Human longevity at the cost of reproductive success: evidence from global data

F. THOMAS,* A. T. TERIOKHIN,*† F. RENAUD,* T. DE MEEÛS* & J. F. GUÉGAN*

*Centre d'Etudes sur le Polymorphisme des Micro-Organismes, CEPM/UMR CNRS-IRD 9926, IRD, 911 Avenue Agropolis, B.P. 5045, 34032 Montpellier Cédex 1, France
†Department of Biology, Moscow State University, Moscow 119899, Russia

Keywords:

comparative analysis;
Homo sapiens;
reproduction;
somatic maintenance;
spatial-series;
trade-off.

Abstract

A trade-off between reproduction and somatic maintenance and hence survival is fundamental to life-history theory. We investigated the relationship between female fecundity and longevity in *Homo sapiens* using data from 153 countries located all over the world. The raw correlation between life span and fecundity was highly significant with a negative trend. After longevity and fecundity estimates were controlled for by confounding factors such as historical (i.e. human ethnic groups), religious, geographical, socio-economical and parasitological components, we still observed a negative relationship between the mean female fecundity and the mean longevity in a country. These findings support the hypothesis for the existence of a trade-off between these two key life-history traits in humans, as also reported by a recent single longitudinal study in England.

Introduction

Ageing, defined as the decline in survival probability and fecundity with advancing adult age, is often viewed as the evolutionary outcome of the declining force of natural selection at older age (Medawar, 1952; Partridge *et al.*, 1999). Ageing can be due to the accumulation of late acting deleterious mutations (Medawar, 1952; Hamilton, 1966; Charlesworth, 1994), and/or due to pleiotropy, as the result of constrained life-history optimization (Williams, 1966; Charlesworth, 1994; Partridge *et al.*, 1999; Zwaan, 1999). For instance, increased allocation of limited resources to reproduction can be an important cause of senescence and later mortality (Medawar, 1952; Williams, 1957; Kirkwood, 1981; Kirkwood & Rose, 1991; Teriokhin, 1998). Most of the evidence for this phenomenon comes from experiments showing the deleterious consequences of an increase in reproductive effort on life span (Partridge & Farquhar, 1981; Van Voorhies, 1992; Chapman *et al.*, 1995; Gems & Riddle, 1996; Prowse & Partridge, 1997; Snell & King, 1997). Artificial selection on age at reproduction showed the reverse effect that selection regime favouring individuals that retained fecundity at a later age resulted in populations with increased life spans (Engstrøm *et al.*, 1992; Zwaan *et al.*, 1995; Partridge *et al.*, 1999). Data for higher organisms, e.g. mammals, have until now been mostly lacking.

The hypothesis that investment in reproduction reduces the resources available for somatic maintenance has recently been tested in *Homo sapiens* by Westendorp & Kirkwood (1998). Using 1200 years of genealogical data on British aristocracy, they showed that the number of progeny was small for women who died at an early age, increased with the age of death, reached a plateau through the sixth, seventh and eighth decades of life, and was lower again for women who died at an age of 80 years or over. This relationship supported the expectation that heavy investments in reproduction diverts resources away from the maintenance and repair of cells, with ageing and earlier death as results (Westendorp & Kirkwood, 1998). For unknown reasons, the authors found a virtually identical pattern among men.

Correspondence: F. Thomas, Centre d'Etudes sur le Polymorphisme des Micro-Organismes, CEPM/UMR CNRS-IRD 9926, IRD, 911 Avenue Agropolis, B.P. 5045, 34032 Montpellier Cédex 1, France.
Tel.: +33 4 67 41 62 32; fax: +33 4 67 41 62 99;
e-mail: thomas@cepm.mpl.ird.fr

J. EVOL. BIOL. 13 (2000) 409–414 © 2000 BLACKWELL SCIENCE LTD

As manipulative experiments on humans are unethical, the statistical search for congruent patterns offers an alternative to understand variation in life-history parameters among human populations. Fortunately, there are considerable statistics on humans and their activities, and other ways of detecting similar patterns and of testing relevant hypotheses are possible. The aim of the present paper is to assess the generality of this trade-off among humans. We test whether the variation of life-history parameters found in the study of British aristocrats is also present across different human populations worldwide. After controlling longevity and fecundity for possible effects exerted by historical, spatial, economical and population patterns, we determined the relationship between longevity and fecundity, using data from 153 countries located all over the world.

Methods

Description of the data

Mean data on life expectancy, on infant mortality and on fecundity were obtained for 153 countries from the statistics of the 1992 World population data sheet (Jones, 1990).

Data on life expectancy and infant mortality were used to calculate longevity (life expectancy of females of different ages). To calculate life span expectations at different ages having only data on life span expectation at birth, L_0, and infant mortality, M_0 (the number of deaths per 1000 births during the first year of life), we had to make assumptions concerning the structure of human mortality. We supposed that human mortality is composed of three components: infant mortality, m_0, defined by the equation

$$e^{-m_0} = 1 - (M_0/1000)$$

and acting only during the first year of life; environmental mortality, m_e, assumed to be constant for all ages but not for different countries; and physiological mortality, m_{ph}, assumed to depend on age, t, in accordance with the law of Gompertz (Gompertz, 1825)

$$m_{ph} = Ae^{Bt}$$

with parameters assumed, for all countries, to be equal to the typical values of $A = 0.00001$ and $B = 0.1$ obtained when fitting demographic data (e.g. Gavrilov & Gavrilova, 1984). These assumptions lead to the following expressions for probabilities p_0, p_1, p_2, ..., p_t of surviving the forthcoming year at ages 0,1, ..., t

$$p_0 = e^{-m_0}; \quad p_1 = e^{-m_e - Ae^{2B}}; \ \ldots; \ p_t = e^{-m_e - Ae^{Bt}}$$

which, in their turn, lead to the following probabilities l_0, l_1, l_2, ..., l_t of surviving from age 0 to the ages of 1, 2, ..., $t + 1$ years:

$$l_0 = p_0 = e^{-m_0};$$
$$l_1 = l_0 p_1 = e^{-m_0 - m_e - Ae^B};$$
$$l_2 = l_1 p_2 = e^{-m_0 - 2m_e - Ae^B - Ae^{2B}};$$
$$l_t = l_{t-1} p_t = e^{-m_0 - m_e t - \sum_{u=1}^{t} Ae^{Bu}}.$$

Using the above equations, we find for the life span expectation at birth

$$L_0 = \sum_{t=0}^{\infty} l_t = e^{-m_0} + \sum_{t=1}^{\infty} e^{-m_0 - m_e t - \sum_{u=1}^{t} Ae^{Bu}}$$

This equation was used to find the environmental mortalities, m_e, for each country (values of L_0 and m_0 being known from our data and values of A and B being set to their typical values). The values of m_e for females ranged from about 0.0005 for Switzerland to about 0.02 for Chad.

With all the parameters in the above equation for L_0 now known, we can calculate the life span expectations at different ages. For this we used the equation of full expectation (e.g. Mangel & Clark, 1988) in which the total life span at birth can be presented as the weighted sum of conditional expectations of life of those who survived up to age t and those who did not:

$$L_0 = l_{t-1} L_t + (1 - l_{t-1}) L_{<t}.$$

Hence

$$L_t = l_{t-1}^{-1} [L_0 - (1 - l_{t-1}) L_{<t}]$$

where

$$L_{<t} = \sum_{u=0}^{t-1} l_u.$$

For example, concerning the life span expectation at 1 year (L_1), we obtain

$$L_1 = \left(1 - \frac{M_0}{1000}\right)^{-1} \left[L_0 - \frac{M_0}{1000}\left(1 - \frac{M_0}{1000}\right)\right].$$

Note, that in this particular case the estimate of L_1 does not depend on our specific assumptions concerning the exact values of parameters A and B in the Gompertz's equation (L_0 and M_0 are supposed to be known from the real data). For consistency, we used only values of life expectancy at 1 year (L_1), but other estimates (i.e. L_5, L_{10}, L_{15}) yielded similar results.

Fecundity (log-transformed) refers to the average number of children born to a woman during her lifetime, i.e. this estimate is only based on the fecundity of females who reached reproductive age and thus it is not influenced by childhood mortality. In addition, an analysis of life-history data should take into account the environmental conditions affecting both longevity and reproduction (Stearns, 1992; Westendorp & Kirkwood, 1998). Consequently, we considered in our analysis historical (i.e. human ethnic groups), geographical,

socio-economical, religious and parasitological components, since these factors are by virtue influencing parameters on human survival and fecundity (Jones, 1990; Anderson & May, 1991).

Data for population geography were obtained from the 1992 World population data sheet (Jones, 1990). We considered four demographic or economic parameters for each country: (i) total population (in number of people per country), (ii) total population growth (per 1000 people), (iii) population density (number of people per km^2) and (iv) per capita gross national product (GNP in US$ per year). These four variables were log-transformed.

Disease occurrences in the 153 countries were compiled from two international health care data bases, i.e. the Centers for Disease Control and Prevention (Atlanta, USA at http://www.cdc.gov/) and the World Health Organization (Geneva, Switzerland at http://www.who.int/). We collected data for a set of 16 categories of human diseases known to affect human survival (i.e. typhoid, hepatitis A, hepatitis B, malaria, schistosomiasis, filariosis, meningococcosis, yellow fever, dengue fever, cholera, trypanosomiasis, dracunculosis, chagas disease, lyme disease, cutaneous leishmaniosis and visceral leishmaniosis). Based on this information, we calculated the disease load as the total number of diseases for each country.

To correct for common history, we used the human group phylogeny based on the work of Cavalli-Sforza (1997), which we coded as categorical variables (Draper & Smith, 1981). We considered the eight largest divisions of ethnic groups: I: Africans and Nilotics (except native people from the Maghreb), II: Europeans (including people from the Middle East), III: Indians, IV: Mongols, Japanese and Koreans, V: American Indians, VI: Papua-New Guineans, VII: Melanesians, VIII: Mhongs, Khmers, Thais, Filipinos, Indonesians and related tribes. Furthermore, we considered five main groups of religion: I: Moslem, II: Christian–Jewish; III: Hindu; IV: Shinto; V: Animist, and we assigned a category when at least 50% of the inhabitants belonged to one major religion. Other independent variables were considered for each country: belonging to the Northern or Southern Hemisphere (coded 0/1), to an island or a landmass (coded 0/1), to a continent, its average position in degree of latitude and longitude and its total surface area (km^2).

Statistical procedure

To model the relationship between female life span and explanatory variables across the 153 countries, we used a general linear model (GLM). Minimal models were selected with a backward elimination procedure. At each iteration, the variable showing highest partial correlation with the dependent variable was included into the model only if its correlation was significant at the 5% level (Zar, 1996). We used the tolerance option with a value of 0.05 which protects against constructing highly multicolinear models tending to generate unstable coefficient estimates (Wilkinson *et al.*, 1992). A similar procedure was performed to model the relationship between fecundity and the explanatory variables across the 153 countries. Then, we plotted residual values of fecundity against residual values of life span and calculated their correlation. All statistical analyses were performed using Systat 8.0, Evanston, IL, USA (Wilkinson *et al.*, 1992).

Results

Mean (±SD) female life span was 67.3 ± 10.9 years (range: 40–83, $n = 153$). Mean fecundity (±SD) calculated from untransformed data was 4.2 ± 1.9 (range: 1.3–8.3, $n = 153$), and from log-transformed data was 1.34 ± 0.26 (range: 0.26–2.11, $n = 153$). The raw correlation between life span and fecundity was highly significant and negative across countries ($n = 153$, $r^2 = 0.70$, $y = 14.13 - 0.15x$, $F = 385.41$, $P < 0.001$), thus indicating that women in rich countries tend to have fewer children and live longer. Results from GLM modelling show that female life span and fecundity were significantly influenced by socio-economic, historical and disease parameters (Tables 1 and 2). Each model was highly significant (Table 1, $R^2 = 0.77$, $n = 153$, $F = 53.1$, $P < 0.001$; Table 2, $R^2 = 0.83$, $n = 153$, $F = 43.1$, $P < 0.001$). Spatial autocorrelation estimates were near zero (Table 1, first-order autocorrelation = 0.086 and Table 2, first-order autocorrelation = 0.193).

Residual distributions for female life span and fecundity were not significantly different from normal

Table 1 Summary of general linear model of female lifespan at 1 year (L_1) vs. significant explanatory variables. Parameter estimates, degrees of freedom (d.f.), *F*-ratio and associated probability (*P*) are given for each significant explanatory variable. For ethnic groups, the dummy variables and their corresponding parameter estimates are illustrated. Results were obtained after a step-down backward elimination procedure with the tolerance option set at 0.05. The final model was highly significant ($R^2 = 0.77$, $n = 153$, $F = 53.10$, $P < 0.001$). Interaction terms which could potentially affect life span variability were not significant.

	Parameter estimates	d.f.	*F*-ratio	*P*
Diseases	−0.833	1	14.101	0.000
GNP (log)	3.165	1	60.541	0.000
Ethnic group				
I	1.597			
II	−0.981			
III	1.294			
IV	−1.250			
V	5.710			
VI	−7.340			
VII	−0.710			
VIII	1.680	7	6.848	0.000

Table 2 Summary of general linear model of female fecundity vs. significant explanatory variables. Parameter estimates, degree of freedom (d.f.), *F*-ratio and associated probability (*P*) are given for each significant explanatory variable. For religion and ethnic group factors, the dummy variables and their corresponding parameter estimates are illustrated. Results were obtained after a step-down backward elimination procedure with the tolerance option set at 0.05 level. The final model was highly significant ($R^2 = 0.83$, $n = 153$, $F = 43.11$, $P < 0.001$). Interaction terms which could potentially affect fecundity variability were not significant.

	Parameter estimates	d.f.	*F*-ratio	*P*
Diseases	0.026	1	5.284	0.023
GNP (log)	−0.144	1	50.371	0.000
Religion				
I	−0.107			
II	0.135			
III	0.349			
IV	−0.335			
V	−0.042	4	2.549	0.043
Ethnic group				
I	0.062			
II	−0.063			
III	−0.207			
IV	−0.177			
V	0.132			
VI	0.412			
VII	0.236			
VIII	−0.271	7	12.793	0.000

distributions using Kolmogorov–Smirnov's *D* statistic (one-sample test, $P > 0.05$ in both cases) and marginally significant when applying Lillifors' test (d.f. = 153, $P = 0.048$ for life span; d.f. = 153, $P = 0.045$ for fecundity).

There was a negative relationship between residuals of fecundity and residuals of female life span (Pearson's correlation coefficient: $n = 153$, $r = -0.27$, $P = 0.0012$) (Fig. 1), indicating that in countries where women had more children the average life span was shorter, after correction for the factors mentioned above.

Discussion

Variations of female life expectancy and of fecundity at a broad scale are explained by numerous factors ranging from socio-economical parameters to disease incidence, geography and phylogeny. This analysis on spatial data confirms the trend in the temporal data for British aristocrats (Westendorp & Kirkwood, 1998) and thus support the hypothesis that human life histories involve a trade-off between longevity and reproduction. As in other species, humans who invest heavily in reproduction while young will, on average, pay for this reproductive success with a shortened life span. The fact that we do not observe in the first part of the curve an increase of fecundity with longevity as observed in Westendorp & Kirkwood (1998) indicates that fecundity is not constrained by short survival in the world. This

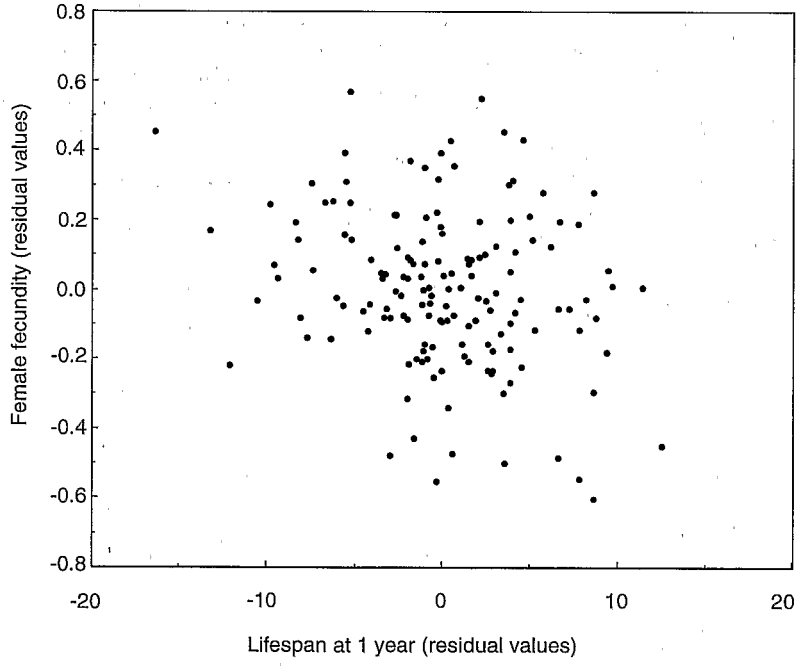

Fig. 1 Relationship between female fecundity (SD = ±0.21) and its corresponding life span (SD = ±4.32) at 1 year across a set of 153 countries ($r = -0.27$, $P = 0.0012$). Corresponding residual values were extracted from models as illustrated on Tables 1 and 2.

phenomenon seems normal here since, as opposed to Westendorp & Kirkwood (1998) who used individual data with a large variance, our study is based on mean longevity and fecundity values. Thus, despite the use of different kinds of data set (temporal vs. spatial data set and individual vs. average values), congruent patterns of life-history trade-offs are observed. All this study concerns phenotypic correlations. However, the data set can potentially address genetic differences as well, as indicated by the significance level of the ethnic group factor. Further investigations would be necessary to assess this point.

Life-history theory assumes that reproduction is costly and competes with other activities of the individuals (Roff, 1992; Stearns, 1992). However, the underlying causes of a cost of reproduction often vary and are difficult to distinguish (Erikstad *et al.*, 1998; Polis *et al.*, 1998; Rose & Bradley, 1998; Telford & Webb, 1998). The idea that parental care is costly is demonstrated in several bird species. Individuals that raised an experimentally enlarged brood have a longer reproductive interval (Deerenberg *et al.*, 1996) or are more sensitive to environmental stress such as parasitism (e.g. Møller, 1993, 1997; Norris *et al.*, 1994; Richner *et al.*, 1995).

Important questions remain, and we would like to underline a potentially strong limitation in our study. In most animals, life-history traits are strongly correlated with environmental variables as the result of natural selection. In this study on *Homo sapiens*, we have made the important assumption that socio-cultural aspects are absent, except maybe those invoked with religion, so that human traits can be analysed exactly like the traits of any animal species. However, as we know, socio-cultural factors are important to understand a large range of human features such as reproduction and are also probably sensitive to general environmental conditions. Although we believe that a substantial part of the fecundity variation among humans explains a significant part of the variability in their longevity through a trade-off, we must be aware that such socio-cultural parameters, because of their complexity, have been neglected in this work and can potentially confound this conclusion.

References

Anderson, R.M. & May, R.M. 1991. *Infectious Diseases of Humans: Dynamics and Control.* Oxford University Press, Oxford, UK.

Cavalli-Sforza, L.L. 1997. Genes, peoples, and languages. *Proc. Natl. Acad. Sci. USA* **94**: 7719–7724.

Chapman, T., Liddle, L.F., Kalb, J.M., Wolfner, M.F. & Partridge, L. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**: 241–244.

Charlesworth, B. 1994. *Evolution in Age Structured Populations,* 2nd edn. Cambridge University Press.

Deerenberg, C., de Kogel, C.H. & Overkamp, G.F.J. 1996. Cost of reproduction in the Zebra Finch *Taeniopygia guttata*: manipulation of brood size in the laboratory. *J. Av. Biol.* **27**: 321–326.

Draper, N.R. & Smith, H. 1981. *Applied Regression Analysis,* 2nd edn. John Wiley & Sons, New York.

Engstrøm, G., Liljedahl, L.-E. & Bjørklund, T. 1992. Expression of genetic and environmental variation during ageing. 2. Selection for increased lifespan in *Drosophila melanogaster. Theor. Appl. Genet.* **85**: 26–32.

Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**: 1781–1788.

Gavrilov, L.A. & Gavrilova, N.S. 1984. Historically stable indices of mortality and their use for medical geography. *Geogr. Med.* **14**: 305–306.

Gems, D. & Riddle, D.L. 1996. Longevity in *Caenorhabditis elegans* reduced by mating but not gamete production. *Nature* **379**: 723–725.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining life contingencies. *Phil. Trans. Roy. Soc. Lond. A* **115**: 513–585.

Hamilton, W.D. 1966. The molding of senescence by natural selection. *J. Theor. Biol.* **12**: 12–45.

Jones, H. 1990. *Population Geography,* 2nd edn. Paul Chapman Publishing Ltd, London.

Kirkwood, T.B.L. 1981. Repair and its evolution: survival versus reproduction. In: *An Evolutionary Approach to Ressource Use* (C. R. Townsend & P. Calow, eds), pp. 165–189. Blackwell Scientific, Oxford.

Kirkwood, T.B.L. & Rose, M.R. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Phil. Trans. R. Soc. Lond. B* **332**: 15–24.

Mangel, M. & Clark, C.W. 1988. *Dynamical Modeling in Behavioral Ecology.* Princeton University Press, Princeton, NJ.

Medawar, P.B. 1952. *An Unsolved Problem of Biology.* Lewis Publishers, London.

Møller, A.P. 1993. Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol.* **62**: 309–322.

Møller, A.P. 1997. Parasitism and the evolution of host life history. In: *Host–Parasite Evolution: General Principles and Avian Models* (D. H. Clayton, & J. Moore, eds), pp. 105–127. Oxford University Press, Oxford.

Norris, K., Anwar, M. & Read, A.F. 1994. Reproductive effort influences the prevalence of haematozoan parasites in great tits. *J. Anim. Ecol.* **63**: 601–610.

Partridge, L. & Farquhar, M. 1981. Sexual activity reduces life span of male fruitflies. *Nature* **294**: 580–582.

Partridge, L., Prowse, N. & Pignatelli, P. 1999. Another set of responses and correlated responses to selection on age at reproduction in *Drosophila melanogaster. Proc. R. Soc. Lond. B* **266**: 255–261.

Polis, G.A., Barnes, J.D., Seely, M.K., Henschel, J.R. & Enders, M.M. 1998. Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. *Ecology* **79**: 2560–2566.

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

Richner, H., Christe, P.H. & Oppliger, A. 1995. Paternal investment affects prevalence of malaria. *Proc. Natl. Acad. Sci. USA* **92**: 1192–1194.

Roff, D.A. 1992. *The Evolution of Life Histories*. Chapman & Hall, New York.

Rose, M.R. & Bradley, T.J. 1998. Evolutionary physiology of the cost of reproduction. *Oikos* **83**: 443–451.

Snell, T.W. & King, C.E. 1997. Lifespan and fecundity patterns in rotifers: the cost of reproduction. *Evolution* **31**: 882–890.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press.

Telford, S.R. & Webb, P.I. 1998. The energetic cost of copulation in a polygynandrous millipede. *J. Exp. Biol.* **201**: 1847–1849.

Teriokhin, A.T. 1998. Evolutionarily optimal age schedule of repair: computer modelling of energy partition between current and future survival and reproduction. *Evol. Ecol.* **12**: 291–307.

Van Voorhies, W.A. 1992. Production of sperm reduces nematode life span. *Nature* **360**: 456–458.

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

Wilkinson, L., Hill, M. & Vang, E. 1992. *Systat: Statistics, Version 5.2. Edition*. Systat Inc., Evanston, IL.

Williams, G.C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evolution* **11**: 398–411.

Williams, G.C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.

Zar, J.H. 1996. *Biostatistical Analysis*, 3rd version. Prentice Hall, Inc., Upper Saddle River, NJ.

Zwaan, B.J. 1999. The evolutionary genetics of ageing and longevity. *Heredity* **82**: 589–597.

Zwaan, B., Bijlsma, R. & Hoekstra, R.F. 1995. Direct selection on life-span in *Drosophila melanogaster*. *Evolution* **49**: 649–659.

Received 26 July 1999; revised 16 December 1999; accepted 22 January 2000