Phenotypic determinants of individual fitness in female fur seals: larger is better

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Inter-individual differences in fitness in female vertebrates have often been related to phenotypic discrepancies, suggesting that bigger individuals exhibit greater fitness. However, the use of the temporally variable indices of quality, such as body mass/condition, may not represent the most reliable index over longer time intervals. Few studies have assessed the direct influence of body size (BS) on individual fitness. We addressed this knowledge gap using data from long-term monitoring of individually marked female subantarctic fur seals. The females of higher quality (i.e. higher lifetime reproductive success) were larger in BS than their counterparts, which correlated with their ability to provision their pup with greater and more regular energy supply, possibly through the maximization of foraging performance and body fat storage. We accordingly found that our study population could be divided into three contrasted categories of maternal quality, with 33% of the females producing over 71% of the viable offspring constituting the next generation. We suggest that a larger BS represents a crucial selective advantage for a central place forager, especially when exploiting remotely available resources.

Keywords: *Arctocephalus tropicalis*; body size; individual fitness; lifetime reproductive success; phenotypic quality; provisioning regularity

1. INTRODUCTION

Studies of reproductive performance offer important insights into evolutionary ecology, because lifetime reproductive success (LRS) represents a measure of individual fitness (Clutton-Brock 1988; Newton 1989). Past investigations of long-term breeding performance have revealed significant individual variation in fitness within a population. Some of these studies focusing on vertebrates have reported that fitness heterogeneity was mostly attributable to differences in parental lifespan and/or in offspring survival (Clutton-Brock 1988; Newton 1989) rather than to any variation in fecundity (Gaillard *et al.* 2000*b*).

Factors such as sex (Clutton-Brock 1988), cohort (Rose *et al.* 1998), diet choice (Annett & Pierotti 1999) and body size (BS; LeBoeuf & Reiter 1988) have also appeared to represent individual characteristics with a potential to affect individual fitness. While the bird studies have reported contrasted correlations between fitness and BS (Newton 1989), the fitness of female ungulates was found to be strongly affected by the lifespan of the mother and its offspring (Clutton-Brock 1988; Bérubé *et al.* 1999), both being related to maternal BS (Gaillard *et al.* 1997; Festa-Bianchet *et al.* 1998). These studies have used body mass and/or body condition as a preferred indicator of BS. Body condition or mass, however, may vary temporally as a function of environment, population status, season, habitat quality or food availability. Repeatable phenotypic measurements would represent a more reliable index of individual fitness over longer time intervals (Arcese 2003). Since some phenotypic traits may infer a reproductive advantage only under particular conditions (i.e. food

availability, population density), long-term monitoring of individuals under a wide range of environmental conditions is necessary to assess the effects of phenotypic characters on reproductive success (Festa-Bianchet *et al.* 1998). Such analyses permit investigation of whether individual quality and its phenotypic determinants represent a dynamic or a constant variable over time (Houston & McNamara 1992; McNamara & Houston 1992).

Tackling the influence of phenotypic traits on individual fitness is of major interest for evolutionary ecology and population dynamics of large mammals. Yet the overwhelming majority of studies using such an approach have been conducted on the terrestrial population (Clutton-Brock 1988; Newton 1989; Arcese 2003). Similar investigations on the marine or coupled marine–terrestrial system would therefore contribute valuable insights on the phenotypic and ecological determinants of fitness. The extreme simplification of parental allocation due to an annual litter size of one offspring maximum raised solely by the female makes pinnipeds very suitable models to examining life-history evolution in a large mammal (Trillmich 1996). Furthermore, the large degree of philopatry on one breeding site exhibited by female fur seals enables long-term monitoring of breeding performances as well as repeated captures.

From a large-scale analysis of long-term individual variation in reproductive output of subantarctic fur seals (*Arctocephalus tropicalis*), we investigated (i) the reliability and repeatability of several predictors of maternal quality, (ii) the phenotypic traits exerting a significant and consistent influence on maternal quality, and (iii) the fitness differences between distinct groups of maternal quality within the population. We used a 10-year monitoring study, a time frame that equals the maximum reproductive lifespan in this female population (Dabin *et al.* 2004). This population has

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shown significant heterogeneity in maternal performances, with breeding females exhibiting higher survival rate than non-breeders and successful breeders having the highest probability to breed successfully during the following reproductive season (Beauplet *et al.* 2006). Consequently, an additional aim of this study was to partition this female population into several classes of maternal quality in order to assess the respective contribution of each class to the next generation.

2. MATERIAL AND METHODS

(a) *Study site and species*

The subantarctic fur seal is a large long-lived marine mammal that hauls out to breed on islands located north of the Antarctic Polar Front (Bester 1984). Births of a single pup occur from late November to early January (Georges & Guinet 2000) followed by approximately 10 months of nursing (Georges *et al.* 1999). During that highly energetically demanding period, females alternate long foraging trips in oceanic waters of the subtropical front where they prey mainly on myctophids (Beauplet *et al.* 2004) with short fasting visits ashore to suckle their pup. Upon weaning, offspring leave their native island and acquire nutritional independence (Oftedal *et al.* 1987; Bowen 1991); they will not return to their native colony before reaching 3–6 years of age (Beauplet *et al.* 2005).

The study was conducted at the 'La Mare aux Elephants' colony, on the northeast side of Amsterdam Island, southern Indian Ocean (37°55′ S, 77°30′ E), where one of the island's largest breeding colonies can be found (Guinet *et al.* 1994). This subantarctic fur seal population has been monitored for over 10 years using capture–mark–recapture methods (Beauplet *et al.* 2005, 2006). Here, we used data collected from 1994 to 2004, when over 60% of the adult females of the study colony were marked with individually numbered plastic tags (Dalton Rototags, Dalton Supply, Nettlebed, UK) in the connective tissue on the trailing edge of both fore flippers (Georges & Guinet 2000). The yearly capture probability of these marked breeding-age females was over 0.90, and rose up to 1.00 when the females experienced a breeding event (Beauplet *et al.* 2006).

(b) *Measuring age, body size and foraging regularity*

In otariids, body length increases throughout life, even after sexual maturation (Trites & Bigg 1996; Dabin *et al.* 2004). During the 1999 breeding season, tooth samples were collected from 108 tagged adult females for age determination (Dabin *et al.* 2004). During the 1996–2004 breeding seasons, we repeatedly measured the body size (BS; tip of nose to tip of tail with the animal lying on its ventral face, ±1 cm, ASM 1967) of known-aged females (from individuals that either had a tooth extraction or were marked as pups) during annual capture events, which allowed us to obtain simultaneously the age and BS of tagged adult females on 223 occasions (Beauplet *et al.* 2006). A mean female age-specific body size (MBS_{AGE}) could therefore be calculated from 5 to 16 years of age. For each individual measurement, we subsequently defined the residual body size (RBS in cm) as $RBS = BS - MBS_{AGE}$ (i.e. females with a positive RBS are larger than the expected size at a given age). We then calculated the individual mean residual body size for each known-aged female for which we have a body size measurement at least during two different breeding seasons over the study period. The mean residual body size value therefore reflects whether the studied female is overall longer or shorter than its conspecifics of the same age.

Throughout lactation, regular searches of the colony were conducted for tagged seals. This enabled the time onshore and the duration of the successive foraging trips to be determined for females breeding during the 1999–2004 seasons. While fur seal foraging trip duration has shown contrasted influence on offspring growth due to food availability affected by season (Beauplet *et al.* 2004) or lunar cycle (Horning & Trillmich 1999), a positive effect of offspring provisioning variability on its growth rate and mass at weaning/fledging has been demonstrated in several marine top predators (Georges & Guinet 2000; Weimerskirch *et al.* 2000). Therefore, for each year, we calculated the foraging trip regularity of the tagged mothers defined by the coefficient of variation of the foraging trip duration experienced by a female during both halves of the rearing period (i.e. before and after mid-April; see Beauplet *et al.* (2004) for further details on seasons). For the analysis, we restricted the sample to the females whose foraging trip duration data were recorded during at least two different breeding events and, thus, subsequently calculated the intra-annual foraging trip variability as the averaging among annual foraging trip regularity.

(c) *Assessment of breeding success and individual fitness*

Intensive observations were conducted on the colony during the 1994–2004 breeding seasons in order to assess the breeding success of tagged females. Each searching session consisted of a 5-h continuous scan in the delimited rookery section and adjacent areas (Beauplet *et al.* 2006). The breeding colony was surveyed every day during the parturition period, and each newborn of a tagged female was sexed, weighed (±0.1 kg) and marked within 12 h after birth (Georges & Guinet 2000; Chambellant *et al.* 2003). Pup–mother relationships were determined when the mother was seen together with her newborn pup during the postnatal period. Between 100 and 200 newborn pups were marked each year and subsequently tagged (as previously described for adults) at one month of age. Tagged pups were then individually weighed regularly throughout the period of maternal dependence to determine the growth rate and to assess their survival throughout the rearing process (Chambellant *et al.* 2003; Beauplet *et al.* 2005). Mean and standard deviation of individual growth rates were then calculated for each breeding season (MGR_Y and SGR_Y, respectively). Each breeding event was subsequently characterized by a standardized yearly growth rate residual, defined as $GR_r = (GR - MGR_Y)/SGR_Y$ (Quinn & Keough 2002). When early mortality by starvation prevented us from calculating offspring growth rate (Chambellant *et al.* 2003), we assigned that pup the lowest individual GR_r value calculated for that breeding season (i.e. from a pup dying from starvation during a later stage of the rearing process).

The majority (above 96%) of the females younger than 7 or older than 16 years of age typically do not produce pups in our study colony (Dabin *et al.* 2004). Hence, we considered the female reproductive lifespan of this population to last a maximum duration of 10 years. Therefore, we restricted our analysis to the 7- to 16-year-old females whose breeding history was recorded during at least 5 years between the first and the last time observed on the study colony. Thus, our study sample is likely to overestimate the proportion of high-quality females as we omitted the lowest-quality individuals, i.e. those not surviving the reproductive costs faced during

Table 1. (*a*) Correlation matrix of the breeding frequency (BF), mean residual pup growth rate (MGR$_r$) and proportion of positive performance (PPP) and (*b*) their respective contribution (eigenvector$\pm$s.e.) on the first two components of the PCA characterizing maternal performances in subantarctic fur seal females breeding at Amsterdam Island.

(*a*)	BF	MGR$_r$	PPP
BF	1		
MGR$_r$	0.077	1	
PPP	0.076	0.840	1

(*b*)	PC1	PC2
BF	0.126$\pm$0.138	0.992$\pm$0.018
MGR$_r$	0.701$\pm$0.024	0.089$\pm$0.102
PPP	0.701$\pm$0.024	$-$0.090$\pm$0.102

the first breeding events (Beauplet *et al.* 2006). Owing to the high degree of philopatry and the capture probability of breeding females being 1.00, a female not seen in the study colony was considered a non-breeder for that breeding season (Beauplet *et al.* 2006). Data were available for 126 females, each contributing an average of 6.1 years of data (s.d.$=1.5$, range 5–10). Each female was then characterized using its breeding frequency (BF, number of breeding events divided by the number of breeding seasons during which individual breeding history was recorded), mean pup growth rate residual (MGR$_r$), and its proportion of positive performance (PPP) defined as the number of breeding events with positive GR$_r$ divided by the total number of breeding events exhibited by the female.

Our statistical analysis to distinguish and define the different categories of maternal fitness followed two steps. First, a principal component analysis (PCA) was run on the correlated variables characterizing females' breeding performances (BF, MGR$_r$ and PPP) in order to reduce these to a smaller number of independent components (table 1). A PCA ordination scatterplot then permitted the visualization of these components, displaying the gradient of reproductive performance exhibited by the females, and a subsequent determination of three categories of maternal quality by maximizing the ratio of between-group to within-group variance (Quinn & Keough 2002). Second, a discriminant function analysis (DFA) standard and jack-knifed classification procedures (Tabachnick & Fidell 1996) assessed the proportion of individuals correctly classified. Hence, it determined how well our three breeding performance variables could be used to characterize the individual fitness of breeding-age females (Quinn & Keough 2002).

Proportion of successful breeding events (RS) was calculated for each mother throughout its period of known breeding history by counting the number of offspring weaned with a sufficient growth rate to allow high postweaning survival probabilities (Pup growth rate>0.04 kg d^{-1}, Beauplet *et al.* 2005). Assuming that individual breeding frequency and success remain similar to the period of known breeding history throughout the 10-year reproductive lifespan (Beauplet *et al.* 2006), the individual lifetime reproductive success was subsequently estimated as: lifetime reproductive success$=(10\times\text{BF}\times\text{RS})$.
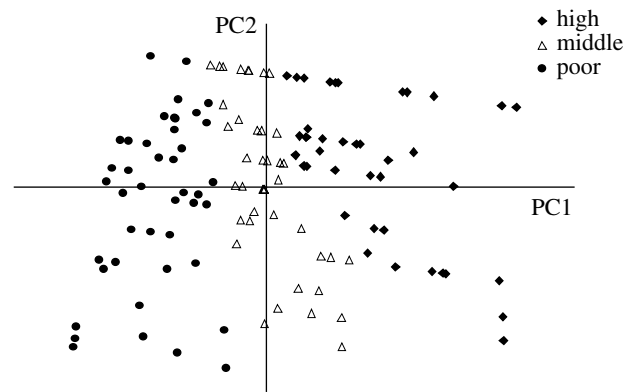
Figure 1. PCA ordination scatterplot of the 126 reproductive females based on a correlation matrix of association between variables related to breeding events observed between 1994 and 2004. The first two components explained over 94% of the total variance, with variables related to pup growth rate having the heaviest loading on PC1, while positive values on PC2 represent individual breeding frequency. Females of high maternal quality are represented by filled diamonds, whereas females of middle and poor maternal performances are represented by open triangles and filled circles, respectively.

(**d**) *Data analyses*

All statistical analyses followed the methods of Sokal & Rohlf (1981) and were performed with the SYSTAT v. 9.0 statistical software (SYSTAT, 9.0 statistics, SPSS, Inc., USA). The Kolmogorov–Smirnov test was used to determine whether the data were normally distributed and an *F*-test was applied to confirm the homogeneity of variances. We then used linear regression to test for the relationship between phenotypic parameters and maternal quality. Comparisons of means between groups of contrasted individual fitness were made using analyses of variance (ANOVAs) with *post hoc* Bonferroni tests. Unless otherwise stated, values are reported as means$\pm$s.e., tests are two-tailed and statistical significance was considered to be $p<0.05$.

3. RESULTS

The first two principal components (PCs) of the PCA accounted for 61.8% (PC1 eigenvalue$=1.85$) and 32.9% (PC2 eigenvalue$=0.99$) of the variability across the female population, respectively (94.8% of the total variance), and were therefore considered in further analyses. The mean growth rate residual and proportion of positive performance had the heaviest loading on PC1 therefore representing a direct and overall measure of maternal quality via pup growth characteristics, while PC2 was mainly driven by breeding frequency (table 1; figure 1).

The estimated lifetime reproductive success averaged 1.95 ± 2.11 for the 126 monitored females, the large standard deviation value underlining the high degree of maternal fitness heterogeneity within the female population. As expected, the fitness of fur seal females was found to be strongly related to PC1 ($p<0.0001$; figure 2). A negative relationship between the estimated lifetime reproductive success and PC2 was also detected ($y=-0.583x+1.948$, $R^2_{adj}=0.069$, $F_{1,124}=10.27$, $p<0.02$), but the low power (0.83) confirms that it was considerably weaker than that observed with PC1. Repeated body size measurements were obtained on 77 monitored females, showing a mean of 136.5 ± 0.4 cm, and a positive relationship was detected
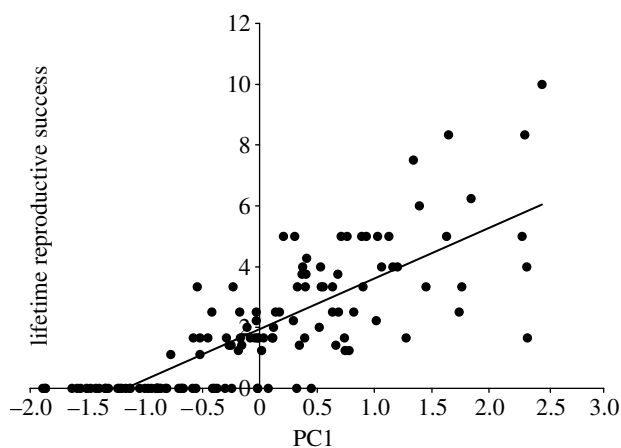
Figure 2. Relationship between the estimated lifetime reproductive success and PC1 representing a direct overall measure of maternal quality in subantarctic fur seal females breeding at Amsterdam Island. The linear regression calculated from individual data is shown ($y = 1.668x + 1.948$, $R^2_{adj} = 0.623$, $F_{1,124} = 207.24$, $p < 0.0001$).
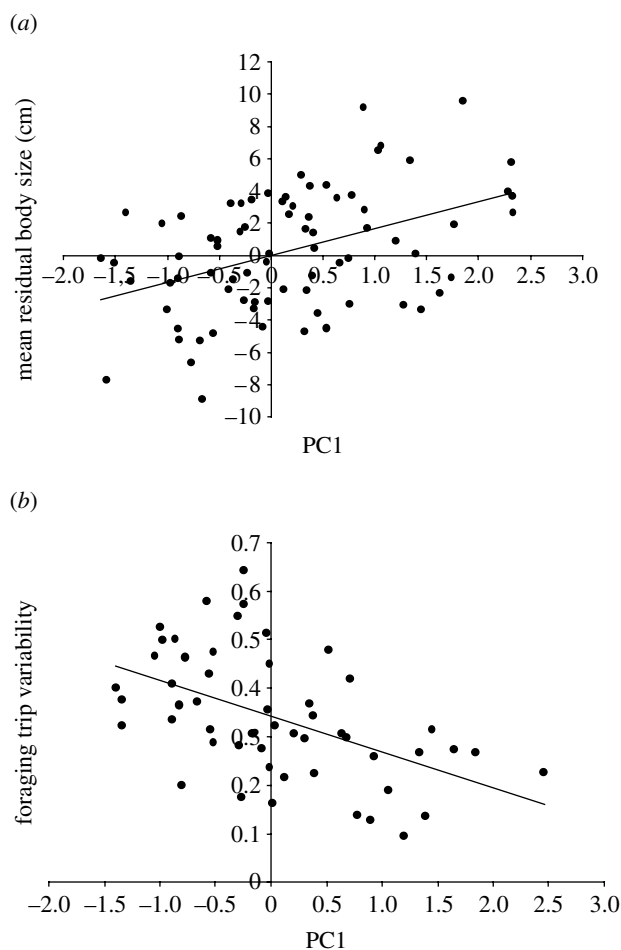
(*a*)

(*b*)

Figure 3. Relationship between two measured phenotypic characters and PC1 representing a direct overall measure of maternal quality in the subantarctic fur seal females breeding at Amsterdam Island. (*a*) The linear regression of the MRBS against PC1 ($y = 1.663x - 0.024$, $R^2_{adj} = 0.176$, $F_{1,75} = 17.24$, $p < 0.0001$). (*b*) The linear regression of intra-annual foraging trip variability during the first half of the rearing period against PC1 ($y = -0.074x + 0.343$, $R^2_{adj} = 0.241$, $F_{1,51} = 17.52$, $p = 0.0001$).

between the mean residual body size and PC1 ($p < 0.0001$; figure 3a). Intra-annual maternal foraging trip variability

Table 2. Differences in mean residual body size ($n = 77$), foraging trip variability ($n = 54$), breeding frequency, breeding success, estimated lifetime reproductive success and respective contribution to the next generation in 126 female subantarctic fur seals at Amsterdam Island, according to their maternal quality class.

maternal quality class	high	middle	poor
mean residual body size (cm)	$+2.43 \pm 0.63$	-0.36 ± 0.58	-1.95 ± 0.74
foraging trip variability (cv)	0.24 ± 0.02	0.38 ± 0.03	0.40 ± 0.02
N	42	41	43
breeding frequency (%)	75.5 ± 3.2	68.6 ± 3.5	58.8 ± 3.8
breeding success (%)	56.6 ± 3.3	25 ± 2.7	1.3 ± 1.1
lifetime reproductive success	4.20	1.58	0.10
contribution to next generation (%)	71.4	26.8	1.8

was assessed throughout the rearing period on 53 monitored females and was found to decrease with PC1 ($p = 0.0001$; figure 3b). Interestingly, no relationship was found between either of these phenotypic parameters and PC2 ($F_{1,75} = 0.20$, $p = 0.66$ for mean residual body size and $F_{1,51} = 0.00$, $p = 0.96$ for foraging trip variability).

Since the PCA ordination scatterplot of the 126 reproductive females did not show a clear aggregation pattern, we constituted three equally sized groups of maternal performance based on the individual PCA scores (figure 1). The results of DFA standard and jackknifed classification accuracies reached 91%, yielding only 11 misclassifications out of a total of 126 individuals. This result suggests that our classification method is robust and, therefore, confirms its ability to distinguish between the categories of maternal performance exhibited by the monitored females.

As expected, all fitness groups appeared to exhibit significant differences in maternal body size for a given age ($F_{2,74} = 11.90$, $p < 0.001$) and to differ in foraging trip variability during the first half ($F_{2,50} = 10.80$, $p < 0.001$), but not during the second half ($F_{2,50} = 1.96$, $p > 0.1$) of the rearing period. High-quality females exhibited lower foraging trip variability during the first half of the lactation period than that of the other fitness classes (*post hoc* Bonferroni: $p < 0.05$ and < 0.001, respectively), while the difference was not significant (*post hoc* Bonferroni: $p > 0.3$) between females of poor and middle quality (table 2). Accordingly, strong between-group differences in maternal breeding success were detected ($F_{2,123} = 125.13$, $p < 0.0001$), whereas differences in maternal breeding frequency were significant only between females of poor and high quality ($F_{2,123} = 5.81$, $p < 0.005$). Overall, 33% of the females successfully weaned on average over four pups, whereas the females of the other groups failed to wean two pups over their 10-year breeding lifespan (table 2).

4. DISCUSSION

In this study, we have shown that the use of a PCA on dependent factors related to pup growth characteristics and female breeding frequency allowed us to define an integrative variable representing maternal quality that was sufficiently distinct (classification success rate of 91%) to distinguish individual fitness categories within the female population. Our classification method was mainly based on PC1, representing the maternal performances of a female (via pup growth characteristics) throughout its breeding history. The lower impact of breeding frequency on maternal fitness variation is consistent with the low and/or variable survival experienced by the offspring until reaching the juvenile stage (Beauplet et al. 2005), and is in accordance with other studies of mammalian systems (Clutton-Brock 1988; Byers 1997).

All groups exhibited remarkably contrasted success rates in weaning pups that had likely high chances of postweaning survival. Accordingly, the lifetime reproductive success of high-quality females was estimated to be 2.6 and 40.0 times higher than the females of middle- and poor-quality class, respectively. Consequently, it appears that 33% of the females (i.e. high-quality group) produced up to 71.4% of the viable offspring, while the middle- and poor-quality groups, representing similar proportions, contributed to only 26.8 and 1.8% of the next generation of the population, respectively (table 2). Although our study underestimated by 4.4% the proportion of poor-quality females by restricting the sample to individuals with a minimum of 5 years of recorded breeding history (fig. 2 in Beauplet et al. 2006), these results confirm the large amount of heterogeneity in maternal quality within this population. Moreover, such an omission of the lowest-quality females dying during the within-cohort selection process prevented this study from reflecting any discrepancy in individual longevity or reproductive lifespan, as each group comprised females exhibiting a similar mean contribution as for the whole population (i.e. 6.1 years).

High-quality females exhibited body sizes of 2.79 and 4.38 cm longer than that of the middle- and poor-quality females of the same age (2.0 and 3.2% longer and, thus, 4 and 9% heavier, respectively), but did not experience a larger number of breeding events than that of the lower fitness categories. In other words, our results indicate a significant influence of individual body size on female fitness, but this relationship could not be related to any difference in female reproductive lifespan. In contrast, a previous study in roe deer (*Capreolus capreolus*) and bighorn sheep (*Ovis canadensis*) reported a positive influence of body mass on females fitness through a longer lifespan experienced by the bigger individuals (Gaillard et al. 2000a). Other studies on vertebrates have attributed the relationship between body mass and individual fitness to larger litter size (Festa-Bianchet & King 1991), greater parasite resistance (Coltman et al. 2001) or behavioural dominance (Murie & Harris 1988; Boag & Wiggett 1994). Since these interpretations are not applicable in our study case, we suggest two possible non-exclusive explanations for this finding.

Firstly, inter-individual body mass effects on reproductive success may in fact be due mostly to differences in skeletal size (Festa-Bianchet 1998), affecting the absolute amount of body reserves accumulated by the animal (Festa-Bianchet et al. 1998). A larger body size may therefore represent a crucial selective advantage for a central place forager, especially when it needs to exploit resources that are distant in space and time and require long-range travel (Beauplet et al. 2004), by maximizing the time spent in the most favourable foraging locations. Larger females also experience lower relative metabolic rates, which may allow them to be more efficient at converting acquired resource into fat reserves (Festa-Bianchet et al. 1998), and subsequently increase their survival under periods of low food availability (Gaillard et al. 2000a). Furthermore, if the capacity to absorb such a mass fluctuation is affected by the body size, then substantial mass loss during a breeding event may be more taxing for smaller females (Bérubé et al. 1999). Therefore, cost of reproduction would become apparent only when individual body reserve depletion is exceeded (Tuomi et al. 1983; Guinet et al. 1998; Loison et al. 2004), which may occur more often in smaller females (Festa-Bianchet 1998). This is in accordance with the lower survival reported in younger breeding females (Beauplet et al. 2006), indicating a higher proportion of lower-quality individuals in younger age classes which experience a within-cohort selection process through effective reproductive costs (Curio 1983; Vaupel & Yashin 1985; Cam & Monnat 2000). Interestingly, a higher long-term reproductive success of larger females has also been detected in a population of bighorn ewes experiencing a high population density (Festa-Bianchet et al. 1998). Hence, our finding confirms the hypothesis of a density-dependence effect (Chambellant et al. 2003; Beauplet et al. 2004), which may further increase the degree of individual heterogeneity within the study population (Toïgo et al. 2002). We suggest that the variability in body size is still maintained in this population because our 10-year monitoring study covered only one generation of breeding females (i.e. 10 years represents the individual maximum reproductive lifetime). However, this female population exhibits the largest average body size of this species (Robinson et al. 2002; Dabin et al. 2004), produces one of the richest otariid milk (Georges et al. 2001), and consequently reflects the position of this species as being further towards the capital breeding end of the spectrum (Trillmich 1996).

Secondly, we can reasonably expect that females with longer body size are probably faster swimmers and more efficient divers (Kooyman 1989) than their smaller counterparts. As such, they may have better abilities to maintain a constant periodicity in their successive foraging trips, providing their pup with regular access to energy supply and avoiding extended periods of fasting (Beauplet et al. 2003). This is supported by our results of the high-quality females exhibiting more regular foraging trips than those of the lower fitness categories. Such influence of foraging trip regularity on individual fitness is perhaps not surprising as a similar trend has been detected over one breeding season (Georges & Guinet 2000), but it is not clear yet what underlying mechanism leads to this relationship. Further studies of maternal foraging strategies in relation to individual fitness should consider the relationship between female lifetime reproductive success and individual phenotypic determinants.

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