
Worldwide Variation in Life-Span Sexual Dimorphism and Sex-Specific Environmental Mortality Rates

ANATOLY T. TERIOKHIN,^{1,2} ELENA V. BUDILOVA,² FREDERIC THOMAS,¹ AND JEAN-FRANCOIS GUEGAN¹

Abstract In all human populations mean life span of women generally exceeds that of men, but the extent of this sexual dimorphism varies across different regions of the world. Our purpose here is to study, using global demographic and environmental data, the general tendency of this variation and local deviations from it. We used data on male and female life history traits and environmental conditions for 227 countries and autonomous territories; for each country or territory the life-span dimorphism was defined as the difference between mean life spans of women and men. The general tendency is an increase of life-span dimorphism with increasing average male–female life span; this tendency can be explained using a demographic model based on the Makeham–Gompertz equation. Roughly, the life-span dimorphism increases with the average life span because of an increase in the duration of expressing sex- and age-dependent mortality described by the second (exponential) term of the Makeham–Gompertz equation. Thus we investigated the differences in male and female environmental mortality described by the first term of the Makeham–Gompertz equation fitted to the data. The general pattern that resulted was an increase in male mortality at the highest and lowest latitudes. One plausible explanation is that specific factors tied to extreme latitudes influence males more strongly than females. In particular, alcohol consumption increases with increasing latitude and, on the contrary, infection pressures increase with decreasing latitude. This finding agrees with other observations, such as an increase in male mortality excess in Europe and Christian countries and an increase in female mortality excess in Asia and Muslim countries. An increase in the excess of female mortality may be also due to increased maternal mortality caused by an increase in fertility. However, this relation is not linear: In regions with the highest fertility (e.g., in Africa) the excess of female mortality is smaller than in regions with relatively lower fertility (e.g., in Asia). A possible explanation of this phenomenon is an evolutionary adaptation of women to the pressures of extremely high fertility by means of some reduction of their maternal mortality.

¹Centre d'Etudes sur le Polymorphisme des Micro-Organismes, CEPM/UMR CNRS-IRD 9926, Institut de Recherches pour le Développement, 911 Avenue Agropolis, B.P. 64501, 34394 Montpellier Cédex 5, France.

²Chair of General Ecology, Faculty of Biology, Moscow State University, Moscow 119899, Russia.

Human Biology, August 2004, v. 76, no. 4, pp. 000–000

Copyright © 2004 Wayne State University Press, Detroit, Michigan 48201-1309

KEY WORDS: SEXUAL DIMORPHISM, LIFE SPAN, MORTALITY RATE.

The existence of life-span sexual dimorphism in humans, characterized by a longer female life expectancy, is commonly recognized and empirically confirmed (e.g., Lopez and Ruzicka 1983; Gavrilov and Gavrilova 1991; Trovato and Lalu 1998; Mathers et al. 2001; Kraemer 2000; Lobmayer and Wilkinson 2000; Kirkwood 2001; Luy 2002). However, there is no established consensus concerning the general worldwide pattern and regional deviations in differences between female and male life spans. Here, we address this question by analyzing global demographic and environmental data.

Evolutionary hypotheses explaining the emergence of female life-span predominance are mainly based on the differences in ecological roles between males and females. Males are expected to maximize their fitness by increasing their mating success, whereas females need to increase their longevity for obtaining maximal reproductive output (Bateman 1948; Williams and Williams 1957; Rolff 2002). An evolutionary optimization model, based on the similar assumption that males should preferentially spend large amounts of energy in short times (mating, hunting) and females should accumulate energy over long periods (gestation and rearing children), results in the emergence of greater female life spans (Teriokhin and Budilova 2000). This “maternal” hypothesis can be completed by the “grandmaternal” hypothesis, which explains both extended female longevity and limited reproductive period (menopause) by advantages of grandmaternal care over maternal care for older females (Hamilton 1964; Trivers 1972; Alvarez 2000; Peccei 2001), and is partly confirmed by the analysis of observed data (Jamison et al. 2002; Sear et al. 2002; Volland and Beise 2002). Although children can inherit up to twice as many of the female’s genes as grandchildren, the risks for an old female not to have enough vital resources and time to gestate and bring up her own child would overcome the advantages of giving a new birth (Teriokhin and Budilova 2000).

A quasi-universal predominance of female life expectancy and especially its persistence in highly developed countries, where differences in ecological roles of males and females are attenuated and environmental mortality risks are reduced, suggest that a substantial component of the sex difference in life expectancy is under genetic control (Wells 2000). We refer to this as life-span sexual dimorphism. However, nongenetic external causes of mortality that affect males and females differently, which we call sex-specific environmental mortality, undoubtedly exist. For example, the consumption of alcohol, usually higher in males, is known to reduce the life span of males (Lunetta et al. 1998; Nolte et al. 2003). Some studies argue that males are more vulnerable to infections (Franceschi et al. 2000; Wells 2000). In contrast, environmental conditions, primarily social ones, might reduce the longevity of females (Klasen 1998; Lavoyin 2001).

We used the Gompertz–Makeham model (Gompertz 1825; Makeham 1860) to divide total mortality into two components: one that reflects the general tendency of age- and sex-dependent mortality and one that takes into account regional deviations (which, in addition, might be sex-specific) from this general tendency.

Materials and Methods

The global demographic and environmental data used in the analyses were collected for 227 countries and autonomous territories (see Appendix) using mainly international electronic databases accessible on the Internet, such as those provided by the World Health Organization (<http://www.who.int>), the Centers for Disease Control and Prevention in the United States (<http://www.cdc.gov>), the United Nations Statistical Division (<http://un.stats.un.org>), the World Bank Group (<http://www.worldbank.org>), and the World Sites Atlas (<http://www.sites-atlas.com>). These data were partly completed by information from other sources (e.g., scientific journals and reports from ministries of health).

Disease occurrences in the different countries were compiled for a set of 324 categories of human parasitic and infectious diseases affecting human survival (see more information at <http://www.cyinfo.com>), and the disease load was calculated as the total number of diseases for each country. The consumption of alcohol per individual was measured in liters per capita per year. Life expectancy at birth and infant mortality were considered separately for each sex. The maternal mortality ratio was defined as the number of maternal deaths caused by deliveries and complications of pregnancy and childbirth divided by the number of live births for a given year; it is expressed per 100,000 live births. The fertility indicates the number of offspring born to a woman per lifetime passing through the child-bearing age. The nutritional conditions were evaluated by the calorie consumption per average inhabitant per day. Mean latitude and mean longitude refer to the value measured at the geographic center of each country.

Instead of life span at birth L_0 , which is presented in our source data and which includes infant mortality of the first year of life, we use the life-span estimate L_1 , which is calculated under the assumption of having survived the first year. L_1 can be obtained from the equation representing L_0 as a weighted sum of $L_{<1}$ (the life span of those who have not survived the first year) and L_1 (the life span of those who did survive the first year):

$$L_0 = p_1 L_{<1} + (1 - p_1) L_1, \quad (1)$$

where p_1 is the probability of dying during the first year, which is also present in our data. Taking into account that $L_{<1}$ is equal to $1 - p_1$ (the probability of surviving the first year), we obtain the following formula for L_1 :

$$L_1 = \frac{L_0}{(1 - p_1)} - P_1. \quad (2)$$

The values of L_1 were calculated separately for women and men using the values of L_0 and p_1 (known for each sex). Only values of L_1 will be used further and will be referred to as female and male life spans.

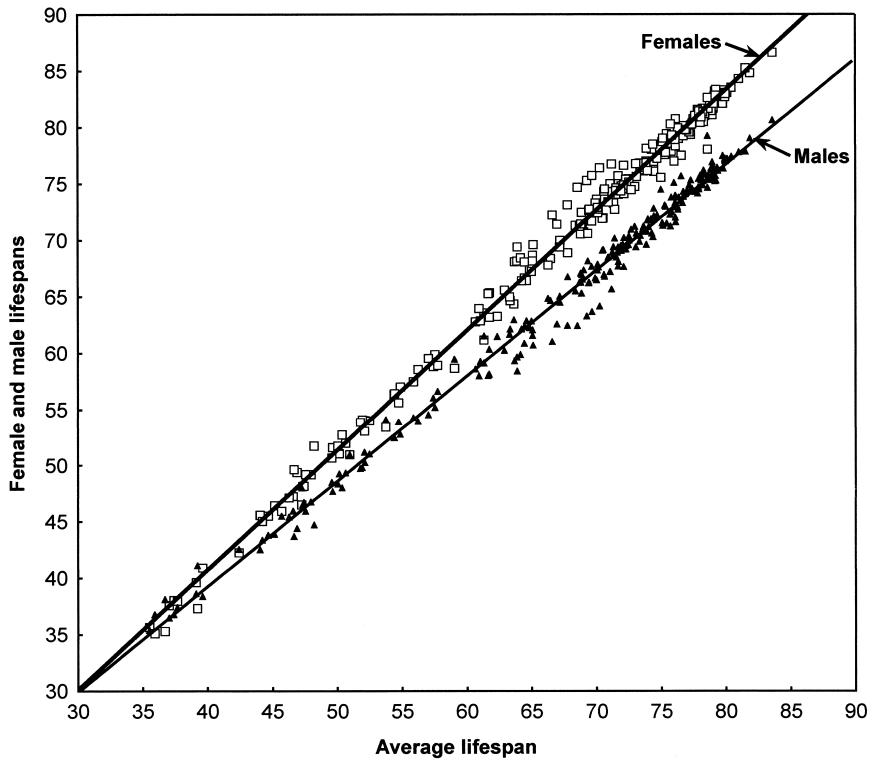


Figure 1. Scatterplots and regression lines of female (upper) and male (lower) life spans on average life span (female–male mean life-span half-sum).

Regression and variance analyses were performed using the S-Plus statistical package (Venables and Ripley 1994).

General Tendency of Life-Span Dimorphism. The general tendency of the global pattern of life-span dimorphism is that dimorphism increases with the average life span (half-sum of female and male mean life spans). This appears clearly in Figure 1, where the dependencies of female and male life spans, L_f and L_m , on their half-sum L are approximated by the linear regressions

$$L_f = -1.822 + 1.0641L, \quad R = 0.996, p < 0.0000001, \quad (3)$$

and

$$L_m = 1.822 + 0.9349L, \quad R = 0.996, p < 0.0000001. \quad (4)$$

In more detail, this tendency is shown in Figure 2, where the dependence of life-span dimorphism, defined as female minus male life span, $d = L_f - L_m$, on L is approximated by a statistically significant linear regression:

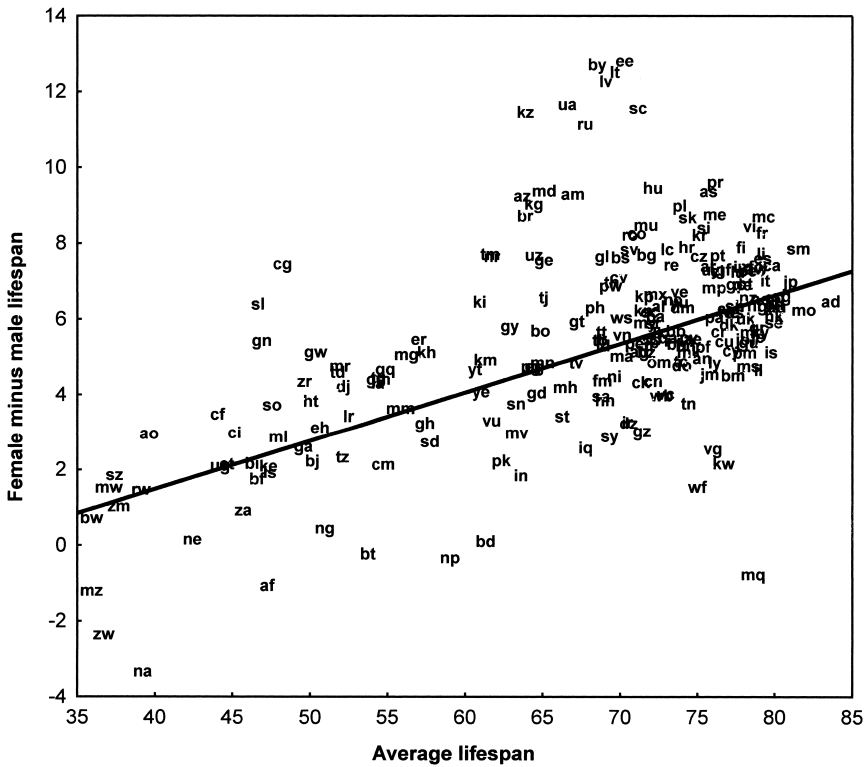


Figure 2. Scatterplots and regression line of female minus male life span on average life span (female–male mean life-span half-sum).

$$d = -3.644 + 0.128L, \quad R = 0.564, p < 0.0000001 \quad (5)$$

(country names are designated by their two-letters codes, given in the Appendix).

Alternatively, the significance of increasing life-span dimorphism with increasing life span can be detected using an approach proposed by Mosimann (Mosimann 1970; Mosimann and Darroch 1985). According to this approach, we should regress the logarithms of L_f on the averages of the logarithms of L_f and L_m and compare the slope of this regression with 1.0. In our case we obtained a value of slope equal to 1.039, which is significantly greater than 1.0 ($p < 0.0000001$), thus indicating that life-span dimorphism does increase with increasing life span.

This tendency can be explained by using the Gompertz–Makeham law (Gompertz 1825; Makeham 1860), which presents the age dynamics of the individual rate of mortality $m(t)$ as the sum of two terms, according to the following equation:

$$m_{(t)} = A + Be^{Ct}. \quad (6)$$

The first term, A , is independent of age and reflects the action of environmental causes of death, whereas the second term increases exponentially with age t . The accelerated increase of mortality with age can be explained by a progressive reduction of an organism's resources allocated to its repair, as is predicted by evolutionary optimization models (Abrams and Ludwig 1995; Cichon 1997; Teriokhin 1998).

The estimations of the parameters A , B , and C from demographic data for different human populations (e.g., Gavrilov and Gavrilova 1991) show that parameters B and C are relatively stable in geographic space and historical time compared to parameter A and that parameter C is more stable with respect to sex. We therefore assume the following model to describe the age dynamics of the mortality rate $m(r, s, t)$ for an individual of sex s (f , female; m , male) living in a region r :

$$m(r, s, t) = A_r + B_s e^{Ct}. \quad (7)$$

When the age dynamics of mortality are known, the individual's expected mean life span can be computed using the equation

$$L_s = 1 + \sum_{t=1}^T \exp \left[-A_r t - \frac{B_s}{C} (e^{Ct} - 1) \right], \quad (8)$$

which approximates the exact integral equation

$$L_s = 1 + \int_{t=0}^{\infty} \exp \left[-A_r t - \frac{B_s}{C} (e^{Ct} - 1) \right] dx. \quad (9)$$

The maximum life span T in the approximated equation must be a sufficiently large age for which the probability to survive up to it is small. We used the value $T = 120$, for which this probability is less than 0.0000001, even in the absence of environmental mortality.

To find the best estimates for the parameters B_f , B_m , and C (i.e., minimizing the sum of squares of differences between observed and estimated life spans through all the countries and both sexes), we assumed that on the global scale the regional sex differences in the parameter A_r are mutually balanced (i.e., that the values of the parameter A_r for each region r were equal for both sexes). Thus we had to estimate $N + 3$ parameters on the basis of $2N$ observations (life spans for males and females for N countries).

The estimates obtained for the parameters were $B_f = 0.0000078$, $B_m = 0.000017$, and $C = 0.101$. In turn, the estimates of life spans computed using the Gompertz–Makeham equation with these parameter estimates (plus corresponding estimates of A_r) do not differ practically (not greater than one-tenth of a year) from the estimates obtained using the linear regressions. Hence

the observed linear trend of life-span dimorphism associated with increasing average life span can be explained by sex differences in the parameter B_s in the Gompertz–Makeham equation.

Regional Deviations from the General Tendency. We then tried to explain the deviations from the general linear trend by using the regional differences in the first term of this equation:

$$m(r,s,t) = A_{r,s} + B_s e^{Ct}. \tag{10}$$

In this second stage of the analysis, values of parameters B_j , B_m , and C were fixed at their estimated values and parameter A was allowed to depend both on region and sex. Fitting this model to the data allowed us to estimate values of environmental mortality rate for each country and for each sex (see Appendix). We then tried to relate mortality sex-specific differences, expressed by $A_{r,s}$, to the environmental conditions in different countries. To attenuate the role of outlying differences between male and female environmental mortality rates, we did not analyze row differences but their logarithmically transformed values d_A , obtained using the equation

$$d_A = \pm(A_{r,m} - A_{r,f})\log[1 + 10,000|(A_{r,m} - A_{r,f})|], \tag{11}$$

which we call male environmental mortality rate excess, or simply male mortality excess.

To evaluate the environmental influence on sexual differences in environmental mortality, we estimated the dependencies of d_A on different environmental factors using regression and dispersion analyses.

These analyses identified several environmental factors significantly related to d_A , some of which were nonlinear. In particular, the excess of male environmental mortality is observed at lower and higher latitudes (lesser than 10° and greater than 45°; see Figure 3). The dependence of d_A on latitude x is described by a second-order polynomial function with a statistically significant quadratic term:

$$d_A = 0.4574 - 0.07736x + 0.001499x^2, \\ R = 0.225, p_x = 0.0037, p_{x^2} = 0.00048. \tag{12}$$

We suggest that such a nonlinear dependence can be explained by opposite linear dependences of d_r with different environmental factors. Factors significantly (at the 5% level) related to the male mortality excess are shown in Tables 1 and 2.

From Table 1 we see that the factor that is the most incontestably correlated with d_A ($R = 0.27$, $p = 0.00024$) is the annual per capita consumption of alcohol. This factor is also positively correlated with latitude ($R = 0.50$, $p < 0.0000001$), so that the excess of male environmental mortality at higher latitudes can, at least

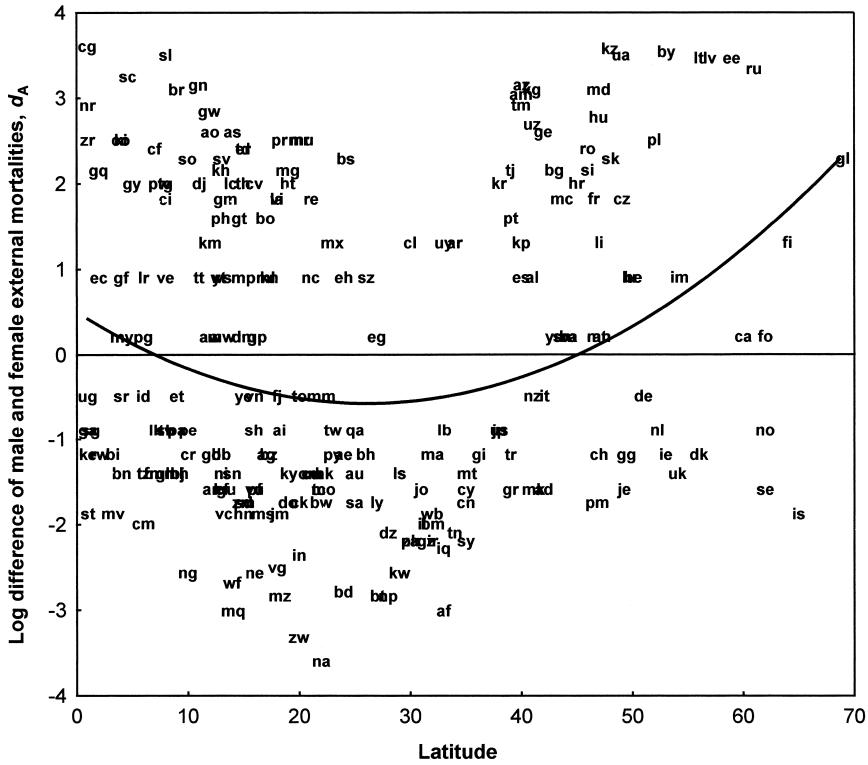


Figure 3. Scatterplots and quadratic regression line of excess of male environmental mortality d_A (see text) on latitude. Names of regions (countries and autonomous territories) are indicated by their two-letter codes (see Appendix).

Table 1. Quantitative Environmental Factors Significantly Correlated to the Excess of Male Environmental Mortality, d_A

<i>Environmental Factor</i>	<i>Correlation with d_A</i>	<i>p Level for Testing $H_0: R = 0$</i>
Alcohol	0.27	0.00024
Infections	0.19	0.013
Physicians	0.22	0.0034

in part, be explained by a negative influence of excessive consumption of alcohol, which affects primarily men (Lunetta et al. 1998; Nolte et al. 2003). On the contrary, another environmental factor, the number of infections (corrected for the logarithm of population number), which also correlated positively with d_A ($R = 0.19$, $p = 0.013$) (see Table 1), increases with decreasing latitude ($R = -0.53$, $p < 0.0000001$). This may explain, at least in part, the increase in male mortality excess at lower latitudes, because, in general, infections affect men more strongly than women (Franceschi et al. 2000; Wells 2000). We might

Table 2. Qualitative Environmental Factors Significantly Related to the Excess of Male Environmental Mortality, d_A

<i>Environmental Factor</i>	<i>Mean Values of d_A in Presence and Absence of Factor</i>	<i>p Level for Testing the Absence of Difference</i>
Europe	0.50 vs. -0.28	0.011
Asia	-0.49 vs. 0.05	0.044
Muslims	-1.07 vs. -0.19	0.0088
Christians	-0.16 vs. -0.74	0.048
Island	-0.48 vs. 0.05	0.044

generalize these two observations by proposing that stressful factors, in particular, those manifested at extreme higher and lower latitudes, influence primarily men negatively, thus increasing the excess of male environmental mortality (Wells 2000).

The same line of thinking can be applied to the negative correlation of insular situation of region with d_A (mean value of d_A is -0.48 on islands versus 0.05 on continents, $p = 0.044$) (see Table 2). We suggest that stressful factors on islands are less expressed than on continental territories. The correlation of d_A with the number of physicians may simply be due to its correlation with other environmental factors, in particular, with alcohol ($R = 0.57$, $p < 0.0000001$). Direct interpretation of this correlation (i.e., that women are more sensitive to an increase or decrease in the number of physicians) is nevertheless also possible.

The significant effect of continent and religion (d_A is higher in European and Christian countries and lower in Asian and Muslim countries; see Table 2) can also be explained by the influence of some environmental factors. Indeed, the consumption of alcohol is significantly greater in Europe than in Asia (11.1 versus 2.8 l, $p < 0.0000001$) and in Christian countries than in Muslim countries (7.3 versus 0.9 l, $p < 0.0000001$).

An additional factor that lowers the excess of male environmental mortality (or rather, increases the excess of female environmental mortality) in Muslim countries compared with Christian countries is higher fertility (4.4 versus 2.8 children, $p = 0.000014$). Higher fertility may decrease d_A because of increasing maternal mortality, which is strongly correlated with fertility ($R = 0.80$, $p < 0.0000001$).

However, the relation of excess male environmental mortality with fertility is not linear. We see in Figure 4 that, although male mortality excess decreases with increasing fertility from lowest to middle values (from 1 to 4.5 children), d_A increases with increasing fertility from middle to highest values (from 4.5 to 8 children). The dependence of d_A on fertility f is well described by a second-order polynomial function with a statistically significant quadratic term:

$$d_A = 2.139 - 1.278f + 0.1467f^2, \quad R = 0.258, p_f = 0.00049, p_{f^2} = 0.0014. \quad (13)$$

of genetic selection or cultural adaptation) may indeed be vitally important for population survival.

Conclusion

The two goals of this study were (1) to identify and explain the general tendency of human life-span sexual dimorphism and (2) to identify and relate the deviations from the general tendency to environmental conditions.

The general tendency consists in an increase of life-span dimorphism with improved environmental conditions and an increase in mean life span. This tendency is observed empirically and can be obtained theoretically if we assume that the age-dependent exponential component of human mortality in the Gompertz–Makeham equation is more conservative than the age-independent (but environment-dependent) component. On the intuitive level this increase in life-span dimorphism with increasing average male–female life span is due to the fact that the longer the life span of men and women, the longer the period for expressing the difference in their age-dependent mortalities.

With regard to deviations from the general trend, the general pattern indicates an excess of male mortality at the highest and lowest latitudes. One explanation is that the stressful factors linked to extreme latitudes affect males more strongly than females. In particular, alcohol consumption increases with increasing latitude and infection pressures increase with decreasing latitude. This pattern agrees with observations that male environmental mortality increases in European and Christian countries and that female mortality increases in Asian and Muslim countries. An increase in the excess of female mortality might also be caused by increased maternal mortality associated with increasing fertility, although this relation is not linear. However, in the regions with highest fertility, notably in Africa, the excess of female mortality is lower than in Asia. A possible explanation may be that African populations have adapted to their highly stressful environment by means of female mortality reduction.

Acknowledgments We thank B. Lafay for helpful comments and an anonymous referee for numerous valuable suggestions. The research was supported by the Centre National de la Recherche Scientifique (CNRS) through a Senior Research Fellowship awarded to A. Teriokhin and by funds from the Russian Foundation for Basic Research (RFBR) (grant 01-04-48384) awarded to E. Budilova and A. Teriokhin.

Received 23 March 2003; revision received 29 October 2003.

Literature Cited

Abrams, P.A., and D. Ludwig. 1995. Optimality theory, Gompertz' law, and disposable soma theory of senescence. *Evolution* 49:1,055–1,056.

- Alvarez, H.P. 2000. Grandmother hypothesis and primate life histories. *Am. J. Phys. Anthropol.* 113:435–450.
- Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Cichon, M. 1997. Evolution of longevity through optimal resource allocation. *Proc. R. Soc. Lond. B* 264:1,383–1,388.
- Franceschi, C., L. Motta, S. Valensin et al. 2000. Do men and women follow different trajectories to reach extreme longevity? *Aging Clin. Exp. Res.* 12:77–84.
- Gavrilov, L.A., and N.S. Gavrilova. 1991. *The Biology of Life Span: A Quantitative Approach*. New York: Harwood Academic.
- 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. R. Soc. Lond. A* 115:513–585.
- Guégan, J.F., and A.T. Teriokhin. 2000. Human life-history traits on a parasitic landscape. In *Evolutionary Biology of Host–Parasite Relationships: Theory Meets Reality*, R. Poulin, S. Morand, and A. Skorping, eds. Amsterdam: Elsevier, 143–161.
- Guégan, J.F., A.T. Teriokhin, and F. Thomas. 2000. Human fecundity variation, size-related obstetrical performance, and the evolution of sexual stature dimorphism. *Proc. R. Soc. Lond. B* 267:2,529–2,536.
- Hamilton, W.D. 1964. The genetical evolution of social behavior. *J. Theor. Biol.* 7:1–16.
- Jamison, C.S., L.L. Cornell, P.L. Jamison et al. 2002. Are all grandmothers equal? A review and a preliminary test of the grandmother hypothesis in Tokugawa, Japan. *Am. J. Phys. Anthropol.* 119:67–76.
- Kirkwood, T.B.L. 2001. Sex and aging. *Exp. Gerontol.* 36:413–418.
- Klasen, S. 1998. Marriage, bargaining, and intrahousehold resource allocation: Excess female mortality among adults during early German development, 1740–1860. *J. Econ. Hist.* 58:432–467.
- Kraemer, S. 2000. The fragile male. *Br. Med. J.* 321:1,609–1,612.
- Lavoyin, T.O. 2001. Risk factors for infant mortality in a rural community in Nigeria. *J. R. Soc. Prom. Health.* 121:114–118.
- Lobmayer, P., and R. Wilkinson. 2000. Income, inequality, and mortality in 14 developed countries. *Sociol. Health Illness* 22:401–414.
- Lopez, A.D., and L.T. Ruzicka, eds. 1983. *Sex Differentials in Mortality: Trends, Determinants, and Consequences*. Canberra: Australian National University.
- Lunetta, P., A. Penttila, and S. Sarna. 1998. Water traffic accidents, drowning, and alcohol in Finland, 1969–1995. *Int. J. Epidemiol.* 27:1,038–1,043.
- Luy, M. 2002. Sex differences in mortality: Time to take a second look. *Z. Gerontol. Geriatr.* 35:412–429.
- Makeham, W.M. 1860. On the law of mortality and the construction of annuity tables. *J. Inst. Actuaries* 8:301–310.
- Mathers, C.D., R. Sadana, J.A. Salomon et al. 2001. Healthy life expectancy in 191 countries. *Lancet* 357:1,685–1,691.
- Mosimann, J.E. 1970. Size allometry: Size and shape variables with characterization of the log normal and generalized gamma distributions. *J. Am. Stat. Assoc.* 65:930–945.
- Mosimann, J.E., and J.N. Darroch. 1985. Canonical and principal components of shape. *Biometrika* 72:241–252.
- Nolte, E., A. Britton, and M. McKee. 2003. Trends in mortality attributable to current alcohol consumption in East and West Germany. *Soc. Sci. Med.* 56:1,385–1,395.
- Peccei, J.S. 2001. A critique of the grandmother hypothesis: Old and new. *Am. J. Hum. Biol.* 13:434–452.
- Rolf, J. 2002. Bateman's principle and immunity. *Proc. R. Soc. Lond. B* 269:867–872.
- Sear, R., F. Steele, I.A. McGregor et al. 2002. The effect of kin on child mortality in rural Gambia. *Demography* 39:43–63.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- Teriokhin, A.T. 1998. Evolutionarily optimal age schedule of repair: Computer modeling of energy allocation between current and future survival and reproduction. *Evol. Ecol.* 12:291–307.

- Teriokhin, A.T., and E.V. Budilova. 2000. Evolutionarily optimal networks for controlling energy allocation to growth, reproduction, and repair in men and women. In *Artificial Neural Networks: Application to Ecology and Evolution*, S. Lek and J.F. Guégan, eds. Berlin: Springer Verlag, 225–237.
- Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871–1971*, B. Campbell, ed. Chicago: Aldine, 136–179.
- Trovato, F., and N.M. Lahu. 1998. Contribution of cause-specific mortality to changing sex differences in life expectancy: Seven nations case study. *Soc. Biol.* 45:1–20.
- Venables, W.N., and B.D. Ripley. 1994. *Modern Applied Statistics with S-Plus*. Berlin: Springer-Verlag.
- Voland, E., and J. Beise. 2002. Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhorn. *Behav. Ecol. Sociobiol.* 52:435–443.
- Wells, J.C.K. 2000. Natural selection and sex differences in morbidity and mortality in early life. *J. Theor. Biol.* 202:65–76.
- Williams, G.C., and D.C. Williams. 1957. Natural selection of individually harmful social adaptation among sibs with special references to social insects. *Evolution* 11:32–39.

Appendix. Regions (Countries and Autonomous Territories)

<i>Region (Country, Territory), r</i>	<i>Code</i>	<i>Life</i>		<i>Female</i>	<i>Male</i>	<i>Difference of Male and Female Mortalities</i>
		<i>Span, L_f</i>	<i>Span, L_m</i>	<i>Mortality, A_{r,f}</i>	<i>Mortality, A_{r,m}</i>	
Afghanistan	af	46.49	48.02	0.0166	0.0142	-0.0024
Albania	al	75.41	69.55	0.0037	0.0038	0.0001
Algeria	dz	71.93	69.15	0.0048	0.0039	-0.0009
Andorra	ad	86.61	80.62	0.0005	0.0001	-0.0004
Angola	ao	40.89	38.38	0.0205	0.0215	0.0010
Anguilla (United Kingdom)	ai	79.63	73.83	0.0024	0.0023	-0.0001
Antigua and Barbuda	ag	73.57	68.90	0.0043	0.004	-0.0003
Antilles (Netherlands)	an	77.54	73.05	0.003	0.0025	-0.0005
Argentina	ar	79.15	72.23	0.0026	0.0028	0.0002
Armenia	am	71.38	62.55	0.005	0.0066	0.0016
Aruba (Netherlands)	aw	82.23	75.37	0.0017	0.0017	0.0000
Australia	au	83.04	77.19	0.0015	0.0011	-0.0004
Austria	at	81.34	74.88	0.0019	0.0019	0.0000
Azerbaijan	az	68.07	59.29	0.0062	0.0081	0.0019
Bahamas	bs	73.60	66.45	0.0043	0.00	50.0007
Bahrain	bh	76.08	71.21	0.0035	0.0032	-0.0003
Bangladesh	bd	61.14	61.50	0.0089	0.0071	-0.0018
Barbados	bb	76.20	70.99	0.0035	0.0033	-0.0002
Belarus	by	74.65	62.40	0.0039	0.0067	0.0028
Belgium	be	81.65	74.84	0.0018	0.0019	0.0001
Belize	bz	74.02	69.36	0.0041	0.0039	-0.0002
Benin	bj	51.03	49.26	0.0138	0.0134	-0.0004
Bermuda (United Kingdom)	bm	79.33	75.29	0.0025	0.0018	-0.0007
Bhutan	bt	53.40	54.09	0.0126	0.0107	-0.0019
Bolivia	bo	67.46	62.24	0.0064	0.0067	0.0003
Bosnia and Herzegovina	ba	75.08	69.48	0.0038	0.0038	0.0000
Botswana	bw	35.64	35.38	0.025	0.0244	-0.0006
Brazil	br	68.13	59.63	0.0062	0.0079	0.0017
Brunei	bn	76.64	71.81	0.0033	0.003	-0.0003
Bulgaria	bg	75.31	68.09	0.0037	0.0043	0.0006
Burkina Faso	bf	47.24	45.95	0.0161	0.0156	-0.0005
Burundi	bi	47.12	45.42	0.0162	0.0159	-0.0003
Cambodia	kh	59.84	55.19	0.0095	0.0101	0.0006
Cameroon	cm	55.58	53.90	0.0115	0.0108	-0.0007
Canada	ca	83.29	76.34	0.0014	0.0014	0.0000
Cape Verde	cv	73.24	66.61	0.0044	0.0049	0.0005
Cayman Islands (United Kingdom)	ky	81.66	76.47	0.0018	0.0014	-0.0004
Central African Republic	cf	45.56	42.54	0.0172	0.018	0.0008
Chile	cl	79.69	72.90	0.0024	0.0026	0.0002
China	cn	74.08	70.19	0.0041	0.0035	-0.0006
Colombia	co	74.97	67.18	0.0038	0.0047	0.0009
Comoros	km	63.54	59.09	0.0079	0.0082	0.0003
Congo, Brazzaville	cg	51.71	44.72	0.0135	0.0164	0.0029
Congo Democratic Republic	zr	51.58	47.69	0.0135	0.0144	0.0009

Life-Span Sexual Dimorphism / 637

<i>Region (Country, Territory), r</i>	<i>Code</i>	<i>Female Life Span, L_f</i>	<i>Male Life Span, L_m</i>	<i>Female Environmental Mortality, A_{r,f}</i>	<i>Male Environmental Mortality, A_{r,m}</i>	<i>Difference of Male and Female Mortalities</i>
Cook Islands (New Zealand)	ck	73.25	69.39	0.0044	0.0038	-0.0006
Costa Rica	cr	78.97	73.77	0.0026	0.0023	-0.0003
Cote d'Ivoire	ci	46.41	43.88	0.0166	0.017	0.0004
Croatia	hr	78.01	70.58	0.0029	0.0034	0.0005
Cuba	cu	79.20	74.26	0.0025	0.0021	-0.0004
Cyprus	cy	79.54	74.84	0.0024	0.0019	-0.0005
Czech Republic	cz	78.69	71.50	0.0027	0.0031	0.0004
Denmark	dk	79.71	74.34	0.0024	0.0021	-0.0003
Djibouti	dj	54.01	50.26	0.0123	0.0128	0.0005
Dominica	dm	76.96	71.13	0.0032	0.0032	0.0000
Dominican Republic	do	76.14	71.83	0.0035	0.003	-0.0005
Ecuador	ec	74.77	69.05	0.0039	0.004	0.0001
Egypt	eg	66.61	62.33	0.0067	0.0067	0.0000
El Salvador	sv	74.29	66.92	0.0041	0.0048	0.0007
Equatorial Guinea	gq	56.97	52.76	0.0108	0.0114	0.0006
Eritrea	er	59.52	54.52	0.0096	0.0104	0.0008
Estonia	ee	76.39	64.12	0.0034	0.0059	0.0025
Ethiopia	et	45.50	43.81	0.0172	0.0171	-0.0001
Faeroe Islands (Denmark)	fo	82.25	75.34	0.0017	0.0017	0.0000
Fiji Islands	fj	71.20	66.23	0.0051	0.0051	0.0000
Finland	fi	81.55	74.13	0.0019	0.0022	0.0003
France	fr	83.17	75.21	0.0014	0.0018	0.0004
Gabon	ga	50.66	48.50	0.0141	0.0139	-0.0002
Gambia	gm	56.39	52.45	0.0111	0.0116	0.0005
Gaza Strip	gz	72.69	70.13	0.0046	0.0036	-0.0010
Georgia	ge	68.63	61.54	0.006	0.007	0.0010
Germany	de	81.12	74.68	0.002	0.002	0.0000
Ghana	gh	58.79	56.01	0.01	0.0097	-0.0003
Gibraltar (United Kingdom)	gi	82.29	76.42	0.0017	0.0014	-0.0003
Greece	gr	81.53	76.22	0.0019	0.0015	-0.0004
Greenland (Denmark)	gl	72.43	65.25	0.0047	0.0055	0.0008
Grenada	gd	66.41	62.83	0.0068	0.0065	-0.0003
Guadeloupe (France)	gp	80.72	74.27	0.0021	0.0021	0.0000
Guam (United States)	gu	80.77	75.86	0.0021	0.0016	-0.0005
Guatemala	gt	69.94	64.47	0.0055	0.0058	0.0003
Guernsey (United Kingdom)	gg	83.05	76.95	0.0015	0.0012	-0.0003
Guinea	gn	49.38	44.41	0.0148	0.0167	0.0019
Guinea-Bissau	gw	52.70	48.03	0.0129	0.0142	0.0013
Guyana	gy	65.56	60.21	0.0071	0.0076	0.0005
Guyana (France)	gf	80.09	73.26	0.0023	0.0025	0.0002
Haiti	ht	51.72	48.36	0.0135	0.014	0.0005
Honduras	hn	70.71	67.33	0.0053	0.0046	-0.0007
Hong Kong (China)	hk	82.74	77.14	0.0015	0.0012	-0.0003
Hungary	hu	76.61	67.62	0.0033	0.0045	0.0012
Iceland	is	82.10	77.45	0.0017	0.0011	-0.0006

Appendix. (Continued)

Region (Country, Territory), <i>r</i>	Code	Life		Female	Male	Difference
		Span, <i>L_f</i>	Span, <i>L_m</i>	Mortality, <i>A_{r,f}</i>	Mortality, <i>A_{r,m}</i>	of Male and Female Mortalities
India	in	64.31	62.93	0.0076	0.0064	-0.0012
Indonesia	id	71.33	66.50	0.005	0.005	0.0000
Iran	ir	71.88	69.07	0.0049	0.004	-0.0009
Iraq	iq	68.85	66.73	0.0059	0.0049	-0.0010
Ireland	ie	80.16	74.45	0.0023	0.002	-0.0003
Israel	il	81.06	76.88	0.002	0.0012	-0.0008
Italy	it	82.67	76.13	0.0016	0.0015	-0.0001
Jamaica	jm	77.83	73.76	0.003	0.0023	-0.0007
Japan	jp	84.28	77.76	0.0011	0.001	-0.0001
Jersey (United Kingdom)	je	81.44	76.38	0.0019	0.0014	-0.0005
Jordan	jo	80.42	75.43	0.0022	0.0017	-0.0005
Kazakhstan	kz	69.38	58.39	0.0057	0.0085	0.0028
Kenya	ke	48.15	46.52	0.0155	0.0152	-0.0003
Kiribati	ki	63.92	57.94	0.0078	0.0087	0.0009
Kuwait	kw	77.46	75.65	0.0031	0.0016	-0.0015
Kyrgyzstan	kg	68.42	59.85	0.0061	0.0078	0.0017
Laos	la	56.31	52.47	0.0111	0.0115	0.0004
Latvia	lv	75.26	63.24	0.0038	0.0063	0.0025
Lebanon	lb	74.50	69.59	0.004	0.0038	-0.0002
Lesotho	ls	48.16	46.70	0.0155	0.0151	-0.0004
Liberia	lr	53.98	51.02	0.0123	0.0124	0.0001
Libya	ly	78.31	73.93	0.0028	0.0022	-0.0006
Liechtenstein	li	82.77	75.52	0.0015	0.0017	0.0002
Lithuania	lt	75.69	63.64	0.0036	0.0061	0.0025
Luxembourg	lu	81.01	74.24	0.002	0.0021	0.0001
Macao (China)	mo	84.77	79.00	0.001	0.0006	-0.0004
Macedonia	mk	76.77	72.11	0.0033	0.0029	-0.0004
Madagascar	mg	58.53	53.93	0.0101	0.0107	0.0006
Malawi	mw	37.57	36.50	0.0233	0.0233	0.0000
Malaysia	my	74.33	68.90	0.004	0.004	0.0000
Maldives	mv	64.60	62.09	0.0075	0.0068	-0.0007
Mali	ml	49.18	46.76	0.0149	0.015	0.0001
Malta	mt	81.00	75.82	0.002	0.0016	-0.0004
Man, Isle of (United Kingdom)	im	81.40	74.49	0.0019	0.002	0.0001
Marshall Islands	mh	68.34	64.61	0.0061	0.0057	-0.0004
Martinique (France)	mq	78.00	79.23	0.0029	0.0005	-0.0024
Mauritania	mr	54.09	49.80	0.0122	0.0131	0.0009
Mauritius	mu	75.68	67.67	0.0036	0.0045	0.0009
Mayotte (France)	yt	62.75	58.55	0.0083	0.0084	0.0001
Mexico	mx	75.37	69.18	0.0037	0.0039	0.0002
Micronesia	fm	70.82	66.92	0.0052	0.0048	-0.0004
Moldova	md	69.57	60.66	0.0057	0.0074	0.0017
Monaco	mc	83.29	75.26	0.0014	0.0018	0.0004
Mongolia	mn	67.19	62.81	0.0065	0.0065	0.0000
Montenegro (Yugoslavia)	me	80.27	71.98	0.0022	0.0029	0.0007

Life-Span Sexual Dimorphism / 639

<i>Region (Country, Territory), r</i>	<i>Code</i>	<i>Female Life Span, L_f</i>	<i>Male Life Span, L_m</i>	<i>Female Environmental Mortality, A_{r,f}</i>	<i>Male Environmental Mortality, A_{r,m}</i>	<i>Difference of Male and Female Mortalities</i>
Montserrat Island (United Kingdom)	ms	80.45	76.17	0.0022	0.0015	-0.0007
Morocco	ma	72.38	67.83	0.0047	0.0044	-0.0003
Mozambique	mz	35.10	36.76	0.025	0.023	-0.0020
Myanmar	mm	57.44	54.27	0.0106	0.0106	0.0000
Namibia	na	37.32	41.11	0.0236	0.0192	-0.0044
Nauru	nr	65.31	58.13	0.0072	0.0086	0.0014
Nepal	np	58.63	59.42	0.01	0.008	-0.0020
Netherlands	nl	81.62	75.74	0.0018	0.0016	-0.0002
New Caledonia (France)	nc	76.42	70.38	0.0034	0.0035	0.0001
New Zealand	nz	81.31	75.22	0.0019	0.0018	-0.0001
Nicaragua	ni	71.64	67.63	0.0049	0.0045	-0.0004
Niger	ne	42.26	42.57	0.0195	0.018	-0.0015
Nigeria	ng	50.95	50.96	0.0139	0.0124	-0.0015
North Korea	kp	74.60	68.47	0.004	0.0042	0.0002
Northern Mariana Islands (United States)	mp	79.26	72.90	0.0025	0.0026	0.0001
Norway	no	82.10	76.04	0.0017	0.0015	-0.0002
Oman	om	74.71	70.32	0.0039	0.0035	-0.0004
Pakistan	pk	63.22	61.44	0.0081	0.0071	-0.0010
Palau	pw	72.60	66.19	0.0046	0.0051	0.0005
Panama	pa	78.88	73.30	0.0026	0.0024	-0.0002
Papua New Guinea	pg	66.37	62.10	0.0068	0.0068	0.0000
Paraguay	py	76.95	71.91	0.0032	0.0029	-0.0003
Peru	pe	73.36	68.47	0.0044	0.0042	-0.0002
Philippines	ph	71.29	65.46	0.0051	0.0054	0.0003
Poland	pl	78.11	69.59	0.0029	0.0038	0.0009
Polynesia (France)	pf	77.75	72.95	0.003	0.0026	-0.0004
Portugal	pt	79.91	72.70	0.0023	0.0026	0.0003
Puerto Rico (United States)	pr	80.72	71.57	0.0021	0.003	0.0009
Qatar	qa	75.61	70.57	0.0036	0.0034	-0.0002
Reunion Island (France)	re	76.80	69.84	0.0033	0.0037	0.0004
Romania	ro	74.51	66.76	0.004	0.0049	0.0009
Russia	ru	73.10	62.42	0.0044	0.0066	0.0022
Rwanda	rw	39.62	38.61	0.0216	0.0213	-0.0003
Samoa (United States)	as	80.27	71.20	0.0022	0.0032	0.0010
San Marino	sm	85.23	77.84	0.0009	0.0009	0.0000
Sao Tome and Principe	st	67.75	64.79	0.0063	0.0056	-0.0007
Saudi Arabia	sa	70.53	67.04	0.0053	0.0047	-0.0006
Senegal	sn	64.94	61.65	0.0074	0.007	-0.0004
Seychelles	sc	76.72	65.62	0.0033	0.0053	0.0020
Sierra Leone	sl	49.63	43.70	0.0146	0.0172	0.0026
Singapore	sg	83.50	77.37	0.0013	0.0011	-0.0002
Slovakia	sk	78.47	70.26	0.0028	0.0035	0.0007
Slovenia	si	79.40	71.46	0.0025	0.0031	0.0006

Appendix. (Continued)

<i>Region (Country, Territory), r</i>	<i>Code</i>	<i>Female Life Span, L_f</i>	<i>Male Life Span, L_m</i>	<i>Female Environ- mental Mortality, A_{r,f}</i>	<i>Male Environ- mental Mortality, A_{r,m}</i>	<i>Difference of Male and Female Mortalities</i>
Solomon Islands	sb	74.54	69.56	0.004	0.0038	-0.0002
Somalia	so	49.19	45.92	0.0149	0.0156	0.0007
South Africa	za	45.94	45.48	0.0169	0.0159	-0.0010
South Korea	kr	79.00	71.26	0.0026	0.0032	0.0006
Spain	es	82.80	75.67	0.0015	0.0016	0.0001
Sri Lanka	lk	75.11	69.95	0.0038	0.0036	-0.0002
St. Helena Island (United Kingdom)	sh	80.37	74.50	0.0022	0.002	-0.0002
St. Kitts and Nevis	kn	74.36	68.61	0.004	0.0041	0.0001
St. Lucia	lc	76.74	69.37	0.0033	0.0039	0.0006
St. Pierre and Miquelon (France)	pm	80.37	75.73	0.0022	0.0016	-0.0006
St. Vincent and Grenadines	vc	74.74	71.19	0.0039	0.0032	-0.0007
Sudan	sd	58.88	56.60	0.0099	0.0094	-0.0005
Suriname	sr	74.84	69.42	0.0039	0.0038	-0.0001
Swaziland	sz	38.02	36.78	0.0229	0.023	0.0001
Sweden	se	82.66	77.22	0.0016	0.0011	-0.0005
Switzerland	ch	82.93	77.01	0.0015	0.0012	-0.0003
Syria	sy	70.55	68.12	0.0053	0.0043	-0.0010
Taiwan	tw	79.76	74.04	0.0024	0.0022	-0.0002
Tajikistan	tj	68.13	62.03	0.0062	0.0068	0.0006
Tanzania	tz	53.05	51.18	0.0127	0.0123	-0.0004
Tchad	td	53.85	49.72	0.0123	0.0131	0.0008
Thailand	th	72.71	66.21	0.0046	0.0051	0.0005
Togo	tg	56.41	52.43	0.0111	0.0116	0.0005
Tonga	to	71.20	66.23	0.0051	0.0051	0.0000
Trinidad and Tobago	tt	71.40	66.21	0.005	0.0051	0.0001
Tunisia	tn	76.08	72.78	0.0035	0.0026	-0.0009
Turkey	tr	74.32	69.49	0.0041	0.0038	-0.0003
Turkmenistan	tm	65.25	58.01	0.0073	0.0087	0.0014
Turks and Caicos Island (United Kingdom)	tc	76.14	71.73	0.0035	0.003	-0.0005
Tuvalu	tv	69.36	64.99	0.0057	0.0056	-0.0001
Uganda	ug	45.03	43.38	0.0175	0.0174	-0.0001
Ukraine	ua	72.20	61.00	0.0047	0.0073	0.0026
United Arab Emirates	ae	77.20	72.19	0.0031	0.0028	-0.0003
United Kingdom	uk	80.88	75.34	0.0021	0.0017	-0.0004
United States	us	80.25	74.55	0.0022	0.002	-0.0002
Uruguay	uy	79.27	72.44	0.0025	0.0027	0.0002
Uzbekistan	uz	68.05	60.83	0.0062	0.0074	0.0012
Vanuatu	vu	63.15	60.30	0.0081	0.0076	-0.0005
Venezuela	ve	76.97	70.72	0.0032	0.0034	0.0002
Vietnam	vn	72.71	67.60	0.0046	0.0045	-0.0001
Virgin Islands (United Kingdom)	vg	76.96	75.07	0.0032	0.0018	-0.0014

Life-Span Sexual Dimorphism / 641

<i>Region (Country, Territory), r</i>	<i>Code</i>	<i>Female Life Span, L_f</i>	<i>Male Life Span, L_m</i>	<i>Female Environ- mental Mortality, A_{r,f}</i>	<i>Male Environ- mental Mortality, A_{r,m}</i>	<i>Difference of Male and Female Mortalities</i>
Virgin Islands (United States)	vi	82.60	74.63	0.0016	0.002	0.0004
Wallis and Futuna Islands (France)	wf	75.54	74.46	0.0037	0.002	-0.0017
West Bank	wb	74.43	70.92	0.004	0.0033	-0.0007
Western Sahara	eh	51.98	49.32	0.0133	0.0134	0.0001
Western Samoa	ws	72.87	67.30	0.0045	0.0046	0.0001
Yemen	ye	62.84	59.23	0.0082	0.0081	-0.0001
Yugoslavia	yu	76.83	70.86	0.0033	0.0033	0.0000
Zambia	zm	37.97	37.40	0.023	0.0224	-0.0006
Zimbabwe	zw	35.31	38.12	0.025	0.0218	-0.0032

