

Good reindeer mothers live longer and become better in raising offspring

Robert B. Weladji^{1,2,3}, Jean-Michel Gaillard², Nigel G. Yoccoz⁴,
Øystein Holand¹, Atle Mysterud³, Anne Loison², Mauri Nieminen⁵
and Nils Chr. Stenseth^{3,*}

¹*Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences,
PO Box 5003, 1432 Ås, Norway*

²*UMR-CNRS 5558, Laboratoire de Biométrie et de Biologie Evolutive, Université Lyon 1,
69622 Villeurbanne Cedex, France*

³*Department of Biology, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo,
PO Box 1066 Blindern, 0316 Oslo, Norway*

⁴*Department of Biology, University of Tromsø, 9037 Tromsø, Norway*

⁵*Finnish Game and Fisheries Research Institute, Reindeer Research Station, 99910 Kaamanen, Finland*

Longevity is the main factor influencing individual fitness of long-lived, iteroparous species. Theories of life history evolution suggest this is because increased longevity allows individuals to (i) have more breeding attempts (time component), (ii) accumulate experience so as to become better able to rear offspring (experience component) or (iii) because individuals reaching old age have above-average quality (quality component). We assess empirically the relative influences of time, experience and quality on the relationship between longevity and individual fitness among female reindeer. Fitness increased with longevity due to all three processes. All females increased in success with age up to their penultimate year of life (experience component), the success of the terminal-breeding occasion was strongly dependent on longevity. Long-lived females had more successful breeding attempts during their life (time component), and had higher reproductive success at all ages, especially during the last year of life (individual quality component) than short-lived females. Our study reveals a more complex relationship between longevity and fitness in large mammals than the simple increase of the number of reproductive attempts when living longer.

Keywords: experience; individual fitness; individual quality; longevity; reproductive success;
Rangifer tarandus

1. INTRODUCTION

Longevity is the main factor influencing individual fitness of long-lived, iteroparous species (Westendorp & Kirkwood 1998; Gaillard *et al.* 2000a). Fitness is a fundamental concept in ecology and evolutionary biology, but is difficult to define and estimate (Brommer *et al.* 2002, 2004). Evolutionary strategies predict how individuals should allocate limiting resources to competing activities in order to maximize fitness. Because of trade-offs (Stearns 1992), increased allocation to reproduction reduces the resources available for somatic maintenance, thereby reducing longevity (Kirkwood 1977; Kirkwood & Rose 1991; Westendorp & Kirkwood 1998). One may thus expect an organism to balance longevity and reproductive success (Kirkwood 1977; Kirkwood & Rose 1991; Westendorp & Kirkwood 1998; Lahdenperä *et al.* 2004). However, previous studies of fitness variation within vertebrate populations have consistently reported that long-lived individuals have higher fitness than short-lived ones (Clutton-Brock 1988; Newton 1989). Thus, a positive relationship generally occurs between longevity and fitness among individuals of a given population. Such a positive effect of longevity on individual fitness could be

accounted for by three different processes—time (number of breeding attempts), experience and individual heterogeneity (i.e. differences of quality among individuals). Disentangling these three processes may help avoid the problem of correlations among fitness components when assessing trade-offs (Reznick 1985). This has not been done previously because of logistic difficulties in collecting adequate data, especially in large mammals.

Using an exceptionally detailed data set collected over 33 years (starting in 1969) on a semi-domestic reindeer (*Rangifer tarandus*) population monitored systematically in Finland, we determine the relationship between longevity and fitness of individual females, and evaluate the relative contribution of three biological processes behind this relationship. The time component *sensu stricto* would correspond to the simple increase of individual fitness with increasing longevity, with a constant reproductive success with age and a constant age-specific reproductive success among females of different longevities. The experience component *sensu stricto* should involve an increase of reproductive success with age for all females, independently of their longevity. Lastly, the quality component *sensu stricto* would correspond to differences of reproductive success according to female longevity, with a constant reproductive success with age. Note that the quality

* Author for correspondence (n.c.stenseth@bio.uio.no).

component we define here corresponds to a special case of individual heterogeneity often pointed out in evolutionary studies. Our quality component is an among-group heterogeneity in overall quality (as measured by longevity) while individual heterogeneity corresponds to the whole set of factors that shape among-individual differences in performance. To identify the respective role of these processes in determining individual fitness, we proceeded in three steps: (i) we evaluated the relationship between fitness and longevity, (ii) we investigated whether annual reproductive success varied according to age (experience component) and individual quality (quality component), as measured by longevity and (iii) we explored how these different models of age-specific variation of reproductive success modify the relationship between fitness and longevity.

2. MATERIAL AND METHODS

(a) Study area and reindeer data

The data are from the Kaamanen Reindeer Research station in Inari, Finland (61° 10'N), where reindeer are free ranging in large-scale seasonal grazing enclosures (all together about 43.8 km²) most of the year, excluding the calving period when they are kept in a more confined calving paddock (about 50 ha). The animals receive supplemental feeding only during winter. The herd was established in the late 1960s with about 20 males and 60 females. Since then, there has been an ongoing systematic monitoring of the animals in several aspects of their biology (e.g. physiology, behaviour).

Newborn calves are caught by hand, individually marked and weighed to the nearest 0.1 kg. The birth dates of the newborns as well as the reproductive status of females (i.e. whether a female had a calf or not) are also recorded. The age and the weight of the mothers are already known as they were marked either at birth or when joining the population. The calving area is examined daily and carcasses found are collected and examined. In this way, mortality among calves during the calving period is recorded as well as the causes of mortality. Additionally, individuals are weighed in spring prior to calving and in autumn during slaughtering (mostly calves), and their fecundity recorded. This allows us to have accurate information about growth, calving success and survival (neonatal, preweaning and adult) for most animals. We used, when assessing lambda, only females that died naturally (i.e. lifespan exactly known) and having reached maturity (i.e. normally at 2 years of age). The population size is kept rather stable over years, as most calves are slaughtered every year to regulate the numbers.

(b) Statistical analyses

We used the two most common measures of individual fitness (Brommer *et al.* 2004), lifetime reproductive success (LRS) that corresponds to the total number of offspring produced and successfully weaned throughout life (Clutton-Brock 1988; Gaillard *et al.* 2000a) and individual lambda (λ), the dominant eigenvalue of an individual-based Leslie matrix (McGraw & Caswell 1996). There is, however, a strong analytical link between these two measures (McGraw & Caswell 1996). Indeed, both are functions of the fertilities (F_i , measured here as the weaning success at each reproductive attempt), but while LRS gives the same weight to all reproductive events irrespective of age, reproductive events occurring at later ages are downweighted (when $\lambda > 1$) or

upweighted (when $\lambda < 1$) compared to early events when using λ (for a given individual m , LRS is defined by $R_0^{(m)} = \sum_{i=1}^{\omega} F_i^{(m)}$ and λ by the equation $1 = \sum_{i=1}^{\omega} F_i^{(m)} (\lambda^{(m)})^{-i}$).

Females' individual fitness (λ) were calculated using R (R Development Core Team 2004) and following McGraw & Caswell (1996)'s recommendations. λ represents one measure of fitness and has recently been applied on a large taxonomic range of populations including humans (Käär & Jokela 1998; Korpelainen 2000; Lahdenperä *et al.* 2004), ungulates (Gaillard *et al.* 2000a; Kjellander *et al.* 2004) and other organisms (Brommer *et al.* 2002). As we used only females that died naturally, lifespan was exactly known as well as yearly reproductive success (measured here as weaning success). Hence, LRS was accurately measured. We divided LRS by two to get a measure comparable to λ .

We used generalized additive models (GAM; Wood 2004; mgcv in R) to assess the shape of the relationship between longevity and both LRS and λ (assessment of the overall increase in fitness as a function of age; see figures 1a and 2a). The relationship between reproductive success and female age was assessed using mixed logistic regression models (Carlin *et al.* 2001), female individual identity being included as a random factor. To estimate the experience versus quality components, we included in the models the fixed factors age (with different definitions of age classes or life history stages as we used a piece-wise like regression model) and longevity. Longevity was included only for the age segment before last year of life (age last year and longevity are obviously identical). The different parameterizations for the age effects were compared on the basis of models' Akaike information criterion (AIC) values, using maximum likelihood methods to calculate AIC and AIC weights (Anderson *et al.* 2001). Estimation based on penalized quasi-likelihood was used for regression parameters and variance components.

3. RESULTS

The relationship between LRS and longevity was linear over the range 4–16 (e.d.f. = 1; $\beta = 0.39$, s.e. = 0.027), whereas the relationship between λ and longevity was not (e.d.f. = 1.91; see figures 1a and 2a).

The model best explaining the variation in annual reproductive success included additive effects of a three-stage life history (age 2, age 3 to penultimate and last year) and of longevity (table 1, selected model shown in bold type). Reproductive success was lower at age 2 than at later ages (table 2), then female reproductive success increased linearly with age between 3 years and the penultimate year of life (table 2), providing evidence for the experience component. Lastly, female reproductive success decreased markedly during the last year of life, and long-lived females were more successful at any stage than short-lived ones (table 2). Looking at stage-specific effects of longevity on female reproductive success, the model including interactive effects between stage and longevity was within 2 AIC units (i.e. AIC = 1.96, see table 1).

In order to assess and quantify the importance of experience and longevity on individual fitness (as measured by LRS and λ), we estimated fitness curves based on the estimated effects of experience and quality (as measured by longevity) on the fertilities F_i . Accordingly, figures were developed (figure 1 and figure 2), showing clearly that experience has a large effect on fitness, particularly for LRS (since λ downweights the

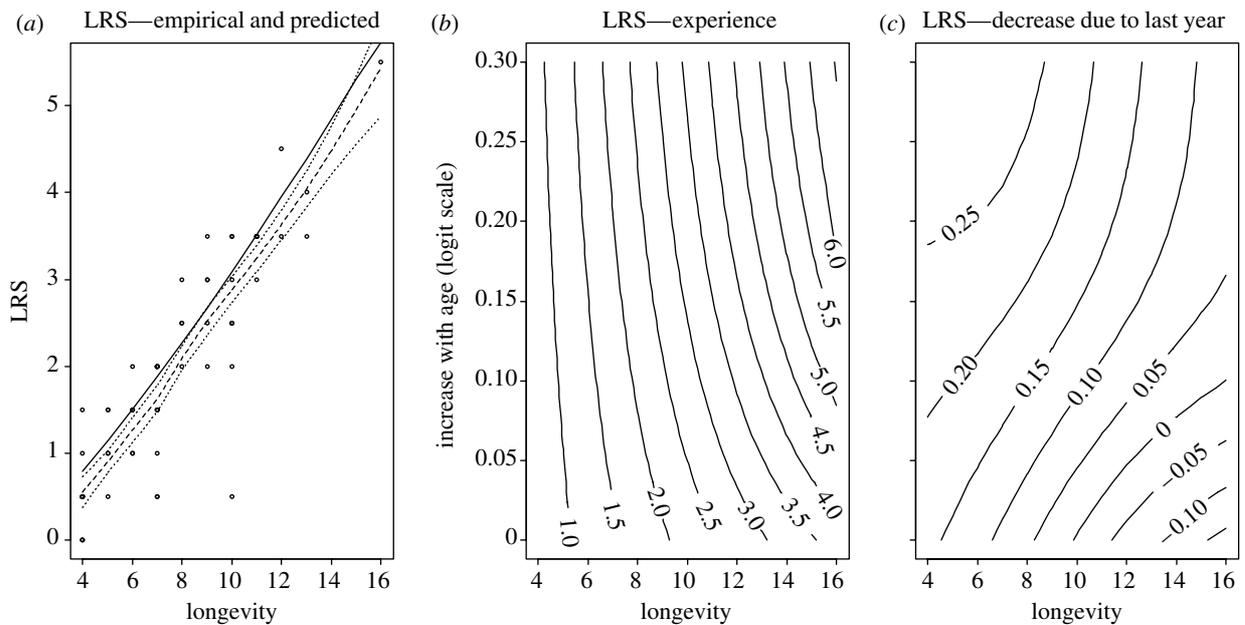


Figure 1. The relationship between longevity and LRS. (a) the relationship between age and LRS is nearly linear (continuous line: LRS based on estimated relationship weaning-success age, dotted line with shaded area, predicted values obtained using an additive model, points are observed values for females with complete observations). (b) The effect of experience (measured by the slope of the regression of weaning success against age) on LRS. A vertical slope (i.e. slope = 0) would indicate no experience i.e. a constant weaning success after three years of age; while a positive slope will reflect the effect of experience. For example, LRS for longevity = 10 will be 2.18 without experience (slope = 0) and 3.090 with experience (i.e. slope = 0.15); demonstrating that individual fitness increases with experience. (c) The consequence on fitness of the lower weaning success observed in the last year of life. The figure shows the difference between a fitness calculated assuming only an effect of experience (measured by the slope weaning-success age) but with no decrease during the last year, and the fitness calculated using the estimated last-year effect.

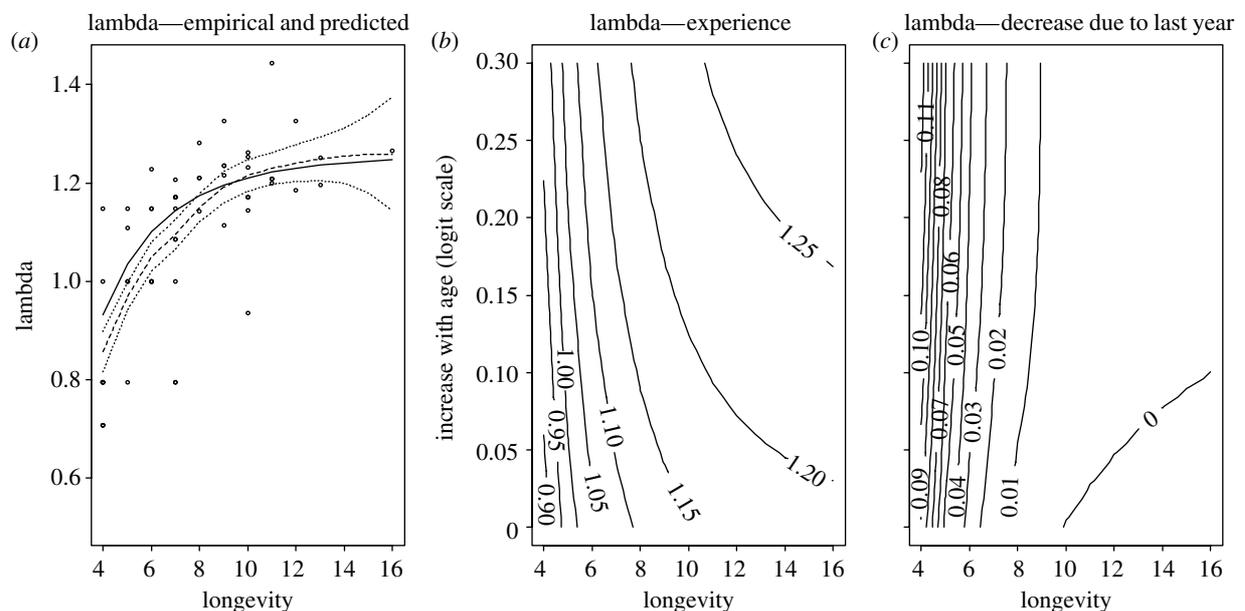


Figure 2. The relationship between longevity and lambda. (a) The relationship between age and Lambda is strongly nonlinear due to reproductive events occurring late in life being strongly downweighted as the estimated lambda are much larger than 1. (b) The effect of experience on lambda. (c) The consequence on fitness of the lower weaning success observed in the last year of life. (see figure 1 for further details).

reproductive events occurring late), and that the effect of the last year is large, especially for short-lived animals (they have a short life, and their last year is very poor).

4. DISCUSSION

As in most previous studies of the relationship between reproductive success and longevity (Stearns 1992; Bérubé

et al. 1999; Korpelainen 2000; Thomas *et al.* 2000; Kjellander *et al.* 2004), reindeer females that live the longest typically enjoyed the highest fitness (time component). That reproductive success was lower at age 2 than at later ages (table 2) is likely because some females have not yet reproduced at all before 3 years of age, but also because primiparous females are generally less successful in raising offspring than multiparous females

Table 1. Results of the Akaike information criterion (AIC)-based model selection procedure for modelling the effect of age on LRS. age.BL, age up to the penultimate year of life; age.LY, last year of life; age2, age = 2, age2.BL, age from 3 to penultimate; age3, age = 3, age3.BL, age from 4 to penultimate. The Δ AIC values are based on maximum likelihood fitting of generalized linear mixed models. The best model is shown in bold type.

age	age ²	poly (age,6)	age.BL	age.BL ²	age.LY	age.LY ²	age2	age2.BL	age > 2	age2.BL ²	age3	age3.BL	longevity	age × longevity	Δ AIC	AIC weights
			x		x	x	x	x					x		0.00	0.40
			x		x	x	x	x					x		0.42	0.32
			x		x	x	x	x						x	1.96	0.15
			x		x	x	x	x		x					2.38	0.12
			x		x			x							12.28	0.00
									x						55.20	0.00
					x		x								8.24	0.01
					x		x								38.73	0.00
					x		x								20.52	0.00
					x		x								21.11	0.00
					x		x						x		21.61	0.00
x					x		x						x		78.93	0.00
x	x														67.20	0.00
x															50.43	0.00
														x	60.22	0.00

(Forslund & Pärt 1995; Gaillard *et al.* 2000b). The linear increase in female reproductive success with age between 3 years and the penultimate year of life (table 2) provides evidence for the experience component. Indeed, experience is often associated with increased reproductive performance (Gaillard *et al.* 2000b; Pyle *et al.* 2001). The success of the terminal-breeding occasion was strongly dependent on longevity, justifying the marked decrease in female reproductive success during the last year of life. As expected from the quality component, long-lived females were more successful at any stage than short-lived ones. Indeed, the effect of age on reproductive success varied with longevity, and we found that marked evidence of the quality component only occurred during the last breeding attempt. Long-lived females were able to keep about the same success until their death whereas short-lived females most often failed during their last attempt.

In addition to the simple increase of the number of reproductive attempts also reported in our study, the occurrence of a higher individual fitness with increased longevity involved an increased yearly reproductive success with age. Moreover, survival is not a random process especially among young animals and a selection against individuals of inferior quality has often been reported (Gaillard *et al.* 2000b). Indeed, the mean quality of animals is expected to increase as they age, masking any trade-off between life history traits (Van Noordwijk & De Jong 1986). However, we found marked effects of female quality on yearly reproductive success only during the last year of life. That the success of the terminal-breeding occasion might be lower than the reproductive success of previous years has been reported in birds (Rattiste 2004) and interpreted as disease-related or condition-related problems. Our study supports this finding of a decreased performance during the last reproductive attempt. In addition, we report for the first time that only the short-lived females show such a decrease in performance whereas the long-lived ones are able to maintain a high reproductive success until the end.

The marked positive effect of experience on reproductive success between 3 years and the penultimate year of life is likely to involve better ability to raise offspring when ageing. This may either be due to a better knowledge of the resource distribution and quality (i.e. foraging ability; Mirza & Provenza 1992; Ortegareyes & Provenza 1993), a higher social rank (e.g. dominance and access to resource), an improved quality of maternal care or a better ability to minimize high mortality risks facing newborn calves. Indeed, loss of newborn pronghorn (*Antilocapra americana*) fawns to coyotes (*Canis latrans*) was less for experienced breeders (Byers 1997). Consequently, greater fitness will evolve when good females learn how to become better mothers, by increasing the success of their offspring (i.e. offspring survival) rather than just breeding themselves (i.e. offspring production).

Hayflick (2000) recently proposed that the question ‘why do we live as long as we do’ might be more appropriate than ‘why do we age’. Since achieving greater fitness is the ultimate goal of any organism, the question ‘how do we achieve greatest fitness by living longer’ is more appropriate in an evolutionary biology perspective. Our study clearly supports this view and demonstrates that fitness of reindeer females increases when they live longer

Table 2. Parameter estimates based on generalized linear mixed modelling assessing the effect of age and longevity on the probability of a female to wean her offspring successfully (i.e. weaning success). Age effects are based on a three-stage model (i.e. piecewise regression): (a) 2 year-old females, (b) females from 3 years of age to penultimate year and (c) the last year of life. In order to get biologically interpretable estimates for the parameters, age > 2 is included as age-2 (so that the intercept corresponds to age 2) and last year is included as last year-7 (so that the coefficients for age represents the slope and curvature in weaning success for a female aged 7, a close to average longevity). Such a parameterization does not affect the predicted values used in figures 1 and 2.

term	without longevity		with longevity	
	estimates	95% C.I.	estimates	95% C.I.
intercept	-0.495	(-1.00;0.013)	-0.216	(-0.833;0.401)
age=2	-0.476	(-0.701;-0.250)	-0.504	(-0.734;-0.274)
age 2 to penultimate	0.139	(0.083;0.194)	0.121	(0.061;0.181)
last year	0.112	(0.033;0.191)	0.137	(0.052;0.221)
(last year) ²	0.033	(0.015;0.052)	0.030	(0.011;0.049)
longevity (for age ≠ last year)			0.0469	(-0.0123;0.106)

not only because they benefit from more breeding opportunities, but mainly because they enjoy the positive effects of experience during their long life, and also because they keep the ability to be successful up to death whereas short-lived females failed most often during their last attempt.

We are grateful to the Finnish Game and Fisheries Research Institute and V. Tervonen and his crew at Kutuharju Reindeer Research Station for the data. This work is supported by funding from the Norwegian Research Council to RBW.

REFERENCES

- Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K. P. 2001 Suggestions for presenting the results of data analyses. *J. Wildlife Manage.* **65**, 373–378.
- Bérubé, C. H., Festa-Bianchet, M. & Jorgenson, J. T. 1999 Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565.
- Brommer, J. E., Merilä, J. & Kokko, H. 2002 Reproductive timing and individual fitness. *Ecol. Lett.* **5**, 802–810. (doi:10.1046/j.1461-0248.2002.00369.x)
- Brommer, J. E., Gustafsson, L., Pietiäinen, H. & Merilä, J. 2004 Single-generation estimates of individual fitness as proxies for long-term genetic contribution. *Am. Nat.* **163**, 505–517. (doi:10.1086/382547)
- Byers, J. A. 1997 *American pronghorn. Social adaptations and the ghosts of predators past*. Chicago, IL: University of Chicago Press.
- Carlin, J. B., Wolfe, R., Brown, C. H. & Gelman, A. 2001 A case study on the choice, interpretation and checking of multilevel models for longitudinal binary outcomes. *Biostatistics* **2**, 397–416. (doi:10.1093/biostatistics/2.4.397)
- Clutton-Brock, T. H. 1988 *Reproductive success*. Chicago, IL: University of Chicago Press.
- Forslund, P. & Pärt, T. 1995 Age and reproduction in birds—hypotheses and test. *Trends Ecol. Evol.* **10**, 374–378. (doi:10.1016/S0169-5347(00)89141-7)
- Gaillard, J. M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. 2000a Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. B* **267**, 471–477. (doi:10.1098/rspb.2000.1024)
- Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toïgo, C. 2000b Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393. (doi:10.1146/annurev.ecolsys.31.1.367)
- Hayflick, L. 2000 The future of ageing. *Nature* **408**, 268–269. (doi:10.1038/35041709)
- Käär, P. & Jokela, J. 1998 Natural selection on age-specific fertilities in human females: comparison of individual-level fitness measures. *Proc. R. Soc. B* **265**, 2415–2420. (doi:10.1098/rspb.1998.0592)
- Kirkwood, T. B. L. 1977 Evolution of ageing. *Nature* **270**, 301–304. (doi:10.1038/270301a0)
- Kirkwood, T. B. L. & Rose, M. R. 1991 Evolution of senescence: late survival sacrificed for reproduction. *Phil. Trans. R. Soc. B* **322**, 15–24.
- Kjellander, P., Gaillard, J. M., Hewison, M. & Liberg, O. 2004 Predation risk and longevity influence variation in fitness of female roe deer (*Capreolus capreolus* L.). *Proc. R. Soc. B* **271**(Suppl), S338–S340.
- Korpelainen, H. 2000 Fitness, reproduction and longevity among European aristocratic and rural Finnish families in the 1700s and 1800s. *Proc. R. Soc. B* **267**, 1765–1770. (doi:10.1098/rspb.2000.1208)
- Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. 2004 Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* **428**, 178–181.
- McGraw, J. B. & Caswell, H. 1996 Estimation of individual fitness from life-history data. *Am. Nat.* **147**, 47–64. (doi:10.1086/285839)
- Mirza, S. N. & Provenza, F. D. 1992 Effects of age and conditions of exposure on maternally mediated food selection by lambs. *Appl. Anim. Behav. Sci.* **33**, 35–42. (doi:10.1016/S0168-1591(05)80082-6)
- Newton, I. 1989 *Life time reproduction in birds*. London, UK: London Academic Press.
- Ortega-eyes, L. & Provenza, F. D. 1993 The amount of experience and age affect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). *J. Anim. Sci.* **71**, 380–383.
- Pyle, P., Sydeman, W. J. & Hester, M. 2001 Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim. Ecol.* **70**, 1088–1097. (doi:10.1046/j.0021-8790.2001.00567.x)
- R Development Core Team 2004 *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rattiste, K. 2004 Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proc. R. Soc. B* **271**, 2059–2064. (doi:10.1098/rspb.2004.2832)
- Reznick, D. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267.

- Stearns, S. C. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.
- Thomas, F., Teriokhin, A. T., Renaud, F., De Meeûs, T. & Guegan, J. F. 2000 Human longevity at the cost of reproductive success: evidence from global data. *J. Evol. Biol.* **13**, 409–414. (doi:10.1046/j.1420-9101.2000.00190.x)
- Van Noordwijk, A. J. & De Jong, G. 1986 Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–142. (doi:10.1086/284547)
- Westendorp, R. G. J. & Kirkwood, T. B. L. 1998 Human longevity at the cost of reproductive success. *Nature* **396**, 743–746. (doi:10.1038/25519)
- Wood, S. N. 2004 Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J. Am. Stat. Assoc.* **99**, 673–686. (doi:10.1198/01621450400000980)