THE ROYAL SOCIETY

Fitness, reproduction and longevity among European aristocratic and rural Finnish families in the 1700s and 1800s

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The life histories of two socio-economically different groups of humans comprising birth cohorts from the 1700s and 1800s were investigated. It was discovered that fertility selection was greater among European aristocrats and mortality selection greater among rural Finns. The life history of the rural Finns involved shorter female life spans, a considerably longer period of reproduction, higher juvenile mortality, a greater total production of offspring and slightly higher individual fitness. In a comparison of parental cohorts, it was discovered that longevity and progeny survival improved significantly from the 1700s to the 1800s. Out of the three factors investigated, longevity was found to influence reproduction and fitness more than socio-economic group or birth cohort. The reproductive efficacy and fitness of women increased along with their life span. However, reproductive success and fitness were lower among women with the longest life span (over 80 years). Among men, reproductive success improved consistently along with the increase in longevity. When birth intervals were examined, it was discovered that the sex of previous offspring did not influence the interval between births.

Keywords: fitness; humans; life history; reproduction; selection; trade-off

1. INTRODUCTION

Life history involves the different components of a life cycle such as birth, growth, survival, number and size of offspring, reproductive investment and death. The success of life histories can be measured by determining the fitness of different life-history variants. Fitness is an important although often vaguely determined concept in ecology and evolutionary biology. Differences in fitness have consequences for gene frequencies and, thus, lead to evolution.

The evolution of the length of the reproductive life span is supposed to be controlled by the relationship between adult and juvenile mortality (Stearns 1992). Increases in the mean and variance of adult mortality are expected to decrease the reproductive life span, while increases in the mean and variance of juvenile mortality can lengthen the reproductive life span. In female humans, the total life span commonly extends far past their reproductive age. It has been suggested that the long human post-menopausal life span is an evolutionary adaptation that allows women to nurture children and grandchildren better without the complications of continued childbirth (Hawkes *et al.* 1998). On the other hand, Packer *et al.* (1998) proposed that reproductive cessation may only be a non-adaptive by-product of senescence, a view based on a test on female mammals in which grandmothers frequently engaged in kin-directed behaviour.

In the theory of life histories, trade-offs have an important role. Within an individual, trade-offs mean energy allocation between different functions competing for the same resources and they could be expressed, for instance, as competition for energy between reproduction and longevity. In effect, organisms may trade a long life span for enhanced reproduction or vice versa.

The goal of the present study was to investigate and compare life-history patterns and potential trade-offs in two socio-economically different groups of humans that engaged in reproduction either before or at the beginning of the demographic transition. As a result of the European demographic transition, which began in the late 1800s in the developed parts of Europe, marital fertility halved in less than 30 years in some countries (Borgerhoff Mulder 1998). A characteristic of the demographic transition was that well-off families reduced their fertility earlier and often to a greater degree (Livi-Bacci 1986). Borgerhoff Mulder (1998) suggested that human reproduction might be driven by psychological reasons and that it responds to modern conditions with a fertility level much lower than that which would maximize fitness.

Fitness values were computed based on the life histories of the human groups investigated. Besides lifetime reproductive success (LRS), individual fitness (λ), which is sensitive to both reproductive quantity and timing, was also calculated for each female using the method of McGraw & Caswell (1996). LRS and λ may rank individuals differently according to their fitness, as discovered by Käär & Jokela (1998), who also claimed that the rate-sensitive measure λ allows for a more accurate estimation of individual fitness.

2. MATERIAL AND METHODS

The data used included European royal and noble families, for which well-documented, demographic information was available and five large rural families from eastern Finland, for which extensive genealogical research had been conducted. The aristocratic families were from Britain, France, Spain, Germany, The Netherlands, Austria, Russia, Denmark and Sweden. Marriages between individuals from different countries had even been common. The rural Finns were mainly either farmers

or landless farm labourers. The data were chosen based on the availability of reliable demographic information and based on the need to have data on people representing socio-economically different groups. All parents in the families were married and they were born between 1700 and 1899, although some offspring were born in the 1900s. The variables recorded for the parents included age at death, number of all progeny, number of surviving progeny, proportion of surviving progeny, age at first childbirth, age at last childbirth and length of reproductive period.

Individual fitnesses (λ) and LRSs were also calculated for women. The method described by McGraw & Caswell (1996) was used for calculating individual fitnesses. For this, a projection matrix including age-specific fertilities and survival probabilities between age classes was constructed for each female based on her life-history data. The age-specific fertility of a female was measured as the number of children surviving to the age of 18 years multiplied by 0.5, because this equals the genetic contribution of one parent to offspring in sexual species. Fertility and survival were calculated in five-year periods throughout the reproductive age. The value of λ was calculated as a dominant eigenvalue of the matrix using MATLAB software (Mathworks, Inc., MA, USA). The value of LRS was calculated as the number of children surviving to the age of 18 years multiplied by 0.5.

Birth intervals, which are important determinants of fertility, were calculated by the sex of children. In the analysis, only those intervals in which the offspring whose birth began the interval did not die within the interval were included.

The effects of the group (aristocratic or rural), birth cohort (1700s or 1800s) and life span (< 50 years, 50–79 years or $\geqslant$ 80 years) on life-history variables and the effects of the group, birth cohort, offspring sex and mother's age (< 30 years, 30–39 years or $\geqslant$ 40 years at the end of the birth interval) on the birth interval were examined using an analysis of variance (SAS Software, SAS Institute, Inc., Cary, NC, USA). Pairwise comparisons of life histories were conducted using Tukey's Studentized range test.

Based on the data for female life histories, Crow's (1958) indices of total selection (I) were calculated and broken down into two components, one associated with mortality differences (I_m) and the other with fertility differences (I_f).

3. RESULTS

Table 1 shows the values for different life-history parameters in married, aristocratic, European, and married, rural, Finnish men and women born in the 1700s and 1800s, while the life-span-dependent values of the parameters are given in table 2. The results of the analysis of variance revealed that the life histories of the aristocratic and rural men and women differed significantly in many respects and that their life histories varied significantly according to the life spans of individuals (table 3). The birth cohort significantly influenced only age at death and offspring survival in both sexes and the total offspring production in men. Interactions between the main effects were not significant except for the interaction between the birth cohort and longevity, which had a significant effect on the number of surviving progeny and age at last child in men.

It was discovered that the aristocratic women had longer life spans than the rural women, but no group

difference was found in men (table 3). The mean life span of both groups and sexes increased from the 1700s to the 1800s. The number of all offspring was greater among the rural Finns and the mean number decreased somewhat from the 1700s to the 1800s. The survival of progeny was significantly higher among the aristocrats and it improved by the 1800s. A slight but not significant increase in the number of surviving offspring was detected. The rural women began their reproduction slightly later than did the aristocratic women and both sexes among the rurals continued reproduction longer. Despite higher offspring mortality, the individual fitness (λ) of the rural women appeared slightly higher than did the fitness of the aristocrats. A small but not statistically significant difference was detected in the LRS between the groups.

The life histories between different longevity groups varied significantly (tables 2 and 3; figure 1). Reproductive success was lowest among individuals who died during their reproductive period. In women, reproductive success peaked in the age group 70–79 years, but decreased among the very old (over 80 years). The offspring production, fitness and LRS of the very old women approached the values detected among the women who died during the age of potential reproduction. Unlike the women's reproductive success, the men's reproductive success increased continuously in accordance with their life span. Age at first reproduction increased continuously in both sexes along with the longevity increase while the period of reproduction decreased in the oldest age group. In addition, offspring survival was lowest among those who died young and highest among those who lived to be the oldest. Therefore, offspring vigour relates to parental longevity. The effect of parental life span on offspring survival was more significant in women than in men.

When conducting pairwise comparisons of the life histories among the different life span groups, pre-menopausal females (< 50 years at death) differed significantly from younger post-menopausal females (50–79 years at death) in all life-history features examined and they differed significantly from the oldest group ($\geqslant$ 80 years at death) in the number and percentage of surviving progeny, in LRS and in age at first and last child. The oldest age group possessed a significantly lower total number of offspring, shorter reproductive period and lower fitness than the younger post-menopausal group. The proportion of childless individuals among the married women and men examined was low, equalling 9.6, 3.0 and 11.8%, respectively, among women in the three age groups, and 8.3, 3.3 and 4.2%, respectively, among men in the three age groups.

The birth intervals including only cases where the offspring whose birth began the interval did not die within the interval are shown in tables 1 and 4. The analysis of variance indicated that the intervals were independent of sex, but that the interactions between the mother's group and birth cohort, group and age, and birth cohort and age significantly affected the interval, with the intervals being shorter among young mothers and increasing among the aristocrats by the 1800s but staying about the same among the rural women. The intervals were somewhat shorter in general among the aristocrats which, however, was apparently mainly due to

Table 1. *Life histories of married, aristocratic, European, and married, rural, Finnish men and women born during the years 1700–1799 and 1800–1899*

(Values are means ± standard deviations unless specified. Surviving progeny includes children surviving to the age of 18 years.)

	aristocrats		rural Finns	
variable	1700–1799	1800–1899	1700–1799	1800–1899
women				
number of individuals	75	91	163	198
age at death (years)	58.6 ± 20.3	66.3 ± 16.3	56.0 ± 15.4	61.1 ± 18.3
number of all progeny	4.36 ± 3.84	3.84 ± 2.46	5.55 ± 2.97	5.20 ± 3.21
number of surviving progeny	3.15 ± 3.05	3.41 ± 2.24	3.29 ± 2.09	3.70 ± 2.57
% surviving progeny	72.2	88.8	59.3	71.1
age at first child (years)	22.9 ± 4.1	22.7 ± 4.4	23.6 ± 4.8	24.4 ± 4.9
age at last child (years)	30.4 ± 6.6	31.7 ± 5.6	37.1 ± 6.0	36.8 ± 6.1
reproductive period (years)	7.5 ± 6.4	8.9 ± 6.0	13.5 ± 6.9	12.4 ± 7.1
fitness	0.92 ± 0.37	0.96 ± 0.39	1.0 ± 0.30	0.98 ± 0.34
lifetime reproductive success	1.57 ± 1.53	1.70 ± 1.12	1.64 ± 1.05	1.85 ± 1.29
birth interval after female child (years)	2.06 ± 1.32	2.66 ± 1.93	2.81 ± 1.54	2.85 ± 1.57
birth interval after male child (years)	1.96 ± 1.32	2.68 ± 2.03	3.09 ± 1.86	2.82 ± 1.79
men				
number of individuals	73	82	149	169
age at death (years)	59.6 ± 13.8	64.4 ± 14.7	58.9 ± 13.1	65.4 ± 13.7
number of all progeny	4.52 ± 4.02	4.15 ± 2.51	6.25 ± 3.00	5.58 ± 3.50
number of surviving progeny	3.25 ± 3.10	3.68 ± 2.26	3.68 ± 2.15	4.10 ± 2.71
% surviving progeny	76.7	89.8	62.0	75.4
age at first child (years)	27.9 ± 8.2	28.7 ± 4.8	26.9 ± 5.9	29.7 ± 6.1
age at last child (years)	36.6 ± 8.8	38.6 ± 7.2	42.3 ± 7.7	42.8 ± 8.3
reproductive period (years)	8.7 ± 7.4	9.9 ± 7.3	15.3 ± 7.5	13.2 ± 8.2

Table 2. *Life histories of married, aristocratic, European, and married, rural, Finnish men and women born during the years 1700–1899 dependent on the age at death*

(Values are means ± standard deviations unless specified. Surviving progeny includes children surviving to the age of 18 years.)

	age at death		
variable	< 50 years	50–79 years	≥ 80 years
women			
number of indviduals	156	303	68
number of all progeny	4.36 ± 3.04	5.40 ± 3.17	4.34 ± 3.18
number of surviving progeny	2.61 ± 2.04	3.88 ± 2.53	3.40 ± 2.51
% surviving progeny	59.9	71.9	78.3
age at first child (years)	22.7 ± 3.8	23.9 ± 5.0	25.0 ± 4.8
age at last child (years)	32.8 ± 6.8	36.3 ± 6.4	35.6 ± 5.8
reproductive period (years)	10.1 ± 7.0	12.4 ± 7.1	10.5 ± 6.7
fitness	0.86 ± 0.42	1.04 ± 0.26	0.94 ± 0.38
lifetime reproductive success	1.30 ± 1.02	1.94 ± 1.26	1.69 ± 1.26
men			
number of indviduals	94	331	48
number of all progeny	4.37 ± 3.07	5.63 ± 3.33	5.67 ± 3.82
number of surviving progeny	2.82 ± 2.33	3.95 ± 2.46	4.29 ± 3.03
% surviving progeny	64.5	70.2	75.7
age at first child (years)	26.5 ± 4.6	28.8 ± 6.3	29.1 ± 7.9
age at last child (years)	36.6 ± 6.6	42.3 ± 8.4	41.1 ± 8.6
reproductive period (years)	10.2 ± 7.4	13.5 ± 8.2	12.0 ± 7.0

the lower mean age of reproduction among the aristocrats.

The index of opportunity for selection among the aristocrats changed clearly from the very high value of the 1700s to the considerably lower value of the 1800s (table 5). The change was only minor among the rural Finns. The fertility component of selection was greater than the mortality component among the aristocrats, while the situation was reversed among the rural Finns.

4. DISCUSSION

Individuals born in the 1700s and most of those born in the 1800s reproduced before effective birth control

Table 3. *Significance levels for the effects of group, birth cohort and life span on the life histories of married, aristocratic, European, and married, rural, Finnish men and women born during the years 1700–1899 as determined by analysis of variance*

variable	effect		
	group	cohort	life span
women			
age at death (years)	$p < 0.05$	$p < 0.001$	—
number of all progeny	$p < 0.01$	n.s.	$p < 0.01$
number of surviving progeny	n.s.	n.s.	$p < 0.001$
% surviving progeny	$p < 0.01$	$p < 0.001$	$p < 0.05$
age at first child (years)	$p < 0.05$	n.s.	$p < 0.01$
age at last child (years)	$p < 0.001$	n.s.	$p < 0.001$
reproductive period (years)	$p < 0.001$	n.s.	$p < 0.01$
fitness	$p < 0.05$	n.s.	$p < 0.001$
lifetime reproductive success	n.s.	n.s.	$p < 0.001$
men			
age at death (years)	n.s.	$p < 0.001$	—
number of all progeny	$p < 0.001$	$p < 0.01$	$p < 0.01$
number of surviving progeny	n.s.	n.s.	$p < 0.001$
% surviving progeny	$p < 0.001$	$p < 0.05$	n.s.
age at first child (years)	n.s.	n.s.	$p < 0.05$
age at last child (years)	$p < 0.001$	n.s.	$p < 0.001$
reproductive period (years)	$p < 0.001$	n.s.	$p < 0.01$

n.s., not significant.

methods and modern medical care, both of which reduce the variance in fertility and mortality. However, a reduction in the variance of fitness components was discovered among the aristocrats reproducing in the 1800s. When the fitness of the aristocrats and rural Finns was broken down into fertility and mortality components, it was apparent that fertility selection was greater in the aristocrats and mortality selection was greater in the rural Finns. Such patterns reflect socio-economic differences between these two groups. High birth rates and low offspring survival are typical features associated with poorer socio-economic conditions. Although the aristocrats and rural Finns are here considered to be two relatively homogeneous but socio-economically different groups, it is possible that substantial environmental variation (due, for example, to contagious diseases, war or wealth differences) was present within each group.

When the life histories of the two groups were compared, the rural Finns were found to possess a shorter female life span, a considerably longer period of reproduction, higher juvenile mortality, a greater total production of offspring and slightly higher individual fitness (λ) than the aristocrats. However, the numbers of surviving children were equal in these two groups. When the parental cohorts were compared, it was discovered that progeny survival improved significantly from the 1700s to the 1800s. An increase in longevity, a slight decrease in the number of all children and a small increase in the number of surviving children were detected in the two birth cohorts. A decrease in reproduction appeared to
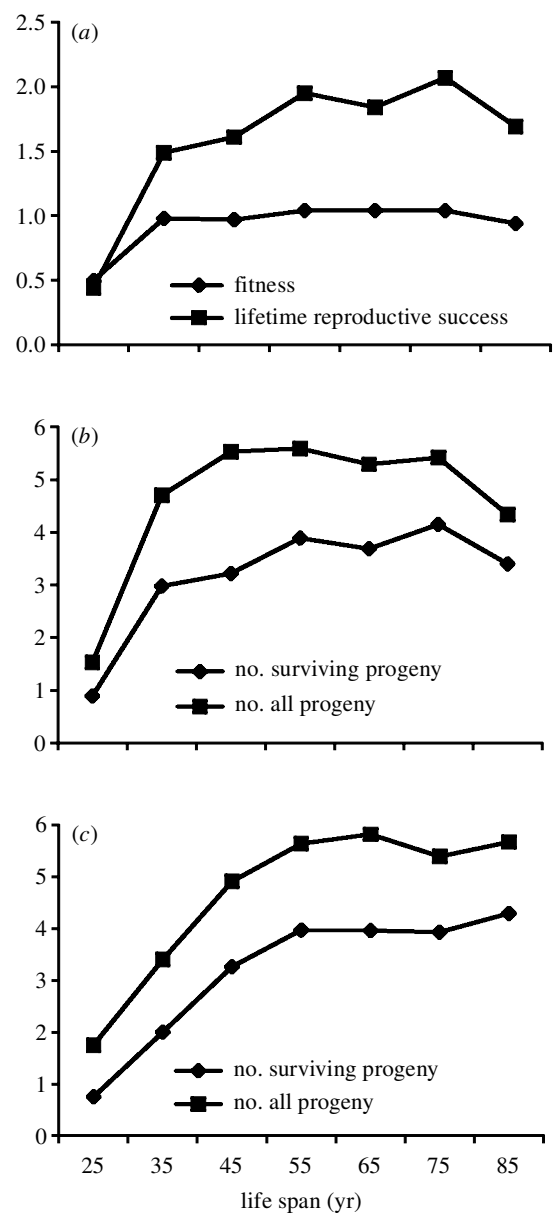

Figure 1. Reproductive success in different life span groups. The data include married, aristocratic Europeans, and married, rural Finns. (*a*) Age-dependent variation in female fitness and lifetime reproductive success, (*b*) age-dependent variation in the number of surviving progeny and number of all progeny in females, and (*c*) age-dependent variation in the number of surviving progeny and number of all progeny in males.

coincide with improved progeny survival but it did not completely prevent an increase in the number of surviving offspring. The data in the present study are mostly from the period before the European demographic transition and the reduction in reproduction occurring from the 1700s to the 1800s had not yet reached the level observed during the last 100 years.

Of the three factors longevity, socio-economic group and birth cohort during a limited time-frame, longevity was found to be the factor that influenced reproduction and fitness the most. The reproductive efficacy and fitness of women increased along with their life span until post-menopausal age. However, among women with the longest life span (over 80 years), reproductive success and

Table 4. *Intervals between two births in aristocratic Europeans and rural Finns dependent on the age of the mother at the end of the interval*

(Values for intervals are means ± standard deviations.)

mother's age	number	interval (years)
< 30 years	795	2.24 ± 1.03
30–39 years	751	3.11 ± 1.95
≥ 40 years	150	3.59 ± 2.53

Table 5. *The index of opportunity for selection and its fertility and mortality components in aristocratic Europeans and rural Finns born during the years 1700–1899*

group	cohort	total index (I)	selection component fertility (I_f)	mortality (I_m)
aristocrats	1700–1799	1.38	0.72	0.39
	1800–1899	0.58	0.41	0.13
rural Finns	1700–1799	1.17	0.28	0.69
	1800–1899	0.94	0.38	0.94

fitness were lower, approaching the level of those women who died during their reproductive period. Among men, whose reproductive costs are lower, reproductive success improved consistently along with the increase in longevity. Comparable trade-offs to those in women have been discovered in *Drosophila melanogaster* flies (Fowler & Partridge 1989; Prowse & Partridge 1997). Using a historical data set including British aristocracy, Westendorp & Kirkwood (1998) detected a trade-off between human longevity and reproductive success. Such discoveries support the disposable soma theory, which predicts that investments in reproduction divert resources away from somatic maintenance, resulting in ageing. Westendorp & Kirkwood (1998) found that the number of progeny was small when a woman died at an early age and increased with age at death, but decreased again among the longest-lived individuals. Unlike the present study, Westendorp & Kirkwood (1998) discovered a comparable pattern in men as well, although the changes were not as great as in the case of women.

Ligtenberg & Brand (1999) claimed that the trade-off Westendorp & Kirkwood (1998) found was instead due to a great proportion of childless women and their over-representation in high age groups. This would imply that, once there are children, the number of them makes no difference to the life span. On the other hand, Westendorp & Kirkwood (1999) argued that any impairment of fertility is likely to increase the likelihood of remaining childless. Therefore, childless individuals should be included in the analysis. In the present study, the proportion of childless individuals was low, which may partly relate to a high level of fertility in the groups examined and partly to a phenomenon that childless families are more easily overlooked in historical genealogical data.

The relationship between high offspring survival and long parental life span reflects the role of a genetic component in human longevity, the presence of which has been proved (Herskind *et al.* 1996; Westendorp & Kirkwood 1998; Korpelainen 1999). In the present study, a significant relationship between maternal longevity and offspring survival was detected, but the comparable trend revealed between paternal longevity and offspring vigour was not as significant. Korpelainen (1999) has previously suggested a hypothesis that the maternally inherited genetic component in the human life span is greater than the paternal component, a discovery that is in accordance with the view emphasizing the role of maternally inherited mitochondrial DNA in ageing (Linnane *et al.* 1989).

Birth interval is an important determinant of rates of reproduction and it also measures parental investment in each child. There is evidence of interval differences depending on the sex of the previous offspring, as discovered by Mace & Sear (1997) in a traditional African population. They found that the intervals after the birth of a boy were significantly longer than those after the birth of a girl, indicating higher parental investment in boys. However, in women of high parity, this difference disappeared. In the present investigation on rural and aristocratic Europeans, the sex of the previous offspring did not influence the interval between births. Yet, the interactions between the mother's group and birth cohort, group and age, and birth cohort and age did affect the intervals. Among the aristocrats the mean interval increased from 2.0 to 2.7 years from the 1700s to the 1800s, while among the rural Finns the birth intervals among mothers born in the 1700s and 1800s were somewhat higher, equalling 3.0 and 2.8 years, respectively. In general, young mothers had short birth intervals.

Longevity has increased considerably during the last 100 years and the extended post-reproductive period covers a greater portion of the total life span. During the same period, the level of reproduction has fallen below the potential reproductive capacity. Although the trade-offs between different functions may be partly responsible for this phenomenon, there are also perhaps psychological reasons, as suggested by Borgerhoff Mulder (1998) and other environmental changes (e.g. improved living conditions and medical care), which have overcome biological control mechanisms and which account for the increases in human life span but decreases in fertility in modern societies.

REFERENCES

Borgerhoff Mulder, M. 1998 The demographic transition: are we any closer to an evolutionary explanation? *Trends Ecol. Evol.* **13**, 266–270.

Crow, J. F. 1958 Some possibilities for measuring selection intensities in man. *Hum. Biol.* **30**, 1–13.

Fowler, K. & Partridge, L. 1989 A cost of mating female fruit flies. *Nature* **338**, 760–761.

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H. & Charnov, E. L. 1998 Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl Acad. Sci. USA* **95**, 1336–1339.

Herskind, A. M., McGue, M., Holm, N. V., Sorensen, T. I., Harvald, B. & Vaupel, J. W. 1996 The heritability of human longevity: a population-based study of 2872 Danish twin pairs born 1870–1900. *Hum. Genet.* **97**, 319–323.

Käär, P. & Jokela, J. 1998 Natural selection on age-specific fertilities in human females: comparison of individual-level fitness measures. *Proc. R. Soc. Lond.* B **265**, 2415–2420.

Korpelainen, H. 1999 Genetic maternal effects on human life span through the inheritance of mitochondrial DNA. *Hum. Hered.* **49**, 183–185.

Ligtenberg, T. & Brand, H. 1999 Longevity—does family size matter? *Nature* **399**, 522.

Linnane, A. W., Marzuki, S., Ozawa, T. & Tanaka, M. 1989 Mitochondrial DNA mutations as an important contribution to ageing and degenerative diseases. *Lancet* **i**, 642–645.

Livi-Bacci, M. 1986 Social-group forerunners of fertility control in Europe. In *The decline of fertility in Europe* (ed. A. J. Coale & S. C. Watkins), pp. 182–200. Princeton, NJ: Princeton University Press.

Mace, R. & Sear, R. 1997 Birth interval and the sex of children in a traditional African population: an evolutionary analysis. *J. Biosoc. Sci.* **29**, 499–507.

McGraw, J. B. & Caswell, H. 1996 Estimation of individual fitness from life-history data. *Am. Nat.* **147**, 47–64.

Packer, C., Tatar, M. & Collins, A. 1998 Reproductive cessation in female mammals. *Nature* **392**, 807–811.

Prowse, N. & Partridge, L. 1997 The effects of reproduction on longevity and fertility in male *Drosophila melanogaster*. *J. Insect Physiol.* **43**, 501–512.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Westendorp, R. G. J. & Kirkwood, T. B. L. 1998 Human longevity at the cost of reproductive success. *Nature* **396**, 743–746.

Westendorp, R. G. J. & Kirkwood, T. B. L. 1999 A reply to Ligtenberg and Brand. *Nature* **399**, 522.