Selection for increased body length in Subantarctic fur seals on Amsterdam Island

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Abstract

The traditional distinction between ecological and evolutionary times is eroding, calling for tighter links between ecology and evolution. An example of such a brigde between the two disciplines is the so-called 'animal model', a methodology initially developed by animal breeders, which has become very popular among ecologists studying contemporary microevolution. Using a Bayesian multi-trait 'animal model', we investigated the quantitative genetics of body size, a fitness-related trait, in Subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Amsterdam Island, Southern Ocean. Our approach jointly modelled the growth and selection processes at work in this population. Body length is heritable for both sexes, and females are under selection for increased body length in this population. We strongly suspect the peculiar ecological context of impoverished, suitable prey availability exacerbated by density-dependence phenomena to be an important selective agent on females breeding on Amsterdam Island.

Introduction

Traditionally, ecologists have assumed the action of natural selection to be negligible on a timescale of decades. The past few years witnessed, however, a surge in studies documenting rapid evolution in a wide range of species and ecological contexts (Hendry & Kinnison, 2001). For a phenotypic trait to evolve by natural selection, (i) this trait must vary, (ii) this variation must give rise to differential fitness, and (iii) finally this trait must be heritable. These three requirements are explicit in the 'Breeder's Equation' of quantitative genetics:

$$R = h^2 * S = \sigma^2_{additive}/\sigma^2_{phenotypic} * S = \sigma^2_{additive} * \beta \quad (1)$$

where R is the population evolutionary response in the next generation (on the same scale as that of the focal trait), $\sigma^2_{additive}(h^2)$ is the standing additive genetic variance (heritability) for the phenotypic trait and β (S) the selection gradient (differential) acting on this trait (Lynch & Walsh, 1998).

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Direct genetic data on wild animals may be scarce in general, whereas long-term demographic data can be more readily available. Although this lack of genetic data impedes our ability to bridge the gap between ecology and evolution, ecologists have embraced the quantitative genetics framework to investigate microevolution in the wild using the so-called animal model (reviewed in Kruuk (2004)). It is a hierarchical model that can handle complex pedigrees and partition the phenotypic variance into many *postulated causal components*, either genetic or environmental. The computer revolution and the availability of popular, friendly, statistical software made ecologists' dreams of analyses of large, unbalanced data sets with sophisticated models come true. The 'animal model' estimates at least one latent (unobservable) trait: an individual genetic merit, and an associated variance parameter: $\sigma^2_{additive}$. Although knowledge of the latter is crucial to our ability to understand the short-term evolutionary potential of wild populations, its accurate estimation is fraught with pitfalls arising from the (usually large) uncertainty inherent in estimating latent variables. This issue is not specific to ecology or quantitative genetics (see for example, Guo & Carlin (2004); Treier & Jackman (2008)), but was recently emphasized by Hadfield *et al.* (2010). With these caveats in mind,

we nevertheless proposed to investigate with the aid of Bayesian methods the quantitative genetics of a fitness-related trait in a wild population of marine mammals: body length of Subantarctic fur seal (*Arctocephalus tropicalis*, Grey 1872).

Ecology of the Subantarctic fur seal on Amsterdam Island

The Subantarctic fur seal is a long-lived, philopatric marine mammal breeding on islands scattered in the Southern Ocean (Wynen *et al.*, 2000). This species went close to extinction: the population breeding on Amsterdam Island (37°55′ S, 77°30′ E), now over 50 000 individuals, is thought to have numbered <150 years ago (Guinet *et al.*, 1994). On Possession Island, Crozet Archipelago (46°37′ S, 51°69′ E), this species is not known to have bred historically, yet a population genetically close to that of Amsterdam Island is currently breeding (Wynen *et al.*, 2000). Female fur seals on Amsterdam Island are 70% heavier and 20% longer than their Crozet conspecifics (for 33 measured females from Crozet, mean body length was 114 ± 7 cm and mean weight, 27.6 ± 4.3 kg; see Results and Fig. 1 for Amsterdam Island individuals). This conspicuous difference may suggest microevolution.

Subantarctic fur seals are central place foragers and yearly breeders. Females haul out on rookeries at the beginning of the Austral summer to give birth to a single pup whose rearing takes 10 months. Females take on all the parental care and alternate between foraging trips and short stays ashore during which they fast while suckling their pup (Georges & Guinet, 2000). As waters around Crozet are rich in Myctophid fish, breeding females take on short foraging trips (Luque *et al.*, 2007). In contrast, fur seals on Amsterdam Island undertake the longest trips described in any otariid species (more than 30 days long and 1000 km away from the rookery) to reach suitable foraging grounds (Beauplet *et al.*, 2004). Consequently, Amsterdam pups have to withstand extreme fasting periods from an early age, resulting in a large preweaning mortality rate of more than one-third (Chambellant *et al.*, 2003). Moreover, the Amsterdam population is very likely to experience density-dependence while the Crozet one is still growing (Guinet *et al.*, 1994). The environmental context of the two populations is thus in sharp contrast and may explain some of the observed morphological differences between females.

Our aim was to address whether the increased body length of female Subantarctic fur seals breeding on Amsterdam Island was consistent with microevolution. First, the variance components of body length in the Amsterdam population were estimated using an 'animal model'. Secondly, we estimated the selection gradient (Lande & Arnold, 1983) acting on body length. Variance components and selection gradients were estimated with
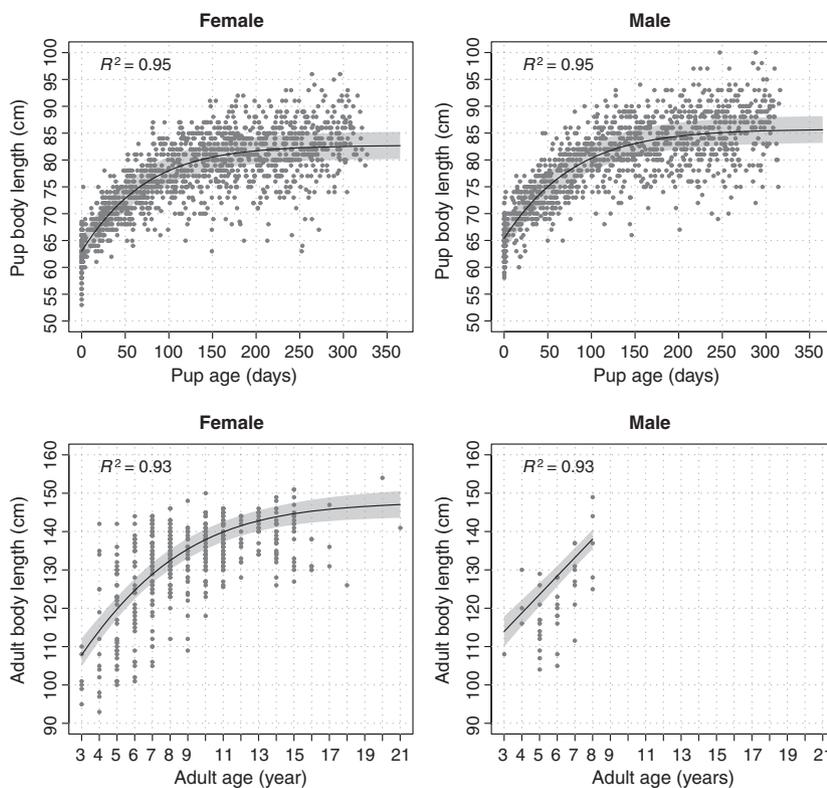
Fig. 1 Fitted growth curves for Subantarctic fur seals on Amsterdam Island. The grey envelope represents the 95% credibility interval.

a joint model to fully account for uncertainties in latent variable estimation (Guo & Carlin, 2004). Such a joint modelling approach provides less biased and more efficient inferences on any association between body length and fitness.

Materials and methods

Data selection and softwares

The breeding colony of 'La Mare aux Éléphants' on the north-east side of Amsterdam Island, Southern Indian Ocean, has been monitored since 1994, as part of a long-term demographic study. Both in 1994 and in 1999, adult females were tagged on the trailing edge of both fore-flippers with an individually numbered plastic tag (Dalton Rototag, Nettlebed, UK). During the 1999 reproductive season, a tooth sample was collected on some breeding females to age them (see Dabin *et al.* (2004) for details). Previous investigations into the at-sea ecology of female fur seals required many capture–recapture events upon which morphometric data were recorded. From 1995 to 2008, all pups of tagged females were captured, marked (using the same methodology as for adults) and measured at several occasions during the rearing period. In addition, tagged juveniles (that is, 3- to 6-year-old nonbreeding individuals) and nonbreeding adults were occasionally captured. On each capture, individual body length was measured (to the nearest centimetre) ventrally as the straight line from snout to the tail tip using a constrain board. Therefore, for most individuals, repeated measurements are available and individual growth trajectory can be reconstructed. As fur seals show a continuous growth throughout their life, knowledge of their age is critical and repeated measurement of adults every year is a necessity.

A pedigree of 939 individuals with 111 maternal lines was extracted from our database. We only included in the pedigree families of at least four members to ensure that each family was informative enough. Ideally, all families should be included but this comes at an increased cost in computation time. Small families contribute little information and 'borrow strength' from larger, more informative, families. Animals of unknown ancestry were assumed to be unrelated. For these 939 animals, 3243 body length measurements (2728 for pups and 515 for adults) were extracted from our database. It must be stressed that this pedigree is shallow and mostly encompass a single generation: the first tagged (adult) individuals are currently reaching the end of their reproductive life while their offspring is starting their own. Moreover, no paternal links are available in this population as breeding adult males, which fiercely defend a harem, are impossible to manipulate without sedating. Moreover, the latter are mostly present during the Austral summer when densities are highest on the colony, adding to the difficulty of handling them while minimizing disturbances.

We excluded some animals from our population pedigree, but we wanted to make full use of all the information at hand. We favoured a Bayesian approach, which provides a suitable framework to incorporate disparate sources of information without invoking asymptotic approximations (Gelman *et al.*, 2003; Guo & Carlin, 2004; O'Hara *et al.*, 2008). In addition to the 3243 measurements aforementioned, 1,364 and 245 measurements were available for 201 pups (from 59 cows) and 167 adults, respectively. Pragmatically, we used data on individuals not in the pedigree to elicit informative priors that were subsequently used in an animal model. For all Bayesian analyses, we used WinBUGS 1.4 (Spiegelhalter *et al.*, 2003) to run multiple chains with over-dispersed starting values and assessed convergence with the Gelman–Rubin diagnostics (Cowles & Carlin, 1996). We thinned chains when needed to reduce autocorrelation and aimed for a sample of 5,000 iterations for each chain. Inferences are thus based on a posterior sample of 15 000 iterations. Analyses were carried out in R 2.9 (R Development Core Team, 2009) using the R2Winbugs (Sturtz *et al.*, 2005) and coda (Plummer *et al.*, 2008) packages. Posterior mean and 95% highest posterior density credibility interval are reported.

Model building, fitting and checking

As some females were marked as adults at the initiation of the study, the beginning of their growth curve is veiled. However, their pups have been monitored and measured. To infer the (unmeasured) growth curve of females marked as adults, we use data from relatives (Hadfield, 2008). Using a multivariate model, we combined parents and progeny information to obtain accurate estimates of body length variance components (Lynch & Walsh, 1998). Therefore, we chose to model body length at two different ontogenetic stages: before weaning (2728 records, pups were measured every month during the rearing period) and after weaning (515 records for adults, defined as >2-year-old individuals). We expected a positive genetic correlation between pup and adult body lengths, which we interpret as a sustained action of genes involved in large body length across life stages. Additional advantages of this multivariate approach are that the hypothesis of constant additive genetic variance across ontogeny is relaxed (Wilson *et al.*, 2005).

Individuals of both sexes were used in the analysis because genes involved in body length are expected to be largely autosomal (Badyaev, 2002; Leder *et al.*, 2010) and inherited equally from both sexes. Pooling males and females also require the hypothesis of equal genetic variances in the two groups, which is reasonable given the lack of evidence for a sex-biased variance in most phenotypic traits linked to body size (Badyaev, 2002). Hence, sex can conceptually be envisaged as providing two different environmental backgrounds in which body

length–related loci are expressed. A sex-specific residual variance, aggregating un-modelled source of variation that may differ between adult males and females, was thus included in the model for adult growth. As breeding females do not invest differentially in either sex (Chambellant *et al.*, 2003), we did not consider sex-specific residual variances for pup growth.

We expected body length to be heritable (that is, $\sigma^2_{additive} \neq 0$). Maternal environment effects (σ^2_{me}), which are common and important in species with extended maternal care (Reinhold, 2002), were also included in the model for pups. Owing to the shallowness of the pedigree and absence of paternal link, genetic maternal effects could not be considered in our analysis (Lynch & Walsh, 1998). Repeated measurements on adults allowed us to include a permanent environment effect (σ^2_{pe}), reflecting the environment an individual is experiencing throughout life (for example, the same territory at each breeding season, or the same foraging strategy). Finally, year (σ^2_{year}) was also considered as a source of variation and included in the model. Adults are harder to handle and measure than pups, and a different field biologist is in charge of measurements each year. Thus, this year effect aggregates variation because of the environment and of the field biologist for adult fur seals.

Growth in pinnipeds is best described with asymmetric, nonlinear functions (McLaren, 1993). We focused on the Gompertz curve (Winsor, 1932) and fitted a model for pups (with age in days) and adults (with age in years). Different curves were used for each sex. Yet, because we had no measurements for males older than 8 years, we used a simple linear function of age to approximate growth in males.

As fur seals have an indeterminate growth, older females are expected to be physically able to give birth to bigger pup. In addition, Beauplet *et al.* (2004) found evidence of maternal body length influencing pup growth at the end of the rearing period. Consequently, maternal age was included for body length at birth and modelled semi-parametrically with linear penalized splines (Gurrin *et al.*, 2005). Finally, we included in the adult model an indicator variable to distinguish between animals marked adults at the beginning (1994–2004) and later part (2005–2008) of the study period. Animals measured at the start of the study were mainly breeding adults, whereas those at the end were mainly nonbreeders (marked as pups), recaptured to prevent identity loss. Hence, the two cohorts differ but not for biological reasons.

In summary, we fitted the following growth curves (so-called random effects are italicized):

- for pups,

  Body length = Gompertz (sex, days) + age of cow at parturition + *additive genetic effect* + *year effect* + *maternal environment effect* + *residual effect*;

- for adult females,

  Body length = Gompertz (years) + cohort effect + *additive genetic effect* + *permanent environment effect* + *year effect* + *residual effect*;

- and for adult males,

  Body length = linear (years) + cohort effect + *additive genetic effect* + *permanent environment effect* + *year effect* + *residual effect*.

The 'animal model' was implemented in WnBUGS using the parametrization of Damgaard (2007). An inverse Wishart prior was used for the genetic variance–covariance matrix. Informative priors for the animal models were elicited with independent data. Model fit was assessed numerically using a R^2-like statistics for nonlinear hierarchical models following Vonesh *et al.* (1996), and graphically with a plot of conditional residuals against fitted values.

Under our current 'animal model', all pups are assumed to be of different bulls, clearly an unrealistic hypothesis given the reproductive biology of Subantarctic fur seals. We investigated the influence on estimates of the absence of paternal links in the pedigree through simulations. We simulated twenty pedigrees under two scenarios (ten pedigrees per scenario). In the first one, a breeding male can defend a harem of five females on average and breed again in subsequent years, but with a small probability. In the second one, a male can *only breed once* but with ten females. Thus, pups under the first scenario are less likely to share the same father than under the second scenario. For each simulated pedigree, we rerun our model with the same phenotypic data and estimated the components of the phenotypic variance. We choose to simulate pedigree data only, as paternal links may be recovered through paternity assignment analysis but phenotypic data are still likely to be missing given the difficulty associated with handling breeding males. It is noteworthy that data are missing for *all* breeding males, that is data is missing completely at random (Rubin, 2005), not withstanding sexual selection. The simulations we performed may be envisioned as some sort of multiple imputation.

Fitness proxies and selection gradients

Because of very limited data on males, we thus focused on females. We used as fitness proxies of a female the probabilities a given female will reproduce, and wean a pup during a breeding season. We selected life-history data for females between the age of 7 and 16 years as these females accounts for 96% of all females reproducing in this population (Dabin *et al.*, 2004). Importantly, the probability of detecting a reproductive female in this population is close to one (Beauplet *et al.*, 2006),

allowing reliable inferences (Gimenez *et al.*, 2008). From our database, 833 and 519 reproductive and weaning events were respectively extracted and analysed with hierarchical generalized additive models. The probability a female (dam_i) would reproduce (wean a pup), $Pr_{breeding}^{dam_i}$ ($Pr_{weaning}^{dam_i}$), was modelled as a Bernoulli trial with a probit link. Covariates were female age, modelled semi-parametrically with linear penalized splines (Gurrin *et al.*, 2005), and year. For both reproduction and weaning success probabilities, a correlated female-specific effect was included (Cam *et al.*, 2002). This female-specific effect was further linked to the 'animal model' described earlier via a variance–covariance matrix. This joint modelling approach is advocated by Hadfield *et al.* (2010) and avoids many of the pitfalls of regressing fitness proxies on genetic merit. We did not fit an animal model for fitness (Morrissey *et al.*, 2010). Our data precluded such an exercise because fitness data on the daughters of the first tagged females in this population are lacking. Having estimated directly the covariance between fitness and (body length) genetic merit, and the genetic additive variance for body length ($\sigma_{additive}^2$), selection gradients were then computed following Janzen & Stern (1998) to permit comparisons with others studies and meta-analyses of the strength of selection. Weakly informative Cauchy priors (Gelman, 2006; Gelman *et al.*, 2008) were used. Model fit was assessed using posterior predictive checking (Gelman *et al.*, 2003; Green *et al.*, 2009). The test statistics used was the proportion of females breeding or successfully weaning a pup (conditional on having bred) at each age from 7 to 16 years old.

Results

Variance parameters

Results from the 'animal model' are summarized in Fig. 1. Model fit was good and examination of residuals plots (see Figs S1 and S2) did not reveal any dramatic model misfit, although pup measurements may be heteroskedastic. The asymptotic length of adult females was 147.8 cm (144.1 : 151.8). Substantial additive genetic variation was found both at the pup and at the adult ontogenetic stage. The genetic correlation between pup and adult body length was 0.85 (0.59 : 0.96). All variance parameters had credibility intervals excluding zero. Body length heritabilities for pups, adult females and adult males were 0.37 (0.19 : 0.52), 0.21 (0.07 : 0.37) and 0.21 (0.06 : 0.36), respectively. The posterior probability that pup heritability was larger than adult heritability ($pr(\mathbf{h}_{pup}^2 > \mathbf{h}_{adult}^2)$) was 0.91.

Female age influenced pup body length at birth in a quadratic-like fashion (Fig. 2). Absence of paternal identities in our pedigree (Supplementary Graph 3) resulted in an underestimation of pup genetic additive variance (by ≈10%), an unsurprising result as we assumed pups to be of different bulls. Maternal environment effects were accurately estimated, at least under the two scenarios for generating paternities in the pedigree.
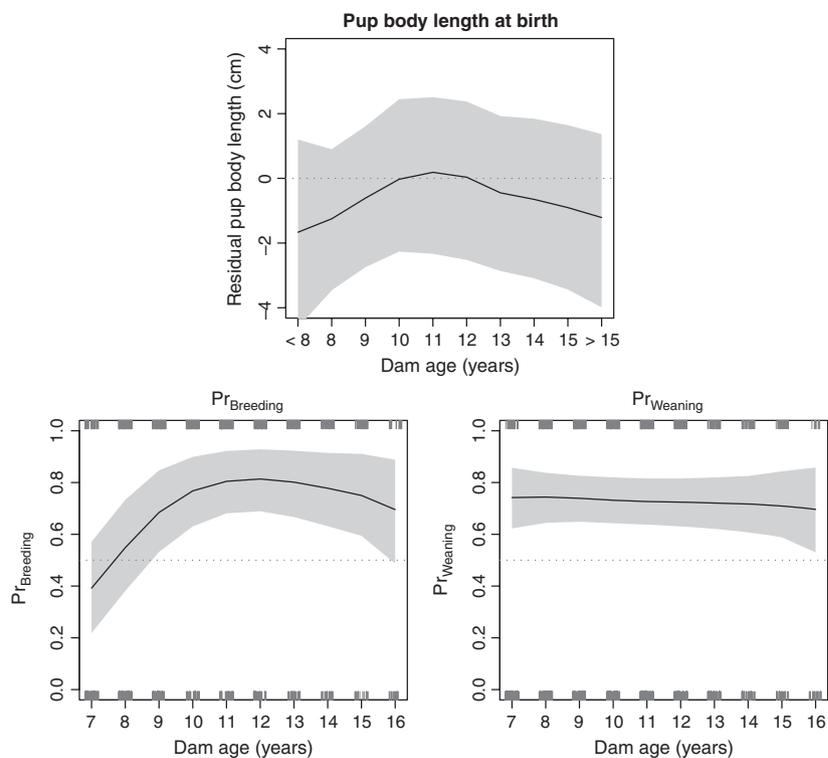
Fig. 2 Age effects of female Subantarctic fur seals. The grey envelope represents the 95% credibility interval. Ticks on the lower graphs represent the data.

Adult genetic additive variance was also accurately estimated. However, there were identifiability issues with permanent environment effects: genetic additive and permanent environment effects were largely (negatively) correlated as seen from the shape of credibility ellipses (Fig. S4). Despite this shortcoming, we chose to be conservative and retained this permanent environment effect for our subsequent inferences. Removing permanent environment effects would inflate the adult genetic additive variance. On the other hand, adult genetic variance and the adult–pup genetic correlation was unaffected by the absence of paternal links in the pedigree, giving some robustness to our results.

Fitness proxies and selection gradients

The posterior mean probabilities a female aged between 7 and 16 years old would breed or successfully wean a pup were respectively 0.62 (0.59 : 0.65) or 0.72 (0.67 : 0.76). Breeding probability showed a steep increase in the first years of reproductive life while weaning probability (itself conditional on breeding) remained fairly constant (Fig. 2). Figure 2 also suggested a small decrease in breeding probability in late reproductive life. There was a slight positive correlation (ρ) between breeding and weaning probability of 0.19 (95% CI −0.24 : 0.58; $Pr(\rho > 0) = 0.80$).

Model fit as assessed from posterior predictive checks suggested an acceptable fit, although the model was over-optimistic in predicting too many females to breed after 12 years-old. This discrepancy was, however, small, except for females aged 16. There were also some discrepancies with weaning probability, but they were small and with no obvious pattern (Fig. S5).

The variance-standardized gradient (β_σ see Hereford *et al.* (2004)) associated with breeding probability and weaning probability were respectively 0.015 (−0.013 : 0.044) and 0.028 (−0.004 : 0.057). The posterior probabilities that these gradients were superior to zero ($pr(\beta_\sigma > 0)$) were respectively 0.87 and 0.97. Posterior distributions of β_σ are depicted in Fig. 3.

Discussion

Quantitative genetics of body length

Body length in Subantarctic fur seals is heritable and under selection. Heritability of body length was not constant and decrease between pup and adult ontogenetic stages. This decrease results more likely from an increase in the magnitude of the total phenotypic variance rather than from a reduction in the additive genetic variance *per se*. Phenotypic variances of body length increased from birth to adulthood (Graph 1). The indefinite growth of Subantarctic fur seals ensures a continuous influx of phenotypic variance as animals age.
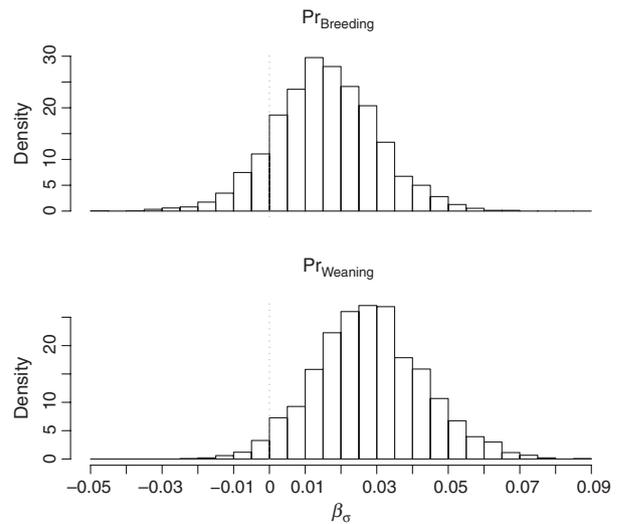
Fig. 3 Posterior distribution of variance-standardized gradients β_σ. These gradients were derived from the covariances between genetic merit and fitness proxies that were estimated using a joint fitness-animal model (Hadfield *et al.,* 2010).

Besides, adults experience a very different and more diverse environment (the open ocean) than pups, which remain around Amsterdam Island before weaning. Hence, a surge in environmental (nongenetic) variance components is expected.

Maternal environment effects were also found on pups, as expected given the complete dependence of pups on their mother during weaning. A more surprising result was the quadratic-like relationship between a breeding female's age and its pup's body length at birth (Fig. 2). We did not anticipate this relationship, but expected *a priori* a curve with a plateau after a given age because of the indeterminate growth of females. In fact, this pattern suggests mid-aged females can give birth to pups bigger than those of older females albeit these old females are expected to be themselves bigger than mid-aged females. The positive genetic correlation between body length in pups and adults means that bigger pups, conditional on them surviving, become bigger, and fitter (Beauplet & Guinet, 2007), adults. Hence, pup phenotypic quality increases with a female's breeding experience but declines towards the end of a cow's reproductive life, suggesting that giving birth to a high-quality pup becomes more and more costly as females age. This finding suggests that bigger is indeed better in female Subantarctic fur seals, but the age at which a female becomes big enough relative to other females is also crucial for producing a high-quality pup.

We did not find that older females were less able to successfully wean a pup. Beauplet *et al.* (2006) found evidence of a survival decline in females older than 13 years (both breeding and nonbreeding). We found that older females were less likely to breed, although the

model we used tended to minimize this effect. In addition, there was a modest, but imprecise, positive correlation between individual breeding and breeding success (weaning) probabilities, suggesting individual covariation (Cam *et al.*, 2002). As these probabilities further positively correlated with female genetic merit in body length, this again suggested that larger females contributed disproportionately to future generations. It should be remembered how we conditioned our inferences on families of at least four members. Thus, we excluded females that rarely breed, irrespective of whether they successfully weaned their pup or not. These females may be those experiencing trade-offs, that is negative covariance between fitness components. This is unlikely to be a big issue for selection gradients as the asymptotic length of females excluded from the pedigree (posterior mean: 144.6; 95% CI, 139.9 : 150.5) was similar to, if slightly smaller and less precise than, that of females included in the pedigree.

Comparison with published estimates

Several meta-analyses of selection gradients are available, yet that of Hereford *et al.* (2004) may be the most comprehensive one as these authors also accounted for bias in estimates, and distinguished between univariate and multivariate selection analyses. We will compare our results with theirs, although this will be tentative as the only study using a Bayesian framework similar to ours we are aware of is Phillimore *et al.* (2010). However, in the latter study, the authors did not have pedigree information on their studied populations. Hereford *et al.* (2004) estimated a median absolute value of variance-standardized gradients for morphological traits and for fecundity fitness proxies to be 0.06 in multivariate studies. This is actually larger (by 300% for breeding probability or 100% for weaning probability) than our own estimates. Taken at face values, this suggests that selection acting on female body length in Subantarctic fur seals on Amsterdam Island is not strong.

Using data collected on a few strayed and South Georgian individuals, McLaren (1993) tentatively estimated the asymptotic length of male Subantarctic fur seals to be 152.3 ± 6.3 cm. This estimate is actually comparable to our own estimate for the asymptotic length of adult *females*! McLaren (1993) felt his estimate to be quite robust, but it would mean that sexual size dimorphism on Amsterdam Island is close to zero, which is clearly not the case (see in Fig. 1 how the male growth curve has not even reached a plateau yet). In fact, males and females are still dimorphic in body length on Amsterdam Island, and this is evident from birth (Fig. 1), but this dimorphism is reduced compared to higher-latitude populations (C. Guinet, pers. obs.). That Subantarctic fur seals are bigger at lower latitudes is at odds with Bergmann's 'rule', a macro-ecological pattern of increased body size at higher latitude in mammals.

Ecological connections

In a recent review, McNab (2010) revisited various macro-ecological patterns of mammalian body size and proposed a unification under an overarching resource rule. McNab (2010) emphasized the primacy and contingency of the ecological theatre (and resource availability) wherein the evolutionary play happens, in shaping mammalian body size trends. In the Amsterdam population of Subantarctic fur seals, Beauplet & Guinet (2007) documented how female body length is a critical determinant of reproductive success, with one-third of females of a given age producing two-thirds of recruited pups. Incidentally, these females were also the biggest. Bigger individuals may have better diving ability, or reach foraging grounds more rapidly, or dive deeper and longer, or store more reserves; or a combination of all. If preys are scarce, even a slight difference in body length between females can make a big difference in foraging success and hence in reproductive success as body weight (that is, both oxygen and fat storing capacity) is a cubic function of total length. However, an increased body length also means a greater investment in structural growth and thus could be responsible for the late start of female reproductive life observed on Amsterdam Island compared to other populations (Dabin *et al.*, 2004). Under this scenario, females would not attempt breeding before reaching a threshold length despite being physiologically mature. We strongly suspect a paucity of specific preys exacerbated by both environmental (the subtropical Front where females forage) and demographic (density-dependence, which may be also reflected in the decreasing trends in breeding success probability across years, Fig. S6) processes to give rise to the observed selection gradient.

Current limitations

Owing to its shallowness, our current pedigree precludes the estimation of a maternal genetic variance. Consequently, the additive genetic variance may be biased upwardly to an unknown degree (Clément *et al.*, 2001). Additive genetic variances and selection gradients may then be over-estimates. Yet, we think this to be unlikely: Wilson *et al.* (2005) investigated the effect of ignoring maternal genetic effect on the heritability of June weight (a trait for which many autosomal loci are likely to be involved) in Big Horn sheep (*Ovis canadensis*). Failure to incorporate maternal genetic effects resulted in a 25% increased additive genetic variance compared to the full model. However, despite a large data set (1884 records on 974 individuals spanning 40 years of monitoring), the increase in model complexity to account for maternal genetic effects was not supported. Big Horn ewes and female Subantarctic fur seals share many biological features: both are philopatric mammals of similar life span, smaller than males, and give birth to one single

offspring per reproductive event (Berubé *et al.*, 1999). Finally, Big Horn ewes are capital breeders (Festa-Bianchet *et al.*, 1998), whereas female Subantarctic fur seals are considered to exhibit a capital breeding strategy (Trillmich, 1996). Given these similarities and the fact that considering maternal genetic effects did not account better for the processes that gave rise to the data in Big Horn sheep, it is reasonable to assume this effect negligible. Another line of evidence comes from our own simulations (akin to missing data imputation) that suggested maternal effects to be accurately estimated.

Our approach is largely correlational, but this may be unavoidable when studying wild populations of large, and elusive, vertebrates. We took, however, great care in using state-of-the-art methods to allow an efficient use of our long-term data set on Subantarctic fur seals. More specifically, we used a joint modelling approach to circumvent some of the statistical issues that have plagued previous studies using 'animal models' on wild populations of vertebrates (Hadfield *et al.*, 2010). We also used posterior predictive checks to investigate which features of the data are not taken into account with our model (Gelman & Shalizi, 2010). In particular, our model does not account properly for the declining breeding probability observed both over a female's lifetime (Fig. 2) and over the course of the study (Fig. S5).

Hadfield (2008) stressed how viability selection may bias the estimation of evolutionary parameters, especially when working on developing traits. In the present study, viability selection may be acting on pups and their growth curve is censored as a result. Here, we assumed that pups differed in asymptotic body length and that the latter is independent of pup survival. Investigating whether there is an association between time to death and growth requires a joint analysis of longitudinal data and event times (Vonesh *et al.*, 2006), which is beyond the scope of this paper.

Finally, we have investigated the quantitative genetics of a single phenotype trait, that is we did not thread out of 'flatland' (Walsh, 2007), although our model looked at two ontogenic stages. We did not address genetic constraints that may act on, and limit the potential evolutionary response of, body length. The pitfalls of ignoring geometry in quantitative genetics are increasingly recognized (Walsh, 2009). These problems are most acute when predicting an evolutionary response using the univariate breeder's equation (see equation 1), which reviewers of the present work convinced us not to attempt.

Conclusions

We documented the quantitative genetics of body length in a wild population of marine carnivores and found strong suggestions that this trait is under positive directional selection. Although our data is limited to a shallow pedigree and very little information on males,

they nevertheless brought to light further insights into the biology of Subantarctic fur seals breeding on Amsterdam Island. Giving birth to big pups becomes more and more costly as females age, yet body length is under selection in females, and likely so in males. Such selection may explain the increased body length of Subantarctic fur seals at lower latitudes. The existence of genes of large effect in carnivores, for example *IGF-1* (Sutter *et al.*, 2007), suggests that rapid and large responses to selection are not wild speculations. In addition, we used in the present study a rigorous statistical framework, allowing the flow of all uncertainties from one level of analysis to the next (O'Hara *et al.*, 2008). We thus have been conservative in our inferences throughout, and yet found evidence of standing genetic variance in body length and selection gradient. Although a nonzero heritability and selection gradient are not sufficient *per se* to infer microevolution, they are consistent with such a pattern. A possible route to further investigation into the causes behind large body size of Subantarctic fur seals could be a candidate gene approach, for example *IGF-1*, using DNA data from females breeding on Possession and Amsterdam Islands, respectively.

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Supporting information

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

Figure S1 Standardized-residuals plot of pup body length measurements.

Figure S2 Standardized-residuals plot of adult body length measurements.

Figure S3 Impact of unknown paternities on estimation of variance components for Subantarctic fur seal pups.

Figure S4 Impact of unknown paternities on estimation of variance components for adult Subantarctic fur seals.

Figure S5 Posterior Predictive Checks for models of fitness proxies.

Figure S6 Year effects.

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