

Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder

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Summary

1. Three hypotheses have been advanced to account for age-related improvement in performance: the selection hypothesis predicts improved due to the loss of lower quality phenotypes, the constraint hypothesis predicts individuals improve function, and the restraint hypothesis predicts younger individuals forego or reduce effort because of mortality risks. A decline in age-related performance (i.e. senescence) is predicted by mutation accumulation, antagonistic pleiotropy and disposable soma (wear and tear) hypotheses.

2. Using five measures of performance – birth rate, maternal and pup birth mass, pup weaning mass, weaning success and lactation length – we tested these hypotheses concerning age-related change in reproduction in 279 female grey seals (*Halichoerus grypus*), ages 4–42 years, over a 23-year period between 1983 and 2005 on Sable Island, Nova Scotia. These females produced 2071 pups.

3. Although body mass of primiparous females increased with age (4–7 years) birth mass of their pups did not, but pup weaning mass did. Second- and third-parity females of the same age as primiparous females gave birth to and weaned heavier pups. However, parity and age were dropped from models when maternal body mass was included.

4. The proportion of females giving birth varied significantly with maternal age, increasing in young females and then declining late in life. Weaning success rate also increased rapidly to about 8 years and subsequently declined in females > 32 years.

5. Generalized additive models indicated nonlinear changes in 3 day body mass (i.e. ~ birth mass) and weaning mass of pups as a function of maternal age, after accounting statistically for the effects of maternal body mass. Mixed-effects, repeated-measures models fitted to longitudinal data further supported the conclusion that pup birth mass and weaning mass vary nonlinearly with maternal age and indicated nonlinear changes in lactation duration.

6. We found some support for the constraint hypothesis, but our findings were not consistent with the selection hypothesis or the restraint hypothesis as the basis for improvement in reproductive performance.

7. Senescence was evident in multiple female and offspring traits, indicating the degeneration in function of several physiological systems as predicted by the disposable soma hypothesis.

Key words: age-specific reproduction, phocid, pinniped, seal.

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Introduction

Life history theory predicts age-specific changes in the reproductive performance of individuals because fitness will depend on the allocation of limited resources to maternal maintenance and growth vs. to offspring

(Roff 1992). The proportion of resources allocated to offspring may vary over the life of an individual female as a function of her physiological state (McNamara & Houston 1996), parity (Broussard *et al.* 2003), experience (Sydeman *et al.* 1991) and age (Derocher & Stirling 1998; Packer, Tatar & Collins 1998). A nonlinear

increase in reproductive success, up to senescence, with parental age has been documented in many species of birds and mammals (e.g. Clutton-Brock 1988; Weimerskirch 1992; Bowen *et al.* 1994; Festa-Bianchet *et al.* 1995; Robertson & Rendall 2001).

Three hypotheses have been advanced to explain this improved performance: (1) the selection hypothesis; (2) the constraint or breeding experience hypothesis; and (3) the restraint hypothesis (Curio 1983; Forslund & Pärt 1995). These hypotheses are not mutually exclusive, but they do stress different mechanisms. The selection hypothesis holds that improved breeding performance is due to the loss of lower quality phenotypes as a cohort ages leading to the appearance of overall improvement of the surviving individuals. The constraint hypothesis predicts that performance improves as individuals acquire or improve skills or physiological function that positively affects reproduction. In contrast, the restraint hypothesis predicts that younger individuals either forego or reduce effort expended on reproduction because of the cost in terms of increased risk of mortality. Thus, according to the theory of terminal investment, individuals should expend more on offspring as they age because of declining residual reproductive value (Gadgil & Bossert 1970).

A decrease in reproductive performance is also predicted by ageing and life history theories (Medawar 1946; Hamilton 1966). Senescence, the progressive loss of physiological function with age resulting in reduced fecundity or survival (Abrams 1991), may constrain the ability of females to increase or maintain investment in offspring later in life. The three leading hypotheses for the evolution of senescence are: mutation accumulation (Medawar 1946), antagonistic pleiotropy (Williams 1957) and a particular form of pleiotropy, the disposable soma (Kirkwood 1981). Senescence evolves because selection acts more weakly on traits that are expressed after individuals have reproduced (Hamilton 1966), permitting either the accumulation of mutations that reduce function or antagonistic pleiotropy whereby traits can evolve that have a positive effect on fitness early in life even though they may reduce function later in life. Trade-offs associated with the cost of reproduction might represent such gene action that generates senescence (Gustafsson & Pärt 1990). The disposable soma theory assumes that ageing results from the accumulation of random molecular and cellular damage as a consequence of evolved limitations in maintenance and repair (Kirkwood & Austad 2000).

Although the pattern of female reproductive performance over a broad range of ages is known for a number of animals, relatively few studies have clearly demonstrated reproductive senescence (e.g. Packer *et al.* 1998). Here, we report on a long-term study of age-specific reproductive performance in female grey seals (*Halichoerus grypus*), ranging from first-time breeders to females approaching the life span of individuals observed in the wild. The grey seal, Family

Phocidae, is well suited for studies of age-related changes in reproductive performance. Females are long-lived (~40 years) and large, with an average body mass of postparturient females of about 197 kg (Mellish, Iverson & Bowen 1999). Females are capital breeders, giving birth to a single pup each year, beginning at age 4–5 years and continuing for several decades or more. During a 16-day lactation period females do not feed, relying instead on body energy stores, in the form of blubber, for both maintenance metabolism and milk production (Iverson *et al.* 1993). Thus, females with low body mass at parturition tend to wean smaller pups or wean pups prematurely (Iverson *et al.* 1993; Mellish *et al.* 1999; Pomeroy *et al.* 1999), increasing the probability of juvenile mortality (Hall, McConnell & Barker 2001). Females end maternal care abruptly by abandoning their pup and returning to sea. This means that female reproductive expenditure can be measured accurately by the duration of expenditure (i.e. lactation length) and the energy allocated to offspring (i.e. offspring mass at weaning).

We tested the hypotheses concerning age-related changes in reproductive performance using our long-term data. The constraint hypothesis predicts that measures of reproductive performance should increase with either breeding experience or body size. As grey seals fast during lactation, maternal body mass is a good indicator of the amount of resources that females can allocate to offspring. If breeding experience has a significant effect on performance, then females of the same age but differing parity should differ in performance. The restraint hypothesis predicts an increase in reproductive effort later in life as the opportunity for future investment declines. This should be reflected in an increase in both the quantity of energy allocated to offspring and the duration of the investment. The selection hypothesis predicts an apparent increase in reproductive performance at the population level as inferior phenotypes are removed from the population with age, leaving behind an increasing proportion of high quality females. Theory predicts that senescence should be more weakly expressed in long-lived species that experience a low risk of extrinsic mortality than in short-lived species (Abrams 1991). Thus, given the longevity of grey seals, we predicted that senescence would occur well after the age at sexual maturity. Finally, because male pups are larger at weaning (Hall *et al.* 2001), and therefore require greater absolute maternal energy expenditure than female pups (Mellish *et al.* 1999), we test the hypothesis that, on average, declining maternal performance is evident earlier in life for females raising male pups than when raising female pups.

Methods

Our 23-year study was conducted on Sable Island (43°55' N, 60°00' W), a partially vegetated sandbar approximately 300 km south-east of Halifax, Nova Scotia, Canada, during the December through early

February breeding seasons from 1983 to 2005. Females give birth on the sand beaches surrounding the island, inland sand flats, and on the vegetated and non-vegetated sand dunes varying from about 3–20 m in elevation. The number of pups born on Sable Island has increased exponentially for the past four decades, with a doubling time of ~6 years (Bowen, McMillan & Mohn 2003). Thus, over the course of the study, the number of pups born increased about 12-fold.

The adult females we studied are a subset of those that were marked with unique permanent hot-iron brands shortly after weaning and were of known age. Females were branded in 1962, 1969, 1970, 1973, 1974, 1985–87, 1989 and 1998–2000. We used two sources of information to test for age-specific changes in reproductive performance. The first was annual resightings of branded adult females during the breeding season to establish the presence of a female and whether or not she was lactating. The second was maternal and offspring trait measurements [maternal postpartum mass (MPPM), pup sex, birth and weaning mass and lactation length] beginning in 1991.

The presence of a study female in the colony was determined from weekly whole-island censuses of all branded females conducted over the course of the breeding season each year. Censuses were conducted using all-terrain vehicles, which permitted the entire colony to be searched thoroughly in a 1–2-day period. In addition to weekly censuses, daily surveys were conducted throughout the colony to dye-mark pregnant study females and those that had recently given birth (within 1–2 days). Thus birth date was known for many of the study females or could be estimated for females with recently born pups based on an assessment of pup age derived from pelage/morphology stage classes (Bowen *et al.* 2003). Given the frequency of whole island censuses and daily searches, it is highly unlikely that a female returning to the breeding colony would have been not detected.

We used these weekly censuses to estimate apparent birth rates for females in three age classes: 4–15 years (young, growing), 16–25 years (prime age, non-growing), and 26–41 years (old age, non-growing). These age classes were based on a growth curve of adult female grey seals (this study). In each age class, only females that could have been observed in ≥ 7 of the 10–12-year intervals were included in the analysis to increase the precision of birth rate estimates. Our estimates are apparent rates, as some females could have died during the study period or emigrated permanently from Sable Island resulting in a downward bias in the proportion giving birth. As few of our branded females have been observed at other colonies, this downward bias is presumably small. Females known to have died were excluded.

Once sighted, study females were visited daily (but not disturbed) to determine weaning date, defined as the day a female left the colony and returned to the sea to feed. For females with known or estimated parturition

dates, the duration of lactation was based on the daily sighting of these marked females. Prior to weaning, pups were sexed and marked with semipermanent, uniquely numbered tags in the hind flipper so that after the female departed the colony, her offspring could be identified. Each year, we weighed a sample of study females and pups, after the female-pup bond was firmly established. These 3-day postpartum masses are used as proxies for pup birth mass and maternal postpartum mass. To the extent possible, pups of all study females were weighed (nearest 0.5 kg) on the day of weaning.

Females were judged successful if they weaned or were last seen with a pup classified as stages 3–5 (i.e. near weaning; see Bowen *et al.* 2003). Females were judged unsuccessful if their pup died prior to weaning or if they weaned/abandoned a pup weighing < 30 kg, as survival probability is low among such small pups (Hall *et al.* 2001). Abandoned pups are rarely fostered by other females in this colony (Perry, Boness & Fleischer 1998) and therefore are almost certain to die.

All procedures used on study animals were in compliance with applicable animal care guidelines of the Canadian Council on Animal Care and were approved by The Department of Fisheries and Oceans Animal Care Committee.

STATISTICAL ANALYSIS

We used both linear and nonlinear models to investigate the variation in three measures of reproductive performance: pup birth mass and weaning mass and lactation length. Each of these response variables was modelled with all possible combinations of three covariates: female body mass, female age, and pup sex. Goodness-of-fit of the models was assessed by comparing more complex models against the means model, examining the patterns of residuals, and by the adjusted R^2 or explained deviance (i.e. relative to the null model of female as a random effect). Given that we expected the relationships to be nonlinear, we used generalized additive models (GAM; Hastie & Tibshirani 1990) with smoothing splines on cross-sectional data to investigate the shape of the relationships. Where a female had more than one observation, we created the cross-sectional data by selecting the most recent observation for each female. This ensured that we would have observations spanning most of the reproductive ages in the population. Splines are piecewise polynomials and the complexity of the curve fitted to the data is controlled by the number of degrees of freedom used. We attempted to determine the optimal complexity of the curve based on a cross-validation analysis with different degrees of freedom, but the results were not biologically realistic. Therefore, we used the default setting of d.f. = 4. Models fitted with 2 and 3 d.f. (i.e. less sensitive to local variation in the data) supported the same conclusions as the models fitted with d.f. = 4. To estimate the ages when pup birth mass, pup weaning mass

and lactation length stopped increasing and began to decline, we performed a series of contrasts (i.e. linear combination of means) within a general linear model (GLM) analysis. The first contrast was performed on the three means centred about the maximum mean of each response variable. Successive contrasts were performed by symmetrically widening the age interval on either side of the maximum mean from 3 to 5, 7, 9, etc. until evidence of a significant quadratic trend in means was found at the 5% level.

Many females were studied in multiple years. Therefore, we also used linear mixed-effects models (LME) to examine changes in pup birth mass, pup weaning mass and lactation length with respect to maternal age and offspring sex. We selected females with ≥ 2 observations, which enabled us to test both linear and quadratic models. Before fitting models with quadratic terms, the predictor variables were standardized to a Gaussian mean 0 and variance of 1 to reduce collinearity. We fitted the following mixed effects model:

$$y_{ij} = \mu + S_i + \beta x_{ij} + \alpha G_{ij} + \varepsilon_{ij}$$

where y_{ij} is the j th measurement on i th seal; μ is the overall mean; S_i is the random effect of the i th seal which is assumed to be distributed $N(0, \sigma_s^2)$; β is the fixed effect of maternal age; x_{ij} is the maternal age of the i th seal for the j th pup; α is the fixed effect of pup sex; G_{ij} is the sex of the j th pup of the i th mother; and ε_{ij} are the errors and are distributed $N(0, \sigma_s^2)$. We fitted an autoregressive correlation structure, where the strength of the dependence between measurements on the same mother depends on how far apart they are in time. Observations that are closer in time tend to be more similar than observations further apart in time; the actual correlation structure is given by:

$$\rho^{|x_{ij} - x_{ik}|}$$

Thus, the correlation decays exponentially as a function of the difference in maternal age between two given pups.

To test the effect of maternal age on weaning success, we fitted a generalized linear mixed model (GLMM) to the weaning success data, using a binomial error distribution and an autoregressive [AR(1)] variance-covariance structure to account for the multiple measurements made on the same female over time.

We tested for the effects of breeding experience and age on performance by comparing females of the same parity among ages and females of different parity within ages. Given the small sample size in some age/parity combinations (Table 1), we conducted several analyses rather than one overall analysis. As birth mass is correlated positively with MPPM in grey seals, we included MPPM as a covariate to control for this relationship in testing the separate effect of maternal age on birth mass. We tested how maternal age and parity influenced MPPM and 3-day pup mass by comparing primiparous-, second- and third-parity females of ages 5–7 years, using a GLM with maternal age and parity as fixed factors.

GAM and LME analyses were conducted in s-PLUS version 7.0; other analyses were conducted in SPSS version 11.5 and SAS version 9.13. Evidence in favour of competing models was evaluated on the basis of lowest Akaike information criterion (AIC), smallest Delta AIC (Δ), and highest AIC weights (w) (Burnham & Anderson 2002). All models having a $\Delta < 2$ were considered as having substantial support, but we preferred the model with fewest parameters. Means are presented with standard errors (SE) throughout and results were judged significant at $P < 0.05$.

Results

Over the 23-year period, we studied 279 females ranging in age from 4 to 42 years. These females produced

Table 1. Maternal and pup body mass at 3 days postpartum and pup weaning mass as a function of age at first parity and number of reproductive events of grey seal females aged 4–7 years. Sample sizes are shown in brackets

Subject	Female Age (year) ^a	Parity					
		1		2		3	
		Mean mass (kg)	SE	Mean mass (kg)	SE	Mean mass (kg)	SE
Female	4	126.7	2.5 (25)				
Pup 3 days		16.7	0.5 (25)				
Weaning		30.7	1.4 (19)				
Female	5	147.6	1.9 (43)	145.7	4.8 (7)		
Pup 3 days		17.3	0.5 (43)	17.5	1.2 (7)		
Weaning		36.2	1.3 (31)	37.6	2.7 (5)		
Female	6	146.6	5.4 (7)	162.3	2.9 (22)	159.8	4.3 (8)
Pup 3 days		16.7	1.0 (7)	19.7	0.7 (21)	20.0	0.9 (8)
Weaning		35.0	3.2 (7)	43.4	1.5 (17)	43.5	1.5 (7)
Female	7	149.8	16.3 (2)	157.6	5.5 (7)	163.9	4.7 (13)
Pup 3 days		17.0	1.5 (2)	18.6	0.9 (7)	21.8	0.9 (13)
Weaning		40.3	0.7 (2)	40.3	1.4 (6)	44.9	2.0 (13)

^aOne second-parity female at age 9 years not included.

a total of 2071 pups, the fate of which could be determined with certainty for 1991 pups. Postpartum body mass of females increased through early to middle teens and remained relatively constant thereafter (Fig. 1). There was no evidence of a decline in maternal mass, and presumably energy stores, in older females.

MATERNAL PERFORMANCE OVER THE FIRST THREE PARITIES

Ages of primiparous and second-parity females ranged from 4 to 7 years and 5–9 years, respectively (Table 1). Of the 82 primiparous females, 30.5% were 4 years old, 57.3% were 5 years old, 9.8% were 6 years old and 2.4% were 7 years old. MPPM of 4-year-old primiparous females was significantly less than that of 5–7-year old females which did not differ from each other (GLM, $F_{3,73} = 18.8, P < 0.001$). For first time breeders, 3-day pup mass did not differ significantly with maternal age (GLM, $F_{3,72} = 0.12, P = 0.94$). Weaning mass did increase with maternal age of primiparous females ($F_{3,63} = 3.4, P = 0.02$), but when MPPM was added to the model ($F_{1,54} = 20.9, P < 0.001$) the effect of maternal age became non-significant ($F_{3,54} = 0.30, P = 0.83$), indicating that female mass and not age presumably accounted for increased pup weaning mass among primiparous females.

Second- and third-parity females were not significantly heavier than primiparous females of the same age ($F_{2,101} = 1.7, P = 0.17$). MPPM tended to increase with age as expected, but this tendency was not significant among the females sampled ($F_{2,101} = 2.1, P = 0.13$). Pup 3-day mass did not differ significantly among females of different ages (GLM with MPPM as a covariate, $F_{2,99} = 0.1, P = 0.89$), but increased significantly with increasing parity ($F_{2,99} = 4.1, P = 0.02$) and there was no maternal age by parity interaction ($F_{3,99} = 1.1, P = 0.35$). Thus, in these young females, increased birth mass was associated with greater breeding

experience after the effects of maternal mass had been removed. Although weaning mass tended to increase, neither maternal age ($F_{3,79} = 0.3, P = 0.72$) nor parity ($F_{2,79} = 1.3, P = 0.28$) significantly influenced pup weaning mass in young females when MPPM was a model covariate ($F_{1,79} = 18.4, P < 0.001$), indicating that only MPPM significantly affected offspring weaning mass, while parity and maternal age had little effect.

APPARENT BIRTH RATE

Birth rate varied by maternal age class (GLM, $F_{2,242} = 17.1, P < 0.001$), with the youngest and middle age classes having a significantly higher birth rate than the oldest age class (Table 2). Among 62 females with estimates in two or all three age-classes, birth rates also differed significantly by age class (linear mixed-effects model, $F_{2,108.6} = 5.87, P = 0.004$), with young and old-age females having significantly lower percentages than middle-age females (Table 2). A 42-year-old female was observed in the colony in 2005; however, she did not appear to be pregnant.

BIRTH MASS

No single model was strongly favoured to account for the observed variation in pup birth mass using the cross-sectional data (Table 3). There was essentially equal support for models 3 and 7, which included a nonlinear term for maternal age (Fig. 2a) or both a nonlinear term for maternal age and pup sex, respectively (Table 3). In both cases, the adjusted R^2 was about 39%. Mean birth mass was highest for females age 18 years. Quadratic contrasts centred on this maximum mean indicated that birth mass increased to about age 14 years and then decreased after about age 24 years ($F_{1,218} = 5.36, P = 0.02$); in the intervening period of 10 years, female age had little effect on pup birth mass (Fig. 2a).

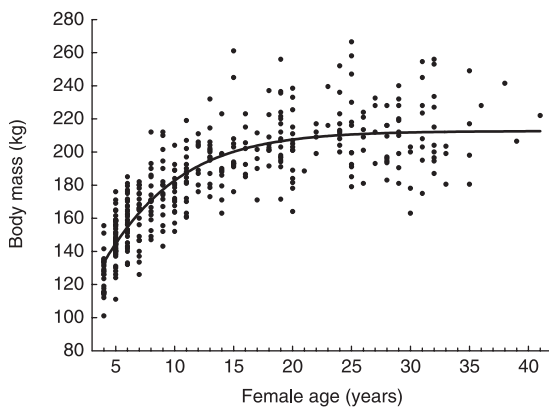


Fig. 1. Body mass (3 days postpartum) of 279 females as a function of age for all years combined. Some females were weighed more than once such that $n = 389$. Curve is a four-parameter Gompertz fitted to the data given by female mass (kg) = $-60.68 + 273.37 \exp\{-\exp[(age - 1.92)/5.53]\}$, $R^2 = 0.704$.

Table 2. Apparent birth rates in 245 grey seal females (cross-sectional analysis) and in 62 females, with 48 of these females represented in the youngest and middle age classes and 56 represented in the middle and oldest age classes (longitudinal analysis)

	Age class		
	4–15 years	16–25 years	26–35 years
Cross-sectional			
Mean (%)	73.1 ^a	83.1 ^a	56.9 ^b
SE	1.5	3.4	3.1
<i>n</i>	174	32	39
Longitudinal			
Mean (%)	68.6 ^a	80.6 ^b	71.1 ^a
SE	3.1	2.8	2.9
<i>n</i>	48	62	56

Values with different superscripts differed significantly based on paired comparisons with Bonferroni correction.

Table 3. General additive models for pup birth mass ($n = 251$), lactation length ($n = 233$) and pup weaning mass ($n = 228$) with Akaike's information criteria (AIC), Delta AIC (Δ) and Akaike weights (w) based on cross-sectional data

ID	Model	Pup birth mass			Lactation length			Pup weaning mass			
		d.f.	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i
0	Intercept	1	686.88	122.13	0.0	418.22	89.12	0.0	1019.74	204.1	0.0
1	Female age (linear)	2	657.24	92.49	0.0	399.98	70.88	0.0	990.46	174.82	0.0
2	Female mass	2	622.93	58.18	0.00	341.48	12.38	0.00	890.27	74.63	0.00
3	Female age (s)*	5	564.746	0.00	0.32	366.07	36.97	0.00	864.56	48.92	0.00
4	Pup sex	2	688.42	123.67	0.00	417.96	88.86	0.00	1020.53	204.89	0.00
5	Female mass + female age (s)	6	565.97	1.22	0.18	331.24	2.14	0.24	819.12	3.48	0.13
6	Female mass + pup sex	3	624.54	59.79	0.00	340.32	11.22	0.00	890.09	74.45	0.00
7	Pup sex + female age (s)	6	564.75	0.00	0.32	363.01	33.91	0.00	859.78	44.14	0.00
8	Female mass + pup sex + female age (s)	7	566.13	1.38	0.16	329.1	0.00	0.69	815.64	0.00	0.74
9	Female mass + pup sex + female age (s_m) + female age (s_f)	11	570.63	5.88	0.02	333.91	4.81	0.06	819.14	3.50	0.13

*Favoured models (bold type) were evaluated on the basis of lowest Akaike's information criterion (AIC), lowest Delta AIC (Δ) and highest AIC weights (w). *(s) = third-order polynomial spline; m = male, f = female.

We then conducted a mixed-effects, repeated-measures analysis using 80 females with ≥ 2 observations (maximum 7) to test whether the same pattern was evident within individual females. This analysis showed that the variation in pup birth mass was best explained by a model with pup sex and a quadratic term for maternal age (model 6, explained deviance = 29.1%, Table 4), again indicating that birth mass increased with maternal age in young females and then decreased with age later in life. There was no evidence for an interaction between pup sex and maternal age, demonstrating that male pups were larger than female pups through the reproductive life of females. Male pups were on average 4.1% heavier than female pups at 3 days postpartum (Table 5).

LACTATION LENGTH

Cross-sectional analysis showed that lactation length varied in a nonlinear fashion, increasing in young females and then decreasing in females older than about 30 years of age (Table 3 and Fig. 2b). The best model (8) explained 35.2% of the variation (adjusted R^2) and also included maternal mass and pup sex as predictors of lactation length. We note, however, that the GAM fit was strongly influenced by the single low point from the 41-year-old female. Removing this point resulted in a fit that showed much weaker evidence of a decline among the oldest females.

Mean lactation duration was highest for females age 16 years. Quadratic contrasts centred on this maximum mean indicated that lactation duration increased to about age 8 years and then decreased after about age 25 years ($F_{1,199} = 4.84$, $P = 0.03$); in the intervening period of about 17 years, female age had little effect on pup birth mass (Fig. 2b).

We had multiple observations (2–13) of lactation length from 220 of our 279 study females. The mixed-effects analysis indicated that lactation length varied with maternal age and with pup sex (model 6, explained

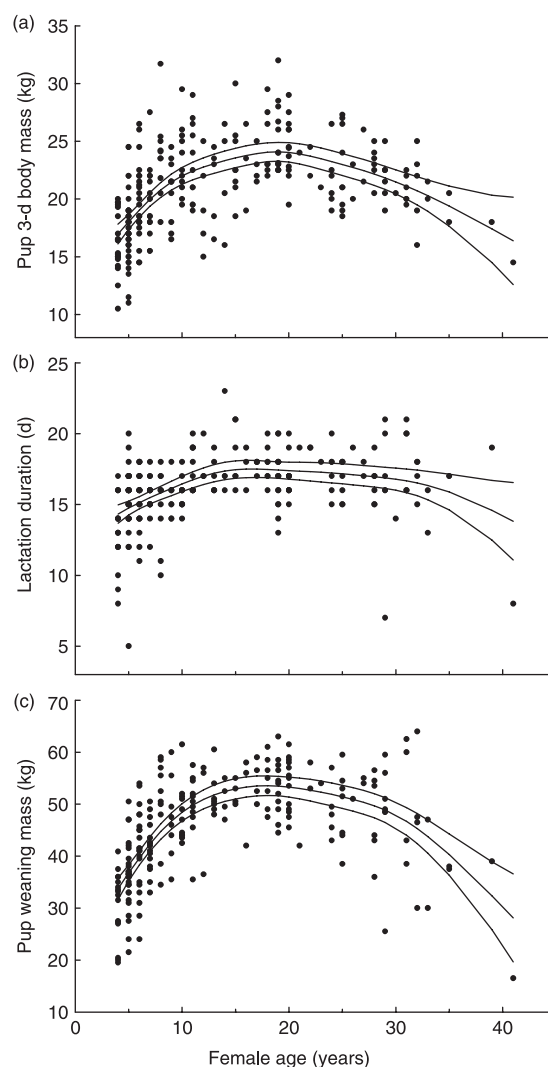


Fig. 2. Three measures of reproductive performance as a function of maternal age (a) pup birth mass (3 days postpartum), $n = 251$ females (b) lactation length, $n = 233$ females, and (c) pup weaning mass, $n = 228$ females. In each plot, the middle solid line is the fit of a generalized additive model and the other lines represent the upper and lower 95% point-wise confidence limits of fitted values.

Table 4. Linear mixed-effects models for pup birth mass ($n = 80$), lactation length ($n = 220$) and pup weaning mass ($n = 237$) with Akaike's information criteria (AIC), Delta AIC (Δ) and Akaike weights (w) based on females with repeated measures (range: 2–14 observations)

ID	Model	Pup birth mass			Lactation length			Pup weaning mass			
		d.f.	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i
1	Female (random effect only)	1	1157.0	47.3	0.00	4998.7	106.7	0.00	11448.8	268.7	0.00
2	Female age	2	1155.5	45.8	0.00	4968.9	76.9	0.00	11406.1	226.0	0.00
3	Pup sex	2	1156.1	46.4	0.00	4998.3	106.3	0.00	11229.3	49.2	0.00
4	Female age + female age ²	3	1114.8	5.1	0.06	4893.7	1.7	0.29	11379.3	199.2	0.00
5	Pup sex + female age	3	1154.5	44.8	0.00	4968.6	76.6	0.00	11379.3	199.2	0.00
6	Pup sex + female age + female age ²	4	1109.7	0.0	0.76	4892.0	0.0	0.68	11180.1	0.0	0.88
7	Pup sex + female age + pup sex × female age	4	1156.3	46.6	0.00	4974.5	82.5	0.00	11383.7	203.6	0.00
8	Pup sex + female age + female age ² + pup sex × female age	5	1112.6	2.9	0.18	4898.2	6.2	0.03	11184.1	4.0	0.12
9	Pup sex + female age + female age ² + pup sex × female age + pup sex × female age ²	6	1120.9	11.2	0.00	4906.5	14.5	0.00	11191.2	11.1	0.00

^aFavoured models (bold type) were evaluated on the basis of lowest Akaike information criterion (AIC), lowest Delta AIC (Δ) and highest AIC weights (w).

Table 5. Parameter estimates for the best (see Table 4) repeated-measures, linear mixed-effects models for age-related variation in pup birth mass and weaning mass and lactation length

Trait	Model	Effect	Sex ^a	Estimate	SE	d.f.	t	P
Pup birth mass (kg)	6	Intercept		23.3	0.38	79	61.00	< 0.0001
		Pup sex	Male	0.95	0.41	43	2.29	0.03
		Female age		0.039	0.023	134	1.66	0.10
		Female age ²		-0.022	0.003	134	-8.19	< 0.0001
Pup weaning mass (kg)	6	Intercept		54.5	0.41	236	133.67	< 0.0001
		Pup sex	Male	2.07	0.29	221	7.11	< 0.0001
		Female age		-0.017	0.038	1442	-0.45	0.65
		Female age ²		-0.060	0.004	1442	-15.53	< 0.0001
Lactation length (d)	6	Intercept		17.9	0.13	219	138.94	< 0.0001
		Pup sex	Male	0.26	0.13	187	1.98	0.049
		Female age		0.037	0.011	871	3.36	0.001
		Female age ²		-0.012	0.002	871	-9.73	< 0.0001
	3	Intercept		18.0	0.11	219	158.05	< 0.0001
		Female age		0.037	0.011	872	3.39	0.001
		Female age ²		-0.011	0.001	872	-9.66	< 0.0001

^aEstimates of female pups are given by the intercepts.

deviance = 12.9%, Table 4). There was some support for model 4 with only a nonlinear maternal age effect, but the Akaike w was only half the strength of the model with pup sex as an explanatory variable. Furthermore, as the difference in lactation length of females nursing male pups was < 0.5 days (Table 5) it seems unlikely that such a difference would be biologically important. Again, there was no evidence of an interaction between pup sex and maternal age.

WEANING MASS AND WEANING SUCCESS

The cross-sectional model (8) that best explained the variation in pup weaning mass included the same terms as that for lactation length, namely a nonlinear maternal age term with maternal mass and pup sex (Table 3 and Fig. 2c). This model accounted for 62.1%

(adjusted R^2) of the observed variability. Mean weaning mass was highest for females age 18 years. Quadratic contrasts centred on this maximum mean indicated that birth mass increased to about age 11 years and then decreased after about age 25 years ($F_{1,194} = 3.89$, $P = 0.03$); in the intervening period of 14 years, female age had little effect on pup birth mass (Fig. 2c).

Mixed-effects, repeated-measures analysis on 237 females with 2–14 observations per female also indicated that pup weaning mass was best explained by a model containing pup sex and female age as a nonlinear term (model 6, explained deviance = 20.5%, Table 4). Again, there was no evidence for an interaction between pup sex and female age. Age-related changes in pup weaning mass within females are illustrated for seven females in Fig. 3. At weaning, male pups averaged 3.8% heavier than females (Table 5).

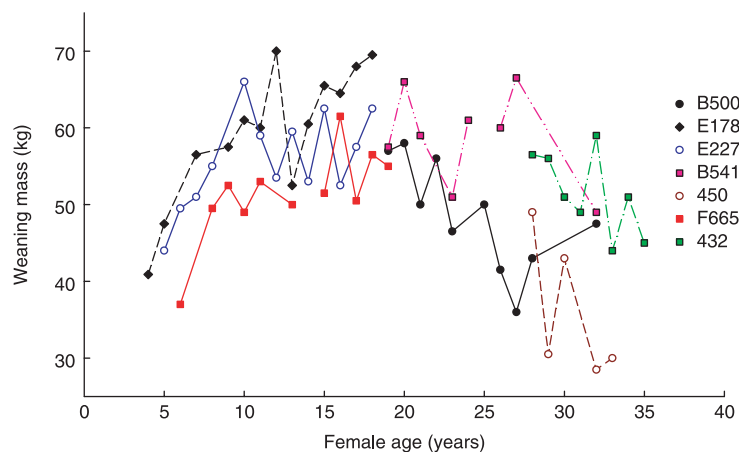


Fig. 3. Pup weaning mass as a function of female age for seven females with five to 13 observations each, illustrating within-female variation.

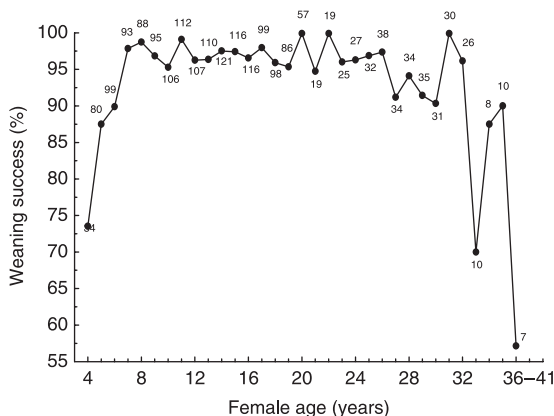


Fig. 4. Percentage of females successfully weaning pups as a function of maternal age. Number of females sampled indicated at each symbol.

The percentage of offspring weaned successfully varied significantly with maternal age (GLMM, $F_{32,1679} = 2.21$, $P < 0.001$) with females 4–6 years of age and those 33 years and older having significantly lower success than other ages (Fig. 4).

Discussion

There are several important findings arising from this long-term study. First, age-related improvement and decline in reproduction were evident in multiple measures of performance. Secondly, our longitudinal data enable us to eliminate the selection hypothesis as an important factor in the observed changes. Thirdly, senescent effects on reproduction did not become evident in females until late in life and a shorter-term cross-sectional study would probably not have detected those changes. This is significant because only relatively recently has convincing evidence for reproductive senescence been demonstrated in several taxa of large long-lived mammals (e.g. Derocher & Stirling 1998; Packer *et al.* 1998; Berube, Festa-Bianchet & Jorgensen

1999; Ericsson *et al.* 2001). Finally, cross-sectional and longitudinal analyses generally provided consistent results regarding the factors influencing maternal performance over the reproductive life span of this long-lived species.

Our long-term study was conducted during a period of sustained exponential increase in the number of pups born at the study site (Bowen *et al.* 2003). In a rapidly growing population, females should reproduce earlier in life and allocate more resources to offspring than would be optimal in a stable or declining population because fitness of an individual declines roughly as a linear function of population size (Roughgarden 1996). The observed exponential growth in pup production indicates that the past several decades was a period of generally favourable environmental conditions. Because age-related degeneration of function may result in lowered survival and reproductive performance only in certain stressful environments, our results may underestimate both the timing and degree of senescent decline in performance. Similarly, we may have underestimated age-related rate of improvement in early reproductive performance given that inexperienced females may be more sensitive to adverse conditions than those with more breeding experience.

Increasing population size could also have increased density in the breeding colony such that some of the age-related changes may, in fact, have been caused by crowding effects. We think this is unlikely, as the adult female response to the increased size of the population was to give birth in a larger fraction of the island and there was still unoccupied breeding habitat at the end of our study. As a result, colony density really did not increase.

CHANGES IN PERFORMANCE WITH PARITY

Earlier age at first parity negatively affects current and subsequent reproductive performance in some taxa (e.g. Huber 1987; Bailey 1991; Fessler *et al.* 2005), but not others (Ozoga & Verme 1986; Festa-Bianchet 1989;

King *et al.* 1991). Age at first parity had no effect on pup birth mass in our study, as has also been reported in other pinnipeds (Lunn, Boyd & Croxall 1994; Ellis *et al.* 2000). Although weaning mass increased with age in primiparous grey seals, age became a non-significant factor when MPPM was included in the analysis. Given the positive correlation between MPPM and body protein and lipid content in this species (Mellish *et al.* 1999), we can be reasonably confident that heavier mothers had more resources to allocate to milk production leading to heavier offspring at weaning (Iverson *et al.* 1993; Mellish *et al.* 1999). Thus even among primiparous grey seals, older and heavier females were able to mobilize their greater energy stores to produce heavier offspring at weaning.

We found that second- and third-parity female grey seals gave birth to heavier offspring than primiparous females of the same age, indicating a positive effect of breeding experience. Similar findings have been reported in other pinnipeds (Trites 1991; Ellis *et al.* 2000) and terrestrial mammals (Cote & Festa-Bianchet 2001; Fessler *et al.* 2005). There is evidence in several other species that changes in uterine blood flow and placental function may account partly for the increase in fetal and birth mass with breeding experience (Wilsher & Allen 2003; Dwyer *et al.* 2005).

AGE-RELATED CHANGES IN PERFORMANCE

Reproductive performance varies with female age in a wide range of mammals [pinnipeds (Reiter, Panken & Le Boeuf 1981; Bowen *et al.* 2001); bears (Derocher & Stirling 1998); whales (Olesiuk, Bigg & Ellis 1990); primates and lions (*Panthera leo*, Packer *et al.* 1998); and ungulates (Clutton-Brock, Guinness & Albon 1982; Ericsson *et al.* 2001)], and birds (Robertson & Rendall 2001, Weimerskirch 1992). However, our study revealed changes in maternal performance with age in multiple aspects of a female's phenotype, including maternal body mass (all traits), placenta and uterine environment (birth rate, birth mass), mammary gland function (weaning mass), and perhaps nursing behaviour and offspring defence (weaning success rate and length of lactation).

The early improvement and subsequent decline in apparent fecundity of grey seals is consistent with similar evidence of changes in birth rates of fur seals (Lunn *et al.* 1994), pilot whales (*Globicephala macrorhynchus*; Marsh & Kasuya 1984) and other mammals (Packer *et al.* 1998; Hewison & Gaillard 2001). Ovulation rates approach 100% in grey seals aged 5 years and older and early term pregnancy rates are almost as high (~90–95%) (Boyd 1985; Hammill & Gosselin 1995). Thus, the increase in birth rate among young females seems more likely to represent an increase in the proportion of females carrying a fetus to term than a change in the proportion becoming pregnant. Body condition plays an important role in both implantation and the maintenance of pregnancy in mammals

(Boyd 1984; White, Rowell & Hauer 1997), with females in poor condition having lower success. Given that older experienced grey seal females (i.e. > 25 years) with reduced birth rates were as heavy as those with the highest birth rates, reduced maternal performance late in life cannot be explained as the result of reduced maternal condition.

Birth and weaning mass of grey seal pups were characterized by a period of rapid increase with maternal age, a plateau of relatively constant offspring mass, followed by a decline in older females (Fig. 2). Similar patterns are evident in the reindeer (*Rangifer tarandus*) (Weladji *et al.* 2002), polar bears (*Ursus maritimus*, Derocher & Stirling 1998), Columbia ground squirrels (*Spermophilus columbianus*, Broussard *et al.* 2003) and lions and chimpanzees (*Pan troglodytes*, Packer *et al.* 1998). Female age was a significant predictor of increasing pup birth and weaning mass in grey seals even after normalizing for the effect of MPPM. In capital breeding pinnipeds, MPPM is thought to play a dominant role in determining both birth and weaning mass (e.g. Bowen, Boness & Oftedal 1987; Fedak, Arbom & Boyd 1996; Pomeroy *et al.* 1999). However, as age was not considered as an explanatory variable in those studies, they provide no information on the relative influence of age and mass on offspring size. Where the effects of maternal body mass and age have been studied simultaneously, significant age effects have been found in harbour seals (*Phoca vitulina*, Ellis *et al.* 2000; Bowen *et al.* 2001) and in northern fur seals (*Callorhinus ursinus*, Boltnev & York 2001). Thus, our results and those on several other pinnipeds suggest that the influence of maternal age on reproductive performance may be more widespread than currently thought.

Because male pups are larger than female pups at birth and weaning, and therefore more energetically expensive to raise, we expected that both young growing females and senescent older females might be less able to raise male pups, resulting in an interaction between pup sex and maternal age. This hypothesis was not supported by our data. This may indicate that pups play an important role in determining how much milk they receive as suggested by the finding that male grey seal pups (with greater energy requirements) spent more time soliciting nursing and suckled longer than female pups (Kovacs 1987).

In addition to the quantity of resources allocated to offspring, we also found that grey seal females seem to vary the length of lactation as a nonlinear function of age (Fig. 3). This indicates that young females alter both the rate and duration of provisioning with increasing breeding experience and mass. However, over a wide range of ages, female lactation length was independent of maternal age even though pup weaning mass declined in older females. This suggests that the oldest females continue to support their young behaviourally (i.e. through attendance and nursing), even though they are physiologically less able to do so.

HYPOTHESES ACCOUNTING FOR
AGE-RELATED IMPROVEMENT

The selection hypothesis posits that improvement in reproductive performance early in life can be accounted for by the selective disappearance of poorer quality individuals over time (Curio 1983). Our cross-sectional data provide clear evidence for age-related improvement in multiple indices of reproductive performance that could have been caused by the selective mortality of poorer quality females. However, our cross-sectional data also indicate a reduction in performance in older females. This reduction would not be predicted by the selection hypothesis. Furthermore, our long-term measurements provide convincing evidence of both early improvement and subsequent decline in reproductive performance within individuals. Thus the selective disappearance of poorer quality phenotypes cannot account for our findings and we conclude there is no support for this hypothesis.

The constraint hypothesis predicts that reproductive performance should improve with increasing parity or body mass, presumably by making the parent better able to provision or to allocate stored energy to offspring. Our results indicate that first time breeders had lower weaning success, gave birth to lighter pups and weaned lighter pups than did second- or third-parity females, providing support for the constraint hypothesis. Over a broader range of ages, we also found that maternal age and MPPM were significant factors underlying the increasing lactation length and weaning mass (Table 3). Thus older and heavier females, with greater resources to support lactation, nursed longer and produced heavier pups, again providing support for the constraint hypothesis. However, the decline in several measures of reproductive performance in older grey seal females argues against this hypothesis, particularly in light of our data showing that those oldest females showed no decline in MPPM, which also has been found in old Columbia ground squirrels (Broussard *et al.* 2003) and wandering albatross (*Diomedea exulans*, Weimerskirch 1992).

As predicted by the restraint hypothesis, reproductive performance increased with increasing age in young females. However, the later decline in multiple measures of performance is not consistent with the predicted increase in reproductive effort in older females. Also, there was a relatively long period of years in which performance was unaffected by maternal age. Finally, although maternal resources continued to increase through the middle teens, measures of reproductive performance levelled off earlier in life indicating that females actually expended relatively less on offspring as they grew older. This finding is at odds with the restraint hypothesis.

SENESCENCE

We found evidence that reproductive performance declined sharply with age and that it occurred at

approximately the same age among four of the five traits measured (apparent birth rate, birth mass, weaning mass and weaning success) with females in their mid- to late 20s or early 30s performing more poorly. We attribute the decline in performance with age to senescence. Senescence could arise due to the wear and tear of accumulated reproductive and other costs of living, the accumulation of late-expression mutations or antagonistic pleiotropy. We do not know the genetic basis of the changes in reproductive performance of grey seals and therefore cannot test directly which of these mechanisms are responsible for the decline in performance. However, few plausible candidates for antagonistic pleiotropy genes have been identified, and there seems little reason to expect the same genes would have a positive effect on fitness early in life and a negative effect later in life (Ricklefs 1998).

Our results indicate that the decline in maternal reproductive performance is not due to loss of body mass, because oldest females were just as heavy as middle-aged females. However, with this exception, our findings are consistent with the disposable soma hypothesis whereby the energy allocated to the maintenance and repair body systems declines with age as the expectation of death increases and residual reproductive value decreases (Kirkwood & Austad 2000). For example, the decline in birth rate in older grey seals may be caused by reduced ovarian function with age, as has been documented in pilot whales (Marsh & Kasuya 1984). The decline in birth rate and pup birth mass for females in aged 25–30 years suggests reduced transfer of nutrients to the fetus, and perhaps through reduced functionality of the placenta and uterus, as has been documented in several domestic species (Wilsher & Allen 2003; Dwyer *et al.* 2005).

In grey seals, weaning mass depends largely on the daily rate of milk consumed by the pup and duration of suckling (Iverson *et al.* 1993; Mellish *et al.* 1999). Consequently, declining offspring weaning mass in older grey seal females presumably reflects reduced functionality in aspects of female physiology associated with the production and transfer of milk, thus particularly in performance of the mammary gland. Serial transplantation of normal mammary gland cells in mice indicates a limited ability to proliferate (Daniel & Young 1971), suggesting the mammary gland has a limited ability to replenish and repair itself and diminished function might be expected in older females.

Grey seals are perhaps the longest-lived pinniped species, with females in their late 30s and early 40s remaining reproductively active (this study). Females can only survive to this age if extrinsic sources of mortality are low. Evolutionary theories of senescence predict that if mortality rate is low, then there is weaker selection on early reproduction and stronger selection for survival and reproductive success later in life (Williams 1957). Our findings that reproductive senescence in grey seals was not evident until females were in their mid-20s are consistent with that prediction.

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