=1.014, t=16.6, *df*=77, $p<0.0001$). Length explained 78.3% of the variability of weight at arrival. The slope of this relationship was homogeneous in the 2 years of study (Chow test: F1,74=0.03, p=0.87), but the residuals of the common regression were lower in 2002 (mean=−128 kg) than in 2003 (116 kg; *t* test: mean diff.=244 kg, t=6.41, *df*=76, $p<0.0001$), suggesting that most males were in better condition at arrival in 2003.

Weight loss

Total weight loss of individual males ranged from 231 to 1,319 kg (n=37, mean=545±243) in 2002 and 189 to 1,300 kg (n=41, mean=556±269) in 2003 and was homogeneous between the 2 years of study (mean diff.=10.6, se=58.3, t=0.18, p=0.8628). The percentage loss ranged from 12.6 to 51.8% (mean=27.1±8.98) in 2002 and 12.3 to 45.2 in 2003 (mean=24.6±8.69) in 2003. It was homogeneous between the years (*t* test, with randomization: mean diff.=2.48%, se=2.0, t=1.24, p=0.2320). The mean daily rate of weight loss was 9.1±2.9 kg/day in 2002 (4.6–16.3) and 9.0±4.1 in 2003 (3–22.5). The mean daily weight-specific loss was 4.7±1.5 g/kg (2.7–9.7) in 2002 and 4.1±1.5 g/kg (1.9–9.1). Pooling the data between the 2 years, males lost a mean of 551 kg, which is 25.8% of their body weight (Fig. 1). Weight loss trajectories of the 2003 males with three or more measures are shown in Fig. 2. The male that had the greatest percentage loss (51.8%) was an adult male who held a big harem, looked exceptionally thin at the end of the breeding season, and did not survive to the following year. Total weight loss of individual males was related to both their length (Linear regression, with randomization: b=6.2 kg lost per cm, se=1.02, t=6.08, p=0.0001), which explained 33% of its variance, and their initial weight ((Fig. 3, b=0.401 kg lost per kg, se=0.047, t=8.52, p=0.0001), which explained 49%. The correlation between body length and weight was not so strong to produce a problem of multicollinearity (tolerance=0.22). Therefore, we ran a multiple regression with both variables, and weight was shown to be the most important of the two in determining weight loss (beta=0.888, $p<0.0001$ vs 0.214, p=0.2321).

To calculate the best population-wide estimate of weight loss rate we ran a mixed model regression on the repeated measures of weights (all weights for all males with three or more weights) with the days from arrival on land as the independent variable and the individual identities as random effect. Weight decrease was linear (Ramsey RESET test: $F_{3,246}$=0.95, p=0.42). In 2002 (n=88 measures of 21 males), weight loss rate was 8.7 kg/day (se=0.46, 95% ci=7.8–9.6). In 2003 (n=163 measures of 33 males), it was 8.8 kg/day (se=0.39, 95% ci=8.1–9.6). The average within male R^2 was 0.85 in 2002 and 0.80 in 2003, showing that the linear model gave an excellent fit of the individual weight loss. The Breusch and Pagan test for the random effect was significant in both cases (2002: $\chi_1^2 = 105.2$, $p<0.0001$; 2003: $\chi_1^2 = 308.6$, $p<0.0001$), showing that different males have

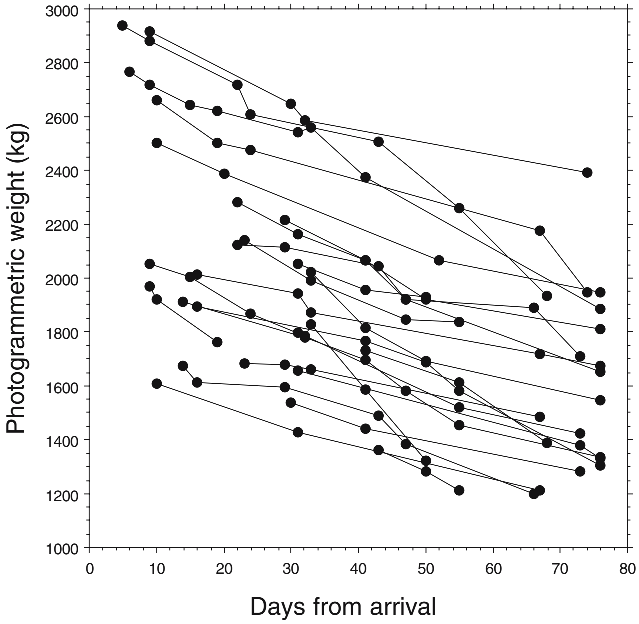

Fig. 2 Individual photogrammetric weight loss trajectories for 2003 males with three or more weights

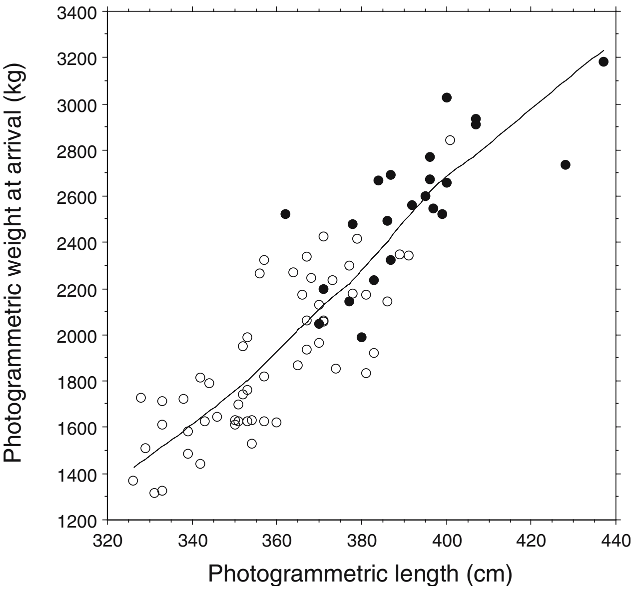

Fig. 3 Scatterplot of photogrammetric weight versus length. The *fitted line* is a LOWESS regression with 0.66 tension (Travis and Trexler 1993). *Filled circles*, mature males; *empty circles*, young males

significantly different rates of weight loss. The difference in weight loss rate was not significant between the two seasons (Wald test on the difference between regression coefficients: $\chi_1^2 = 1.49$, $p=0.22$). The weight loss rate estimated for the pooled data was 8.8 kg/day (95% ci=8.1–9.3).

Age-specific variation of weight loss

Mature males had a higher total (i.e., non size-independent) weight loss than young ones (748±61.7 kg, $n=23$ vs 468±24.8, $n=55$; *t* test, with randomization: mean diff.=280 kg, se=55.1, $t=5.07$, $p=0.0001$) and a higher percentage loss (28.9±2.1 vs 24.5±1.1; mean diff.=4.4%, se=2.2, $t=2.06$, $p=0.0326$). Total loss increased with age (Fig. 4) at a rate of 113 kg/year (Linear regression, with randomization test: se=19.9, $t=5.69$, $p=0.0001$, $R^2=0.31$) and percentage loss at 1.70% (se=0.81, $t=2.10$, $p=0.0393$). Size-independent loss (i.e., the loss after removing the effect of length) was not related to age ($b=20.5$, se=19.4, $t=1.06$, $p=0.2913$). Males measured three or more times in both 2002 and 2003 had a higher weight loss in 2003 (Paired *t* test, with randomization: mean diff.=160 kg, $t=2.27$, $p=0.0369$).

Weight loss and male status

Main breeding males ($n=30$) were both longer (387±18.7 cm vs 357±18.0; *t* test: mean diff.=30.3, se=4.25, $t=7.12$, $df=76$, $p<0.0001$) and heavier upon arrival (2,403±392 kg vs 1,898±359; mean diff.=505 kg, se=86.6, $t=5.84$, $df=76$, $p<0.0001$) than peripheral males ($n=48$). Total weight loss was higher for main breeding males (704±50.6 kg) than for peripherals (455±27.1; mean diff.=249 kg, se=52.6, $t=4.03$, $p=0.0001$), while percentage loss was similar (28.8±1.6 vs 23.9±1.2, mean diff.=4.9, se=2.0, $t=2.48$, $p=0.1111$). The total weight loss increased with the increase in the total number of females held (Linear regression, with randomization: $b=0.191$, se=0.050, $t=3.80$, $p=0.0007$), but the variance in loss explained by the females days index was rather small (adjusted $R^2=0.16$). Both percentage loss ($b=0.005$, se=0.002, $t=2.66$, $p=0.0084$) and size-independent loss increased slightly with the females days index ($b=0.079$, se=0.044, $t=1.80$, $p=0.0516$).

Behavioral factors affecting weight loss

Males were present on land for a mean of 61.6±15.0 days. Weight loss increased with the duration of presence on land (Linear regression, with randomization test: $b=9.4$, se=1.59, $t=5.88$, $p=0.0003$). Weight loss was not related to general activity ($b=-244$ kg, se=173.4, $t=-1.14$, $p=0.1863$). Weight loss increased with the rate of interaction with other males ($b=63.0$, se=21.9, $t=2.88$, $p=0.0060$, beta=0.314), but the proportion of variance associated with the regression model was small ($R^2=0.10$). Aggression rate had a stronger effect ($b=96.3$ kg, se=16.5, $t=5.82$, $p=0.0001$, beta=0.556) and explained a bigger proportion of variance in weight loss ($R^2=0.31$). Aggression rate had a slight effect on percentage loss ($b=1.63\%$, se=0.66, $t=2.45$, $p=0.0149$, beta=0.271) but not on size-independent loss.

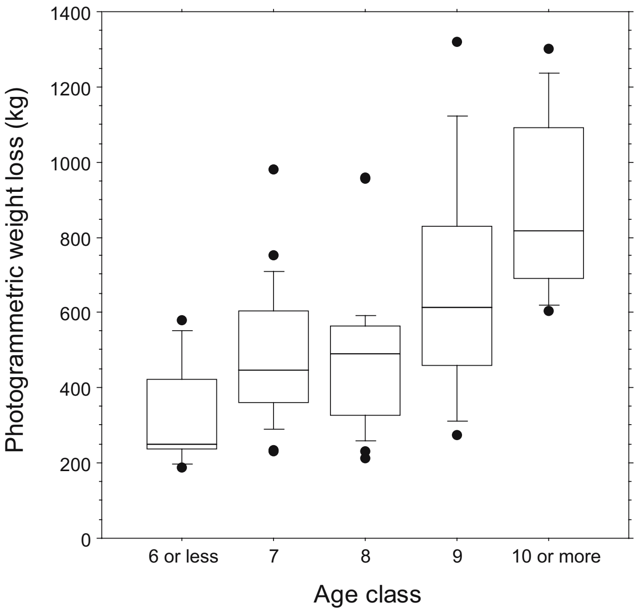

Fig. 4 Boxplot of photogrammetric weight loss versus age class (males of age 6 or less, and males of age 10 or more, were pooled). The *box* represents the range between the 25th and 75th percentile, and the *horizontal line* within the box is the median; the *two lines* outside the box represent the 10th and 90th percentile; the *black points* are the observation <10th or >90th percentile

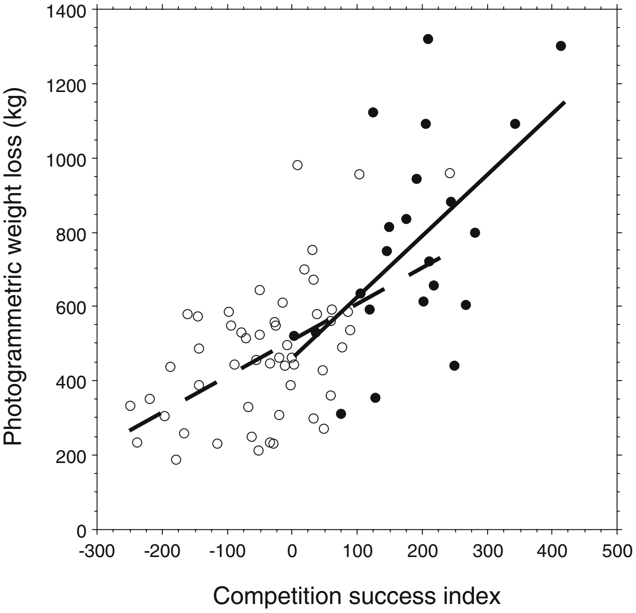

Fig. 5 Scatterplot of photogrammetric weight loss versus success in competition, as measured by the David's score, with regression lines for young and mature males. *Filled circles* and *plain line*, mature males; *empty circles* and *dashed line*, young males

Weight loss increased with the individual rate of interaction with females (b=124 kg, se=17.9, t=6.92, p=0.0001, beta=0.621), and the proportion of explained loss variance was rather large (R^2=0.39). The rate of interaction with females also affected the percentage loss (b=2.9%, se=0.72, t=4.08, p=0.0002, R^2=0.18) and the size-independent loss (b=63.1 kg, se=17.4, t=3.63, p=0.0004, R^2=0.15).

Weight loss increased with the increase in the competition success index (Fig. 5; b=1.23, se=0.15, t=7.97, p=0.0001, beta=0.685), and this factor explained a rather large proportion of the variance in loss (adjusted R^2=0.47). The slope of the model was steeper for mature males (b=1.67) than for young males (b=0.946), but the difference was not significant (Chow test: $F_{2,70}$=0.8728 p=0.42). Success in competition increased also the percentage loss (b=0.026, se=0.007, t=3.94, p=0.0002, R^2=0.18) and the size-independent loss (b=0.476, se=0.165, t=2.89, p=0.0048, R^2=0.10).

To test the combined effects of the structural and behavioral factors that affect weight loss, we ran a multivariate regression of weight loss vs length, age, aggression rate, competition success, and rate of interaction with females. We included length instead of weight because it is a better measure of structural size. These variables were themselves correlated (all r>0.50) but not so much to produce a serious multicollinearity problem (all tolerances> 0.23). The model explained 57% of the variance in loss, and the most important factors were behavioral, the competition success, and the rate of interaction with females, while the structural factors had nonsignificant regression coefficients (Table 1).

Effect of weight loss on individual fitness components

The weight loss of unsuccessful individuals (ENFI≤10, n=58) was significantly lower than the weight loss of successful ones (n=20; t test, with randomization: mean diff.=−262 kg, se=66.3, t=−3.95, p=0.0001). Mating success increased with weight loss (b=0.018, se=0.004, t=4.35, p=0.0001, beta=0.446, R^2=0.20) but not with percentage loss (b=0.21, se=0.13, t=1.61, p=0.1064). ENFI increased with total weight loss (b=0.055, se=0.008, t=6.72, p=0.0001, beta=0.610, R^2=0.37) and percentage loss (b=0.914, se=0.281, t=3.26, p=0.0019, beta=0.350, R^2=0.12). A model including length, age, weight loss, and competition success explained 62% of the variance in ENFI, but the standardized regression coefficients of weight loss (beta=0.163) and length (0.145) were not significant and smaller than the significant coefficients of age (0.280) and competition success (0.301).

There was no difference in weight loss between males that survived to the next breeding season (n=22, mean=572±50.4) and males that did not (n=15, mean=590±93.6; t test, with randomization: mean diff.=17.6, se=98.3, t=0.18, p=0.4135).

Table 1 Multiple regression of weigh loss versus body length, age, aggression rate, competition success, and rate of interaction with females

Variables	*b*	se(*b*)	beta	*t*	p	95% CI (*b*)	
Length	1.69	1.60	0.154	1.05	0.2778	−1.51	4.89
Age	0.17	29.87	0.001	0.01	0.8954	−59.50	59.84
Aggression rate	−38.35	26.25	−0.225	−1.46	0.1521	−90.78	14.09
Competition success	0.93	0.28	0.518	3.28	0.0016	0.37	1.50
Rate of interaction with females	74.65	24.70	0.375	3.02	0.0031	25.30	124.00

b Partial regression coefficient; *se(b)* standard error of the partial regression coefficient; *beta* standardized partial regression coefficient; *t t* test statistics; *p* result of the randomization test on the null hypothesis H0: *b*=0, with 10,000 resamplings, 95% ci(*b*)=95% confidence interval of the partial regression coefficient calculated using the bootstrap (1.000 samples)

Discussion

Assumptions and limitations of our study

Our study was observational, with no control of the study setting and of the subjects included. Moreover, the evidences we produced are purely correlational, and correlation does not mean causation. The modelling of optimal life history evolution assumes the presence of a genetic basis for the life history traits involved. Phenotypic correlations are not always a good index of genetic correlations because they measure both environmental and genetic effects on a trait. Therefore, the ideal methods to deal with reproductive effort are quantitative genetic designs and selection experiments (Reznick 1985). On the other hand, phenotypic correlations are often a good index of genotypic correlations (Cheverud 1988). Moreover, experimental genetic approaches to the study of reproductive effort often require such a simplification of the study settings compared to the natural settings that they measure only a part of the true reproductive effort (Bell 1980; Reznick 1985). Many species, and many interesting biological questions, are not amenable of experimentation, and even when experiments in natural setting are practically feasible, they may present a high ethical cost (Cuthill 1991).

The photogrammetric method of weight loss estimate proved effective because it produced a large sample of repeatable measures. The method is particularly suitable for male elephant seals (see also Bell et al. 1997). Direct weighing may provide better estimates of each weight but also has drawbacks. Strongly invasive methods, which requires physical or chemical restraint, present risks (Deutsch et al. 1990), have an ethical cost (Wilson 2002), are difficult to apply serially to the same individual, and may disrupt behavior. All these problems are amplified by the large size of elephant seal males (e.g., Bryden 1969). The use of a weighing platform (Deutsch et al. 1990), although ingenious and effective, is difficult to implement in the field, requires a large effort to obtain each weight, presents the risk to disrupt behavioral activity (due to the methods used to lure the male on the platform), and has a moderate success rate (42% successful attempts, Deutsch 1990 p. 26). The photogrammetric method is fast (each picture/weight requires a modest effort), produces a large sample of serial measurements, is cheap to implement, and has a high success rate (the percentage of pictures suitable for measurement was 81.8%, n=1,974 pictures). Therefore, the photogrammetric estimation of weight is a valuable alternative to direct weighing, but also to the behavioral estimation of reproductive effort, the reliability of which is questionable (Mysterud et al. 2004).

In our study, a small number of older males were measured. This was not due to a sampling bias because we measured most breeding males in our study population and all males of the older classes. In the only other study available on breeding male age distribution, the percentage of males older than 10 years was 22.5% (South Georgia; McCann 1980), higher than the 5.1% of SLI. Therefore, our results would be conservative because we expect that more males of the oldest age classes would increase the difference between young and mature males.

Components of reproductive effort in male elephant seals

Reproductive effort has three components, energy, time, and risk (Warner 1980). In this paper we considered just one component of male effort, the energetic one, as measured by photogrammetric weight loss. Although this is the method of choice to estimate reproductive effort in capital breeders (Mysterud et al. 2004), the importance of other components should be assessed. There is a large variation in the importance of the time component between species (Owen-Smith 1984). The time component can be important in species with a complex mating pattern, where a male may require a significant amount of time to find an oestrus female, where courtship can be complex and time consuming and copulation itself can be a long process, and where postcopulatory mate guarding may be crucial for reproductive success. Moreover, in species with stable, long-term, social bonds between males and females, the male may need to allocate a considerable amount of time outside the strict mating period to interact with females, to maintain the cohesion of the breeding unit and be able to mate (e.g., this “loyalty” problem is the core of male reproductive effort in another harem breeding mammal, the gelada baboons, Dunbar 1984). In all these species, males are clearly time limited, and time allocation is an important component of their reproductive strategies and effort. Nothing of this applies to elephant seals: males keep no social bond with females; reproduction is gregarious and there is no searching phase for oestrus females; males are not selective in their choice of females to mate with and copulation takes a negligible amount of time (Galimberti et al. 2000a); mate guarding is a minor and occasional component of mating behavior (Galimberti et al. 2000b). Altogether, elephant seal males seem not to be limited by mating time, at least at the high level of polygyny of our study population. The same seems to happen in South Georgia, where harems are bigger (McCann 1983). In our study population, the average time budget comprises about 85% of time dedicated to resting and just about 5% to social activities. It is rather unlikely that the differential allocation among males of this small amount of social time will produce any significant difference in total reproductive effort. This is in accordance with the lack of a relationship between our index of general activity and weight loss.

The risk component of reproductive effort is difficult to assess. Physical damage due to male competition is frequent in some species (Wilkinson and Shank 1977; Silverman and Dunbar 1980; Geist 1986; Drews 1996; Pack et al. 1998), but its effect on reproduction and survival is unclear. In elephant seals, although fights are an important component of agonistic behavior (Haley 1994), most social interaction are settled without physical contact (Sandegren 1976; McCann 1981) and vocalizations convey reliable information about the contestants phenotype (Sanvito et al. 2007a), permitting the resolution of conflicts through assessment. At SLI, only 3% of the interactions are actual fights, and most interactions are settled by vocalizations (Sanvito et al. 2007b). Notwithstanding this, males were frequently wounded, although wounds were never so severe as to stop a male's breeding activities, and we observed just one case of lethal fight in 12 breeding seasons. In northern elephant seals, wounds appear to be a minor cost of reproduction (Deutsch et al. 1994), and lethal fights are exceptionally rare (Deutsch 1990). Other risk components are possible, including predation and disease transmission, but, altogether, the risk component seems to be of minor importance in male elephant seal reproductive effort.

Patterns of weight loss

SLI males were heavier at arrival (mean=2,092 vs 1,704 kg, max=2,265 vs 3,182) and lost more weight (vs 198–1,049 kg) than northern elephant seals of Año Nuevo (Deutsch et al. 1990). They had a lower mean percentage loss (25.8 vs 35.6), but a higher maximum (51.3 vs 46.3%) and a higher variability (CV=0.343 vs 0.160). This difference could have been an artefact of the different protocol, but it seems too large to be explained just by this due to the low variability of individual estimates at both sites. The growth trajectory of SLI males (personal observation) is quite different from the northern elephant seals one (Clinton 1994). In the northern species, the growth rate shows a fast reduction between age 6 (relative growth about 9%) and 8 (2%), and then reaches a plateau. At SLI, the growth rate is similar at age 6 (8%), but the decrease is less steep (>5% at age 8), and the growth rate remains above 2% up to age 12. Therefore, although the age range of males present during breeding was similar between our study and the northern elephant seal study, the body size range was smaller in the northern elephant seal sample (see also Clinton 1990), and the observed higher variability in reproductive effort at SLI can be a result of this larger spread in body size.

The causes of the huge sexual size dimorphism in elephant seals are not clear. A large size confers a fecundity advantage to females (Le Boeuf and Reiter 1988) and is an important component of male competition for mates (Haley et al. 1994). At SLI, length explained about 56% of variance in the competition index, and initial weight explained 57% of it. Moreover, a large size may improve fasting endurance (Andersson 1994; Murphy 1998) because the exponent of the allometric scaling of metabolic rate with body size is lower than 1 in seals (Lavigne et al. 1986; Boyd 2002) and mammals at large (Reiss 1989), although this point is somehow controversial because most evidence comes from inter-specific studies (Millar and Hickling 1990). The effect of body size on both competition and endurance may well explain why male elephant seals are so big, and so much bigger than females. On the other hand, bigger individuals require bigger amount of food to survive, and this may put an upper limit to size evolution (Blanckenhorn 2000). In southern elephant seals, males demand a much greater proportion of resources than females, both individually and at the population level (Boyd et al. 1994). At SLI male size showed a reduction of about 32 cm in photogrammetric length from 1995 to 2003 (personal observation). The reduction in mean size of breeding males observed at SLI, and the almost complete disappearance of the very large males present in the first years of our long-term study could have been the product of a shortage of food resources that made it impossible for the largest males to recover from the weight loss suffered during breeding. Therefore, the ecological constraints set forth during the aquatic feeding phase may be the limiting factor in the increase in reproductive effort.

Data on the reproductive effort of male mammals is scanty and almost limited to seals only (Table 2). The absolute and percentage weight loss of southern elephant seals at SLI was bigger than in any other species except the northern elephant seal. In northern elephant seals the lifetime pattern of reproductive effort, and life history at large, present striking differences between the sexes (Reiter and Le Boeuf 1991; Clinton and Le Boeuf 1993). Notwithstanding this, the mean reproductive effort of each breeding season is quite similar between the sexes, although it is more variable in males (Deutsch et al. 1994). Southern elephant seal females of the South Georgia population (Arnbom et al. 1997) had a higher mean percentage effort than males at SLI (34.6 vs 25.8%) but a lower maximum effort (42.0 vs 51.8%) and a lower variability (CV=0.104 vs 0.343). Daily rate of weight loss was only slightly lower (7.9 vs 9.1 kg/day), but again the variability was much lower (CV=0.177 vs 0.392). Our study confirms the higher variability of male reproductive effort, as expected for a polygynous species in which females have few opportunities to increase their seasonal reproductive success, being limited to a single pup per breeding season.

Reproductive effort and age

Reproductive effort is expected to increase with age when the adult mortality is low, when individuals continue to

Table 2 Summary of the information available on pinniped male reproductive effort

Species	Data set	Body weight	Presence on land	Weight loss	Percentage loss	Weight loss rate	Reference
Mirounga leonina	Pooled	2,092±445 (0.213)	61.6±15.0 (0.244)	551±255 (0.463)	25.8±8.9 (0.343)	9.1±3.6 (0.393)	This study
.	Adults	2,592±306 (0.119)	68.7±16.1 (0.235)	748±296 (0.396)	28.9±10.2 (0.353)	11.0±3.9 (0.354)	
.	Subadults	1,896±333 (0.176)	58.0±13.8 (0.238)	468±184 (0.392)	24.5±8.0 (0.326)	8.3±3.1 (0.377)	
M. angustirostris	Adults	1,704±213 (0.125)	91.0±14.8 (0.163)	622±171.5 (0.276)	36.2±6.6 (0.182)	7.08±1.54 (0.218)	Deutsch et al. 1990
.	Subadults	1,178 (737–1,403)				4.55±0.83 (0.182)	
Halichoerus grypus	Pooled	235–245	36 (32–41)		17	2.1–2.3	Anderson and Fedak 1985
.	Pooled	298±29.5 (0.099)	21	41.9±17.7 (0.422)	14.3±5.8 (0.406)	2.9±0.9 (0.310)	Tinker et al. 1995
Cystophora cristata	Pooled	312.5±53 (0.170)	17.5	44	14	2.5±1.1 (0.440)	Kovacs et al. 1996
Phoca vitulina	Adults	108±5.6 (0.052)	29	max 26.5	max 24	0.913±0.07 (0.067)	Walker and Bowen 1993
.	Subadults	76±6.6 (0.087)				0.229±0.142 (0.620)	
Arctocephalus gazella	Pooled	188±1.92 (0.010)	30.7±2.21 (0.072)		24 (4–41)	1.53±0.04 (0.026)	Boyd and Duck 1991

Values are mean±standard deviation and coefficient of variation (or range) in parentheses, if available. Depending on the study, we present, the statistics for the full data set, or the statistics for the data set split between adults and subadults, or both

grow after puberty, and when the allocation of resources required for breeding is so large that it can significantly affect maintenance and growth (Charlesworth and Leon 1976; Charlesworth 1994). The reverse conditions favor an early start of breeding and a constant or reduced effort with age. Elephant seal males seem to meet the condition of an increase in reproductive effort with age. Mortality rates of mature males are low (Clinton and Le Boeuf 1993), growth continues after physiological maturity (McLaren 1993), and a massive resource allocation is required to breed at all. Contrary to expectation, in the northern species, Deutsch et al. (1990) found no differences in reproductive effort between subadult and adult males. At SLI, total reproductive effort and percentage effort increased with age, although the increase in size-independent effort was not significant. There is contrasting evidences about the age-specific allocation of reproductive effort in male mammals (Clutton-Brock 1984; Mysterud et al. 2003). Yoccoz et al. (2002) studied reproductive effort in the red deer (*Cervus elaphus*), a species with a harem-based mating system quite similar to elephant seals (Clutton-Brock et al. 1982), although with a lower male reproductive effort (Bobek et al. 1990). They compared two models: the "terminal investment" model, which forecast an increased terminal reproductive effort due to the reduction in reproductive value (Clutton-Brock 1984), and the "mating strategy-effort" model, which forecast a peak in breeding effort for prime-aged males, which usually are harem holders, followed by a decline in the older age classes. Red deer age-specific allocation of reproductive effort seems to fit the second model better. Southern elephant seals, on the other end, show a regular increase in reproductive effort, with no late decline and no signs at all of male reproductive senescence. At SLI, all males that were able to breed showed a clear increase in breeding success up to their last breeding season, and then died, without any sign of breeding senescence.

The much bigger total reproductive effort shown by adult males at SLI should have important consequences on feeding strategies due to the need to recover a much greater energy loss in the same time span of the subadult males. Therefore, we may expect to observe differences in the migration and feeding patterns among males displaying different total reproductive effort. Unfortunately, although there is a rich database of information about feeding strategies of elephant seal females obtained by telemetry during the aquatic phases of the lifecycle, this sort of information is rare for males. There is evidence for a feeding segregation between the sexes, and for a large variation of feeding strategies between individual males, but no evidence of a relationship between male reproductive effort and feeding strategies (southern elephant seals: Campagna et al. 1999; northern elephant seals: Stewart

1997; Le Boeuf et al. 2000). This could be due to the small samples (<30 individuals even in the largest study, Le Boeuf et al. 2000).

The cost of success

Southern elephant seals are the most striking example of intrasexual selection (Andersson 1994) and the most extreme case of inequality of breeding success (Galimberti et al. 2002). Such an extreme system offers unique opportunities for males, but this clearly comes at a cost. Weight loss, both absolute and percentage, increased with both the index of success in competition and the rate of interaction with females. In northern elephant seals, a "dominance" index was the single strongest correlate of weight loss (Deutsch et al. 1990), explaining about 49% of the variance in loss (52% in combination with body weight). At SLI, the body weight and the competition index explained together about 47% of variance in loss. Social status is usually assumed to be related to reproductive effort, with higher-ranking males having a bigger effort than subordinates (but see Senar et al. 2000). In elephant seals, access to females is constrained by dominance relationships between the males (Le Boeuf 1974; McCann 1981), although there is room for alternative tactics (Baldi et al. 1996), and the resulting level of monopolization of females by main breeding males is lower in the northern species (Hoelzel et al. 1999). At SLI, a high rank in local dominance hierarchies, and a high global success in competition, which are costly factors in term of energetic expenditure, are smoothly converted to fitness currency because hierarchies are strongly linear (Galimberti et al. 2003) and harem size is moderate (Galimberti and Boitani 1999). These factors favor a strict control of the mating system by the dominant males and a strong monopolization of copulations (see also Modig 1996). Moreover, contrary to most seals including the northern elephant seal, male southern elephant seals show good skills to herd females both by recruiting females to their harem and by stopping them from leaving (Galimberti et al. 2000a). Herding improves the breeding performance of harem holders but comes at a cost, reflected in the effect of the rate of interaction with females on weight loss. Unfortunately, a measure comparable to our index of interaction with females was not calculated for the northern elephant seals study of Deutsch et al. (1990). We suspect this component to be less important in the northern species because of the lack of a well-developed herding behavior.

Acknowledgments We would like to thank C. and A. Galimberti for their long-lasting support of our researches on elephant seals, the Falkland Islands Government for the research licence, the Falkland Islands Development Corporation for letting us do the field work at Sea Lion Island, Mr. D. Gray and Miss Jenny Luxton for their help with the logistics. Many people helped us in the field, too many to be mentioned here, we wish to thank them all. Our research at Sea Lion Island was partially funded by Earthwatch Institute grants and by Strachan Visick Ltd. The comments of the Editor, Dr. Vincent Janik, and of two anonymous Referees greatly improved the manuscript.

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