Evolutionary Ecology Research, 2003, **5**: 1199–1221

The impact of environmental factors on human life-history evolution: an optimization modelling and data analysis study

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ABSTRACT

A model of human life-history evolution based on the optimization of resource partition by an individual between its growth, reproduction and survival is used for searching evolutionarily optimal state-dependent strategies of energy allocation under different combinations of the model parameters representing food availability and environmental stresses. Using these strategies, we compute the corresponding optimal life histories and determine the dependency of their characteristics on both environmental parameters. Then, using a statistical analysis of global social and demographic data for 131 countries, we examine relationships between human life-history traits and environmental characteristics. Finally, we compare the dependencies obtained by modelling with those derived from data analysis. We show that such observed phenomena as a decrease in fertility with an increase of wealth (known as demographic transition), an increase in birth weight, age at maturity, size at maturity and life expectancy with a decrease of infection and an increase in food availability can be viewed as consequences of evolutionary optimization of the human life-history strategy of resource allocation.

Keywords: age at marriage, age at maturity, availability of food, birth weight, demographic transition, dynamic programming, fertility, human life-history evolution, infection stresses, life expectancy, optimal energy allocation, size at maturity

INTRODUCTION

Evolutionary optimization models of life histories (e.g. Hamilton, 1966; Perrin and Sibly, 1993; McNamara and Houston, 1996; Guégan *et al.*, 2000; Teriokhin and Budilova, 2001) have been used successfully to explain and predict many general relationships between environmental conditions and life-history traits in populations evolving in such given conditions. In many studies, it has been demonstrated that some life-history traits (e.g. age at

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maturity, body size at maturity, life expectancy) depend on different environmental factors, in particular food availability and environmental mortality (e.g. Stearns, 1992; Teriokhin, 1998; Kozlowski and Teriokhin, 1999). The present study uses a similar approach based on the optimization of state-dependent partitioning of the individual's resources between its basic needs, such as growth, reproduction and survival, by applying a standard technique of stochastic dynamic programming (e.g. Mangel and Clark, 1988). The study consists of three stages. First, using evolutionary modelling, we evaluate the joint effects caused by changing two model parameters representing resource availability and environmental mortality stress on six human life-history characteristics (age at maturity, age at release from parental care, body size at maturity, body size at release, number of children, life expectancy). Second, using global social and demographic data, we evaluate by multiple regression analysis the joint effects of two environmental factors (food availability and infection stress) on several real human life-history characteristics (age at menarche, age at marriage, adult female body size, weight at birth, fertility, female life expectancy). Third, we compare the results obtained by optimization modelling with the results obtained by statistical analysis in order to understand to what extent the empirical dependencies of human life-history traits on environmental conditions may be explained by the process of evolutionary adaptation of human populations to their environments and whether this adaptation is ensured by biological or cultural means.

EVOLUTIONARY MODEL

We use a discrete time dynamic model to describe the life history of an individual (e.g. Mangel and Clark, 1988). We assume that at time 0 (the moment of birth), the individual's body size (mass) is X_0 and at each time step t from 1 to $T_{\max}$ it increases by the value $w_t E_t$. That is,

$$X_t = X_{t-1} + w_t E_t \tag{1}$$

where X_t and X_{t-1} are the individual's body sizes at the beginning and the end of step t, E_t is the amount of energy (measured in units of mass) produced by the individual during this step, and w_t is the fraction of this energy allocated to growth. In our computations, we use the values $X_0 = 3$, which is close to the typical human weight at birth (kg), and $T_{\max} = 100$, the age (years) that represents the limit not attained by most people.

If at some step t no energy is invested in body growth (i.e. $w_t = 0$) and hence body size remains equal to its value X_{t-1} at the beginning of the step, we use the commonly accepted allometric equation (e.g. West *et al.*, 1999) to compute the amount of energy produced during this step:

$$E_t = aX_{t-1}^{b} \tag{2}$$

The multiplier a is varied from 1.6 to 2.1 to roughly mimic the variability of food availability and the exponent b is set equal to 0.25. The range of variation of a and the value of b were so chosen to ensure that adult body weight would lie approximately within its typical limits of 40–80 kg (e.g. Eveleth and Tanner, 1976).

If $w_t > 0$ (i.e. individual body size increases in the time interval from $t - 1$ to t), then we used the following more precise equation:

$$E_t = \{[X_{t-1}^{1-b} + a(1-b)w_t]^{1/(1-b)} - X_{t-1}\}/w_t \tag{3}$$

This equation takes into account the increase in body size in the time interval from $t - 1$ to t. To obtain this equation, we note that from (1) it follows that

$$E_t = (X_t - X_{t-1})/w_t \tag{3'}$$

and from (1) and (2) it follows that

$$\mathrm{d}X_t = w_t a X_t^b \mathrm{d}t \tag{3''}$$

Integrating (3″) through the interval $(t - 1, t)$ (with w_t assumed constant) and substituting the found expression for X_t into (3′), we obtain (3).

Still one other fraction of energy u_t is allocated to reproduction. We assume that an individual can accumulate the energy allocated to reproduction during several time-steps (maybe only one) to release it in bigger portions (the moment of release can be interpreted as the cessation of parental care for a child). The reproductive energy Y_t accumulated by the end of step t is obtained by adding the value u_tE_t to the energy Y_{t-1} accumulated by the beginning of this step:

$$Y_t = Y_{t-1} + u_tE_t \tag{4}$$

If the accumulated reproductive energy is released at the end of some step t, then it is set equal to 0 at the beginning of the next step $t + 1$ (we set $Y_0 = 0$).

We assume, in addition, that the effective reproductive output F_t is not equal to the amount of released reproductive energy Y_t, but that it depends sigmoidally on it (see also Teriokhin and Budilova, 2001):

$$F_t = F_t(Y_t) \tag{5}$$

This was done because only under such an assumption may it be advantageous to accumulate energy instead of releasing it at each time-step. Here we used a sigmoid function of the following form:

$$F_t = \begin{cases} 0 & \text{if } Y_t < Y_{\min} \\ \dfrac{Y_{\max}}{Y_{\max} - Y_{\min}}(Y_t - Y_{\min}) & \text{if } Y_{\min} < Y_t < Y_{\max} \\ Y_{\max} & \text{if } Y_t > Y_{\max} \end{cases} \tag{6}$$

The parameters $Y_{\min}$ and $Y_{\max}$ are set equal to 0.45 and 90, respectively, because these values ensure that the number of children is not significantly greater than 8, the maximum average fertility observed in our data.

The remaining fraction of energy $v_t = 1 - w_t - u_t$ is assumed to be allocated to survival. We take into account two sources of mortality for an individual. The first, ‘environmental mortality’, cannot be reduced by the individual, whereas the second, ‘individual mortality’, can be reduced by allocating some energy to survival. More exactly, we assumed that the probability P_t for an individual to survive at step t is given by the equation

$$P_t = \exp(-m)\frac{(v_tE_t)^d}{c + (v_tE_t)^d} \tag{7}$$

The first multiplier, $\exp(-m)$, gives the probability to survive irremovable environmental stresses. The second multiplier gives the probability to survive the reducible causes of mortality. The closer to 1 is v_t, the greater is v_tE_t, the amount of energy allocated to individual survival. We varied m from 0.001 to 0.011 to roughly mimic the variability of real environmental mortality (e.g. Thomas *et al.*, 2000) and we use the values 0.0025 and 2 for parameters c and d to obtain a realistic mean life span range from 40 to 85 years observed across countries.

So, the values and ranges of the model parameters a, b, c, d, m, X_0, $Y_{\min}$, $Y_{\max}$ and $T_{\max}$ were chosen to make the resulting ranges of life-history traits obtained in optimization modelling as close to those observed in the data as possible.

But when the values of these parameters are fixed, we can compute the dynamics of the state variables of the model, X_t and Y_t, if there is a rule to determine at each time step t and for each combination of values of X_t and Y_t the values of the control variables u_t, v_t and w_t, mentioned above, and of one additional control variable z_t necessary to identify the moments of releasing the accumulated reproductive energy (it can take only two values, 'yes' or 'no'). We searched for the rule which maximizes the expected lifetime reproductive output using stochastic dynamic programming (e.g. Mangel and Clark, 1988). It can be shown (Mylius and Diekmann, 1995; Teriokhin, 2002) that the strategy maximizing the reproductive output is evolutionarily optimal when the population is stable and this stability is attained by exercising density pressure only on offspring or only on adults.

The dynamic programming searches for an optimal strategy in the form of a rule matching a set of values of control variables to each admissible set of values of state variables. It operates by iterating backwards from $T_{\max} - 1$ to 0 and at each age step and for each set of values of state variables X_t and Y_t it searches for a set of values of u_t, v_t, w_t and z_t which maximizes the following gain function:

$$G_t(X_t, Y_t) = [G_{t+1}(X_{t+1}(u_t,v_t,w_t,z_t),\ Y_{t+1}(u_t,v_t,w_t,z_t)) + F(Y_t(u_t,v_t,w_t,z_t))]P_t(u_t,v_t,w_t,z_t) \qquad (8)$$

(To find the optimum numerically, we discretize both the state and control variables.) It is natural to assume that $G_{T\max}(X_{T\max}, Y_{T\max}) = 0$ for all pairs of values of $X_{T\max}$ and $Y_{T\max}$; that is, to assume that there is no reproductive output at the maximum age $T_{\max}$. Knowing $G_{T\max}(X_{T\max}, Y_{T\max})$ and using (8), we can calculate $G_{T\max-1}(X_{T\max-1}, Y_{T\max-1})$ for all pairs of values of $X_{T\max-1}$ and $Y_{T\max-1}$, searching for each pair the optimal combination of control values of u_t, v_t, w_t and z_t (i.e. those which maximize the right-hand side of (8)). Then, knowing $G_{T\max-1}(X_{T\max-1}, Y_{T\max-1})$, we can calculate $G_{T\max-2}(X_{T\max-2}, Y_{T\max-2})$, and so on to $G_0(X_0, Y_0)$. What is remarkable is that during these calculations we find for each t not only $G_t(X_t, Y_t)$, the expected future fitness of an individual in state X_t, Y_t at time t, but also the optimal values of control variables u_t, v_t, w_t and z_t.

DATA

The data for the analysis were compiled for 131 different countries using mainly Internet global databases (WHO, UNICEF, World Bank, GIS). Variables representing the environmental conditions were 'food' and 'infection'. For each country, the first variable was based on the average number of calories for a person per day and the second was approximated by the parasite species richness per country for the 16 most dangerous infectious diseases (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) (Guégan *et al.*, 2001). Work in progress indicates that this environmental parasitic pressure index for the 16 most potent killers correlates strongly with a new index based on the 350 parasitic and infectious diseases infecting human populations in the world, thus indicating that the 16 pathogens estimate is a good indicator of overall parasitic stress. Other variables were used to describe the average human life-history traits of females in the population for each country. Only female characteristics were used to simplify the analysis of data and modelling. Questions pertaining to human sexual life-history dimorphism are treated elsewhere (Guégan *et al.*, 2000; Teriokhin *et al.*, 2000). Six life-history characteristics were analysed: average age at menarche, average female age at marriage, average adult female stature, weight at birth, average lifetime number of children per female, and female life expectancy at 1 year old.

The dependency of each of these life-history characteristics on the two environmental characteristics (i.e. food and infection) were analysed using a two-factor linear regression (e.g. Sokal and Rohlf, 1994). The regression equations obtained were illustrated by two-dimensional contour graphs with contour lines corresponding approximately to the mean value of the analysed life-history trait and to the values distant by a half and by a full standard deviation from the mean.

RESULTS OF EVOLUTIONARY MODELLING

The evolutionary modelling results present the dynamics of the state and control variables and of survival in the course of an individual life history. We computed such life histories for 36 combinations of values of environmental parameters obtained by setting $a = 1.6, 1.7, 1.8, 1.9, 2.0, 2.1$ and $m = 0.001, 0.003, 0.005, 0.007, 0.009, 0.011$. An example of evolutionarily optimal life-history results (for $a = 1.7$ and $m = 0.9$) is presented in Appendix 1.

Based on Appendix 1, it is possible to compute several derivative characteristics of life history. Age at maturity, T_{mat}, can be viewed as the age reached by the beginning of investment of energy in reproduction (i.e. before the first value of t when $u_t > 0$). Using Appendix 1, we obtain $T_{\text{mat}} = 20$. Body size at maturity, X_{mat}, is the body size attained at the age at maturity. Using Appendix 1, we obtain $X_{\text{mat}} = 53.6$. Life expectancy, T_{exp}, is calculated as the sum of probabilities, S_t, to survive from 0 to 1, 2, . . . , 100 years:

$$T_{\text{exp}} = \sum_{t=1}^{T_{\max}} S_t \tag{9}$$

where S_t is computed as the product of probabilities to survive the periods from 0 to 1, from 1 to 2, . . . , and from 99 to 100:

$$S_t = \prod_{i=1}^{t} P_i \tag{10}$$

Using Appendix 1, we obtain $T_{\text{exp}} = 62$. The number of children, N_{chi}, is calculated as the sum of reproductive releases occurring before the age at menopause, which we set equal to $T_{\text{mnp}} = 50$ (Thomas *et al.*, 2001). Using Appendix 1, we obtain $N_{\text{chi}} = 5$. The body size at release, X_{rel}, is defined as the average amount of energy at reproductive releases before age $t = 50$. Using Appendix 1, we obtain $X_{\text{rel}} = 13.6$. The period of parental care, T_{rel}, is defined as the average period between consecutive releases of reproductive energy. Using Appendix 1, we obtain $T_{\text{rel}} = 4$.

Some irregularities (in particular, the non-monotonicity) in the dependencies of modelled life-history traits on the parameters a and m observed in several tables accompanying the figures are due to the discretizing of time and of the state and control variables.

Age at maturity

We obtained the following values for age at maturity, T_{mat}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	17	18	17	17	17	17
0.009	19	19	18	19	18	18
0.007	19	20	20	20	19	19
0.005	21	22	22	21	21	21
0.003	23	23	23	22	22	22
0.001	23	24	24	24	24	24

The corresponding dependency of T_{mat} on a and m is illustrated in Fig. 1. We see that the age at maturity increases with a decrease in environmental mortality (i.e. the part due to parasitic pressure) and it depends very weakly on resources.

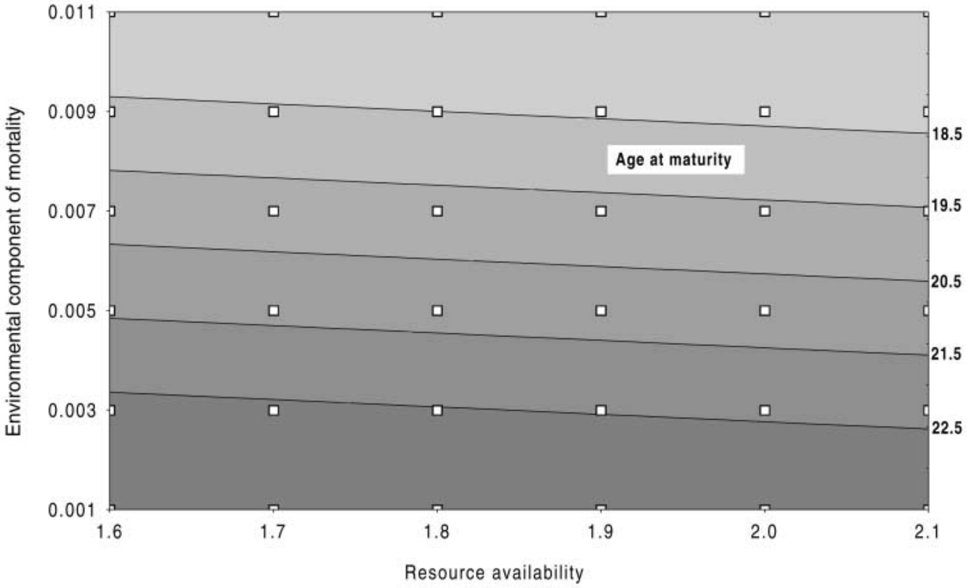

Fig. 1. A linear approximation of modelled dependency of T_{mat}, the age at maturity, on a and m presented as a contour plot of T_{mat} on a and m. The levels of T_{mat} are shown by the different hatching and by the numbers on the right-hand side.

Age at release

We obtained the following values for age at release, T_{rel}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	4.5	4	4	4	4	4
0.009	4.5	4	4	4	4	5
0.007	4.5	4	6	5	5	5
0.005	7	6	5	5	5	5
0.003	6.5	7.5	5	7	6	6
0.001	10	8	9	8	8	8

The corresponding dependency of T_{rel} on a and m is illustrated in Fig. 2. We see that age at release, like age at maturity, increases with a decrease in environmental mortality and it depends again very weakly on resource availability.

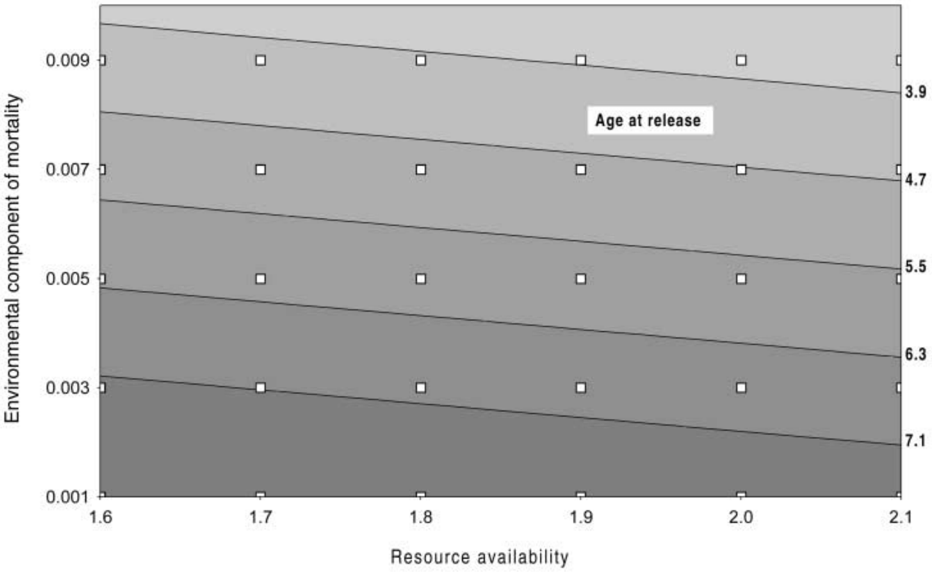

Fig. 2. The linear approximation of modelled dependency of T_{rel}, the age at release, on a and m presented as a contour plot of T_{rel} on a and m. The levels of T_{rel} are shown by the different hatching and by the numbers on the right-hand side.

Body size at maturity

We obtained the following values of body size at maturity, X_{mat}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	41	48	49	53	57	61
0.009	46	51	52	60	61	65
0.007	46	54	59	64	65	70
0.005	52	59	66	68	73	78
0.003	58	62	69	71	76	83
0.001	57	65	71	78	85	90

The corresponding dependency of X_{mat} on a and m is illustrated in Fig. 3. We see that body size at maturity increases as environmental mortality decreases and as resource availability increases.

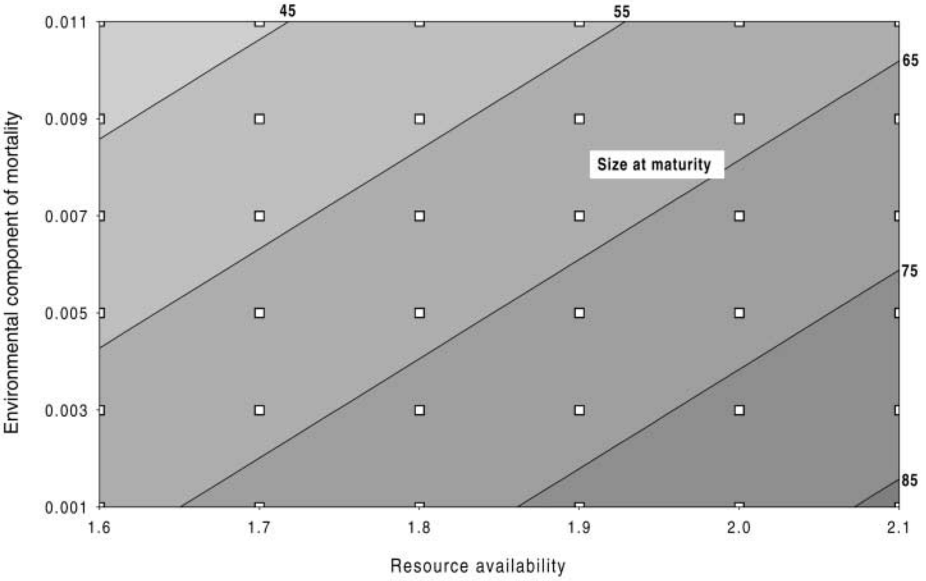

Fig. 3. The linear approximation of modelled dependency of X_{mat}, the body size at maturity, on a and m presented as a contour plot of X_{mat} on a and m. The levels of X_{mat} are shown by the different hatching and by the numbers at the top and on the right-hand side.

Body size at release

We obtained the following values of body size at release, X_{rel}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	13.8	13.3	14.7	15.2	16.2	17.3
0.009	12.4	13.4	14.3	15.6	16.5	22
0.007	13.3	13.6	22.1	19.8	20.9	22.3
0.005	20.4	20.8	18.8	20	21.4	22.9
0.003	19.5	21.1	19.1	28.4	26	27.8
0.001	32.8	32.6	34.6	33.2	35.6	37.8

The corresponding dependency of X_{rel} on a and m is illustrated in Fig. 4. We see that body size at release, like body size at maturity, increases with a decrease in environmental mortality and with an increase in resource availability in the environment.

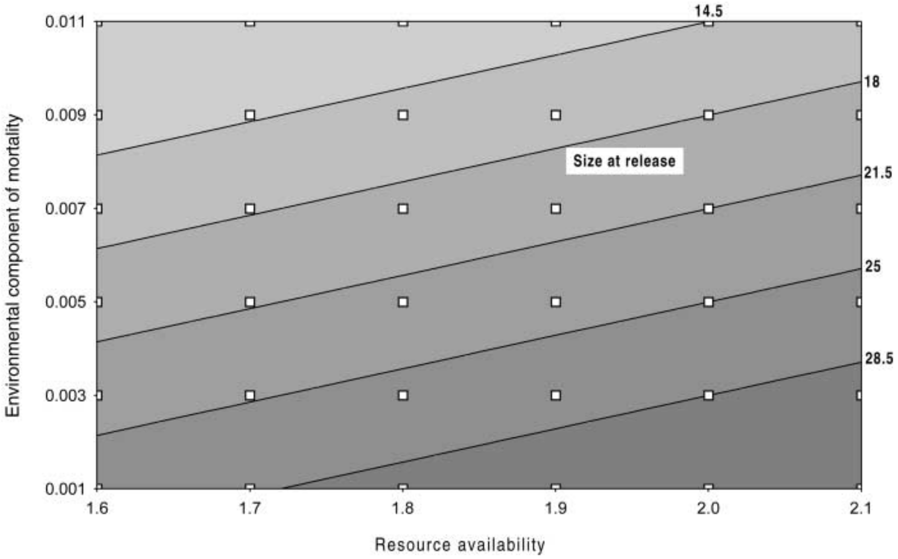

Fig. 4. The linear approximation of modelled dependency of X_{rel}, the body size at release, on a and m presented as a contour plot of X_{rel} on a and m. The levels of X_{rel} are shown by the different hatching and by the numbers at the top and on the right-hand side.

Number of children

We obtained the following values of number of children for a woman, N_{chi}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	6	7	7	8	8	8
0.009	6	7	7	7	7	6
0.007	6	7	4	5	6	6
0.005	4	4	5	5	5	5
0.003	4	4	5	3	4	4
0.001	2	3	2	3	3	3

The dependency of N_{chi} on a and m is illustrated in Fig. 5. We see that the number of children per woman decreases with a decrease in environmental mortality and it depends very weakly on resource availability.

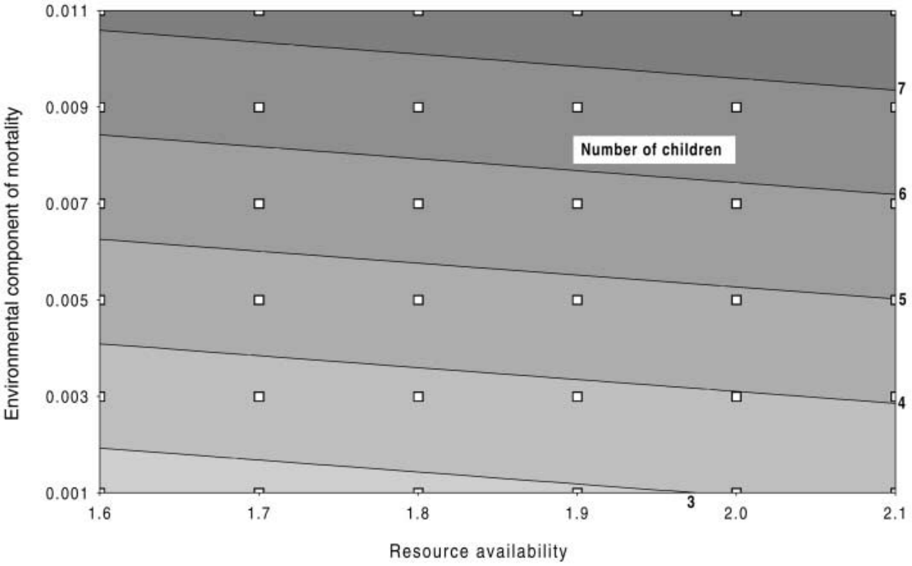

Fig. 5. The linear approximation of modelled dependency of N_{chi}, the number of children, on a and m presented as a contour plot of N_{chi} on a and m. The levels of N_{chi} are shown by the different hatching and by the numbers on the right-hand side.

Life expectancy

We obtained the following values of life expectancy, T_{exp}, for different combinations of values of a and m:

	a					
m	1.6	1.7	1.8	1.9	2.0	2.1
0.011	52	52	53	53	54	54
0.009	56	57	57	58	58	59
0.007	62	62	62	63	64	64
0.005	68	68	68	69	70	70
0.003	74	75	75	76	77	77
0.001	82	83	83	84	85	85

The corresponding dependency of T_{exp} on a and m is illustrated in Fig. 6. We see that life expectancy increases as environmental mortality decreases, while the relationship with resource availability is weak.

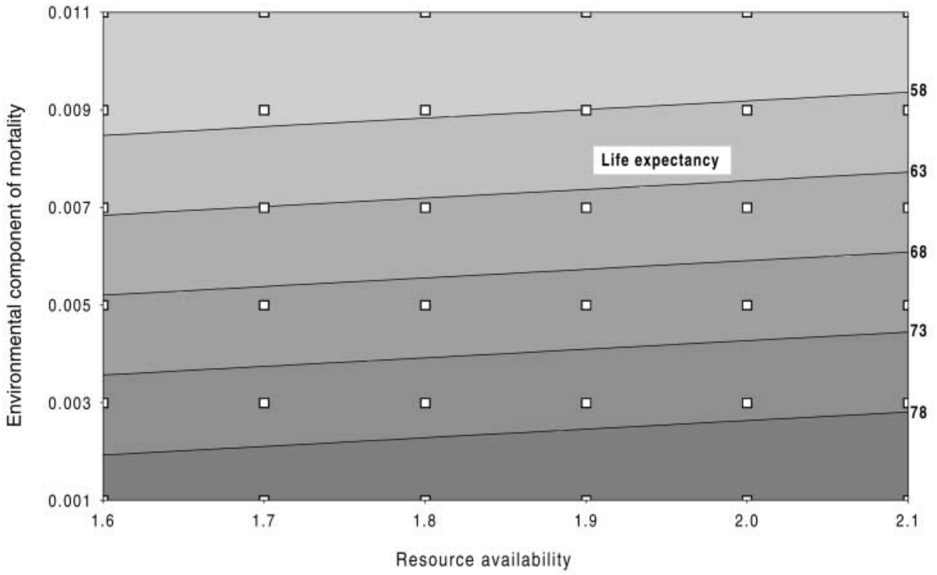

Fig. 6. The linear approximation of modelled dependency of T_{exp}, the life expectancy, on a and m presented as a contour plot of T_{exp} on a and m. The levels of T_{exp} are shown by the different hatching and by the numbers on the right-hand side.

RESULTS OF DATA ANALYSIS

Our results for the relationships between the life-history traits under study and the two environmental factors (i.e. food and infection), which can be considered as good surrogates of resource availability and environmental mortality, are as follows (names of countries and areas are indicated on the figures by their Internet codes as given in Appendix 2).

Female age at menarche

The age at menarche T_{mnr} is one life-history trait that characterizes the age at maturity. The regression of T_{mnr} on 'food' and 'infection' is as follows:

$$T_{\mathrm{mnr}} = 16.304 - 0.981 \times \text{food} - 0.0114 \times \text{infection}$$

$$(n = 65,\ R = 0.26,\ P_{\mathrm{food}} < 0.002,\ P_{\mathrm{infection}} > 0.83)$$

This dependency is illustrated in Fig. 7. We see that female age at menarche is a decreasing function of food supply, but does not depend significantly on infection.

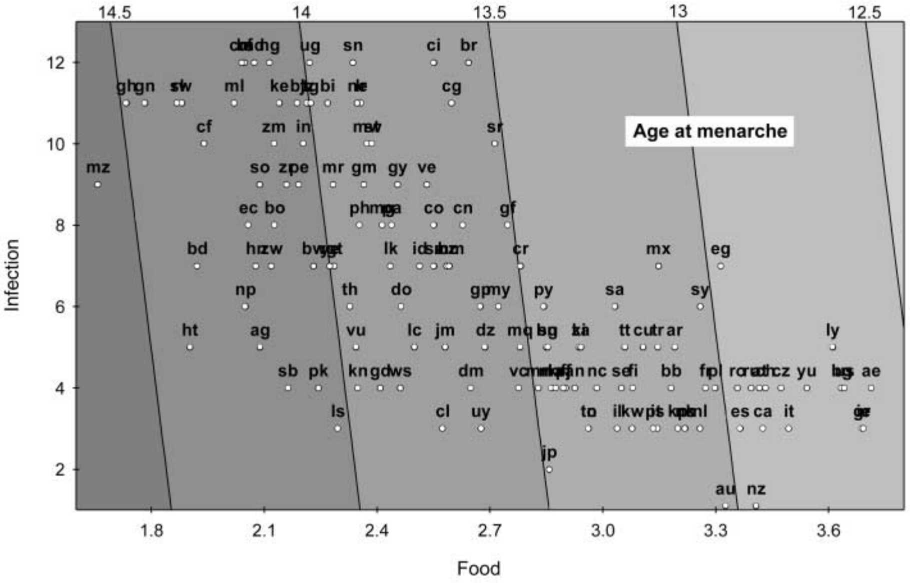

Fig. 7. A linear approximation of observed dependency of age at menarche, T_{mnr}, on food and infection presented as a contour plot of T_{mnr} on food and infection. The levels of T_{mnr} are shown by the different hatching and by the numbers at the top. The country codes are given in Appendix 2.

Female age at marriage

The female age at marriage, T_{mrg}, is another life-history trait that characterizes the female age at maturity because it is closely associated with the beginning of reproduction. The regression of T_{mrg} on 'food' and 'infection' is as follows:

$$T_{\text{mrg}} = 26.598 - 0.162 \times \text{food} - 0.555 \times \text{infection}$$

$$(n = 90,\ R = 0.48,\ P_{\text{food}} > 0.83,\ P_{\text{infection}} < 0.0001)$$

This dependency is illustrated in Fig. 8. We see that female age at marriage across countries increases as infection decreases, but does not depend significantly on food availability.

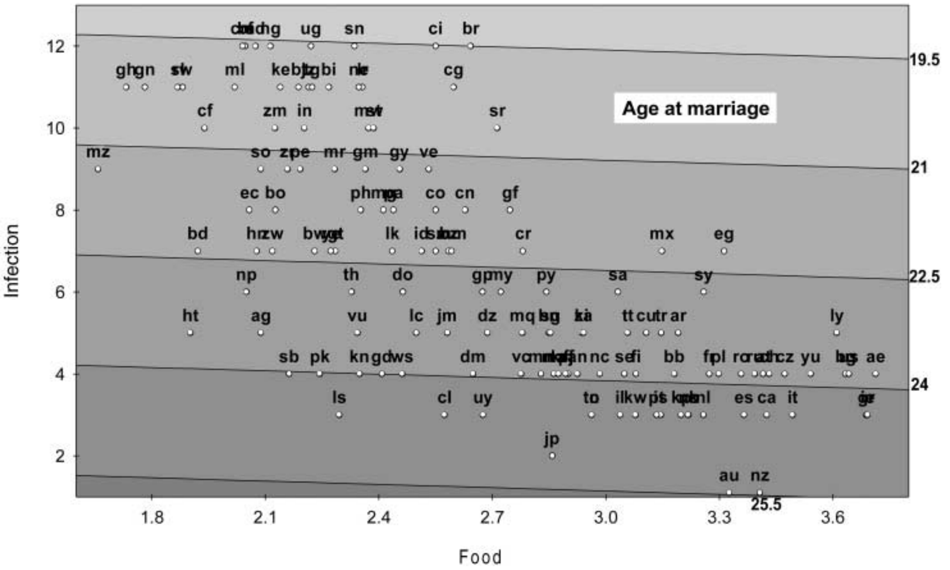

Fig. 8. A linear approximation of observed dependency of age at marriage, T_{mrg}, on food and infection presented as a contour plot of T_{mrg} on food and infection. The levels of T_{mrg} are shown by the different hatching and by the numbers on the right-hand side. The country codes are given in Appendix 2.

Female adult stature

We use female adult stature, X_{fem}, to characterize body size at maturity because stature is highly correlated with body weight. The linear regression of this variable on 'food' and 'infection' is as follows:

$$X_{\text{fem}} = 135.304 + 7.440 \times \text{food} + 0.366 \times \text{infection}$$

$$(n = 44,\ R = 0.64,\ P_{\text{food}} < 0.00005,\ P_{\text{infection}} > 0.18)$$

This dependency is illustrated in Fig. 9. We see that female adult stature increases with an increase in food availability, but does not depend significantly on infection.

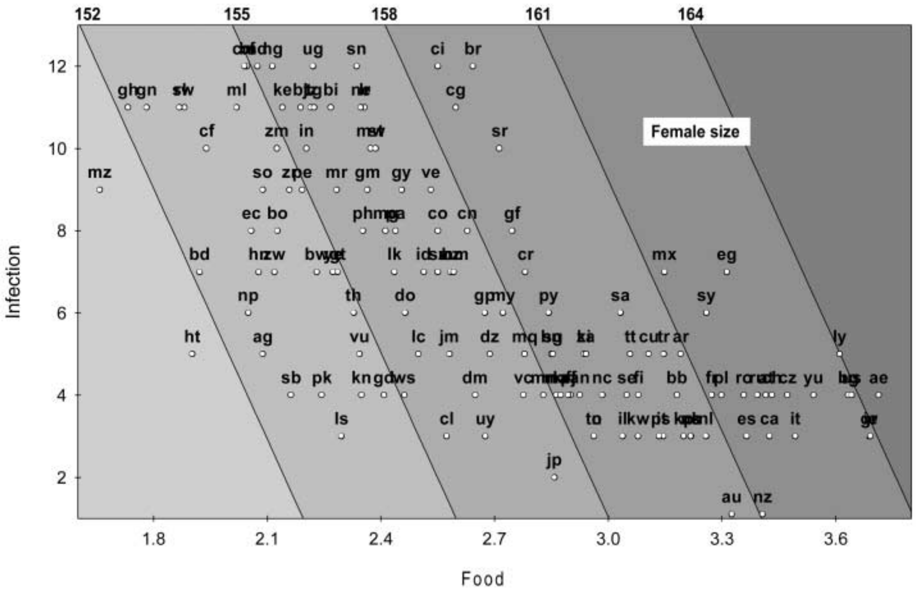

Fig. 9. A linear approximation of observed dependency of adult female stature, X_{fem}, on food and infection presented as a contour plot of X_{fem} on food and infection. The levels of X_{fem} are shown by the different hatching and by the numbers at the top. The country codes are given in Appendix 2.

Weight at birth

The regression of weight at birth, X_{bth}, on food and infection is as follows:

$$X_{\text{bth}} = 2.631 + 0.219 \times \text{food} - 0.0116 \times \text{infection}$$

$$(n = 108,\ R = 0.73,\ P_{\text{food}} < 0.00001,\ P_{\text{infection}} < 0.04)$$

This dependency is illustrated in Fig. 10. We see that weight at birth increases significantly with a decrease in infection and with an increase in food.

Fertility

The regression of female fertility, N_{frt}, measured as the mean lifetime number of children for a woman, on food and infection is as follows:

$$N_{\text{frt}} = 5.982 - 1.378 \times \text{food} + 0.298 \times \text{infection}$$

$$(n = 130,\ R = 0.76,\ P_{\text{food}} < 0.00001,\ P_{\text{infection}} < 0.000001)$$

This dependency is illustrated in Fig. 11. We see that human fertility across countries is a decreasing function of both parasitic pressure and food availability in the environment.

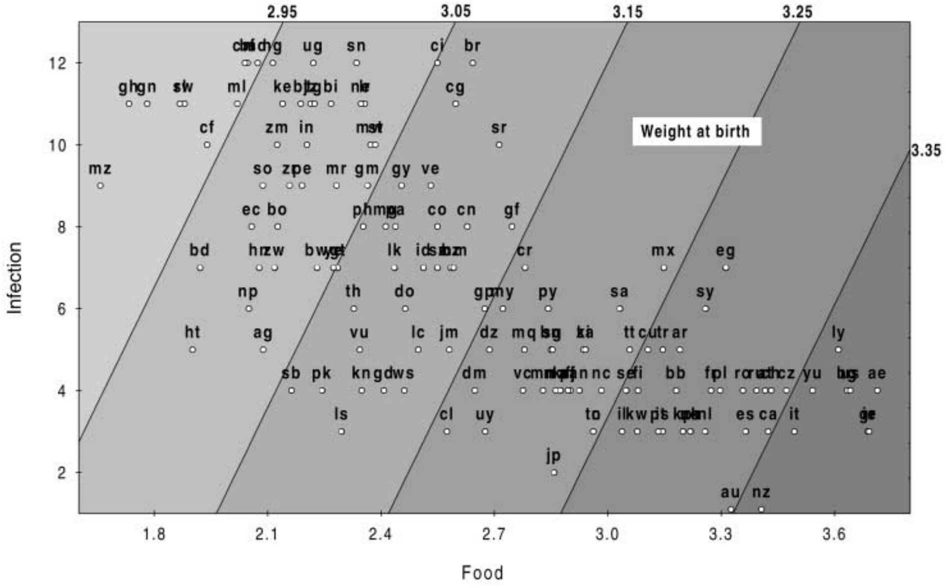

Fig. 10. A linear approximation of observed dependency of weight at birth, X_{bth}, on food and infection presented as a contour plot of X_{bth} on food and infection. The levels of X_{bth} are shown by the different hatching and by the numbers at the top and on the right-hand side. The country codes are given in Appendix 2.

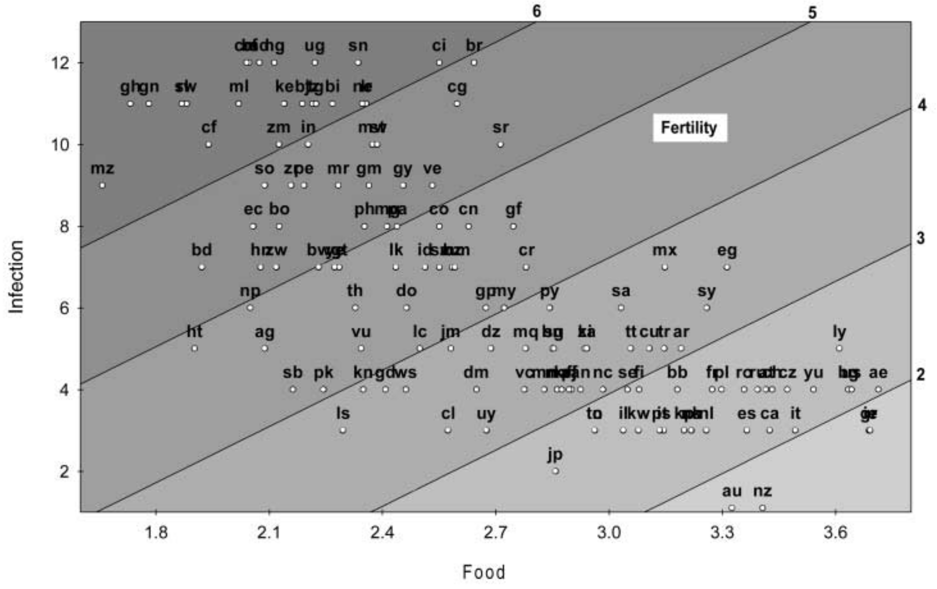

Fig. 11. A linear approximation of observed dependency of female fertility, N_{frt}, on food and infection presented as a contour plot of N_{frt} on food and infection. The levels of N_{frt} are shown by the different hatching and by the numbers at the top and on the right-hand side. The country codes are given in Appendix 2.

Female life expectancy

The regression of female life expectancy at 1 year old, T_{fem}, on food and infection is as follows:

$$T_{\text{fem}} = 54.721 + 8.521 \times \text{food} - 1.361 \times \text{infection}$$

$$(n = 127,\ R = 0.80,\ P_{\text{food}} < 0.000001,\ P_{\text{infection}} < 0.000001)$$

This dependency is illustrated in Fig. 12. We see that female life expectancy increases as parasitic pressure decreases and as food supply increases.

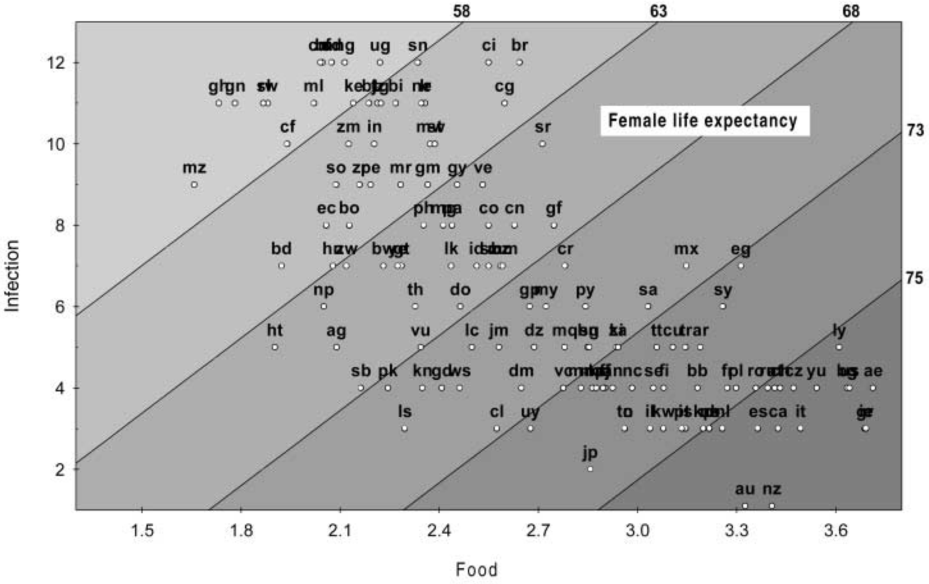

Fig. 12. A linear approximation of observed dependency of female life expectancy, T_{fem}, on food and infection presented as a contour plot of T_{fem} on food and infection. The levels of T_{fem} are shown by the different hatching and by the numbers at the top and on the right-hand side. The country codes are given in Appendix 2.

DISCUSSION

In this study, we have built a dynamic model of human female body growth and reproduction based on evolutionary optimization of the strategy of partitioning an individual's resources between the needs for growth, reproduction and survival. We have tried to make this model as simple as possible because analysing results obtained with complex models is usually cumbersome. We disregarded some aspects of the evolutionary optimization of human life histories considered elsewhere, as some previous analyses have suggested that their role would be unimportant in the present analysis.

In particular, we did not take into account the investment of resources into repair. The effect of such investment was considered in detail in Teriokhin (1998). In addition, the evolutionary optimization of human sexual dimorphism in body size and in life expectancy were investigated by Guégan *et al.* (2000) and Teriokhin *et al.* (2000), respectively. Here we restricted our analysis to the consideration of only female life histories. We did not optimize the age at menopause in females as this was done by Teriokhin and Budilova (2000). We simply took its average value of 50 years. In accordance with our data, the age at menopause does not depend significantly on food and infection, and in any case its worldwide variation of the order of 1 or 2 years is much less than that predicted by optimization models (Teriokhin and Budilova, 2000; Thomas *et al.*, 2001). We were obliged, however, to complicate the model by allowing the accumulation of reproductive energy to make possible the modelling of the dependency of female fertility on environmental factors.

In this study, we used two model variables associated with age at maturity. These were age at maturity, T_{mat} (i.e. the age at the beginning of reproductive accumulation), and age at release, T_{rel} (i.e. the duration of parental care). Both of these variables depend strongly on environmental mortality (e.g. parasitic pressure), m, and very weakly on resource availability, a. In addition, both increase when environmental mortality decreases. There are also two empirical characteristics of age at maturity. These are the age at menarche, T_{mnr}, and the age at marriage, T_{mrg}. The first characteristic increases with decreasing food availability, and the second increases with decreasing infection – that is, it is the age at marriage which matches the optimal dependency predicted by the model. We may thus suppose that this rather cultural rather than biological characteristic better reflects the optimal age of maturity. The importance of cultural aspects in human evolution has been discussed in particular by Laland *et al.* (2001).

The two model variables associated with female body size at maturity – that is, body size at maturity, X_{mat} (i.e. the body size at the beginning of reproductive accumulation), and body size at release, X_{rel} – both increase with an increase in resources and a decrease in environmental mortality. The two empirical characteristics of age at maturity, female stature and weight at birth, decrease with decreasing food supply too, but only weight at birth decreases significantly with an increase in infection. Female stature was observed not to decrease with increasing infection (there was even some increase in stature with increasing infection in our analysis, although not significantly so), though it is predicted by our simple optimization model. This phenomenon was considered in detail by Guégan *et al.* (2000), who conjectured that some increase in female stature with increasing fertility (which increases with increasing environmental mortality due to parasitic pressure) might be an adaptation for mitigating high risks of maternal mortality caused by an insufficient female body size.

The number of children, N_{chi}, in accordance with the optimal model should increase with increasing environmental mortality, and we also observed a similar trend for empirical fertility, N_{frt}, with increasing infection. Fertility varies significantly throughout the world with a tendency to decrease with increasing wealth. This phenomenon, known as demographic transition, has been investigated using different approaches (see Mason, 1997; Borgerhoff Mulder, 1998; Mace, 1998, 2000). In our model, the effect of a decrease in the number of children with an amelioration of environmental conditions (see Fig. 5) emerges as a consequence of the maximization of lifetime reproductive output under the assumption of non-linear dependence of reproductive output on reproductive investment.

Observed fertility, N_{frt}, increases significantly not only with increasing environmental mortality but also with decreasing food supply, whereas this is not the case for N_{chi}, the model characteristic of fertility. One possible explanation is that the variable ‘food’, which is highly correlated with the general level of development of a country, contains some information on mortality additional to that contained in the variable ‘infection’ (e.g. the level of medical care);

Comparing the tendency for increasing N_{chi} with the tendency for decreasing T_{rel} and X_{rel} in the model, we conclude that the increase in the number of children is accompanied by a decrease in the duration of parental care and body size of offspring at release.

The modelled life expectancy, T_{exp}, increases with increasing environmental mortality but it depends very weakly on resource availability. Similarly, the empirical life expectancy, T_{fem}, increases significantly with decreasing infection, but it also increases with increasing food. One explanation for this disparity in results obtained from modelling and statistical analysis is the same as for fertility: the variable ‘food’ may also contain some information about mortality. A more detailed statistical analysis of the influence of infection on human life expectancy has been conducted by Guégan and Teriokhin (2000).

CONCLUSION

We conclude that the empirical dependencies of some human life-history traits on environmental conditions roughly coincide with the predictions obtained from optimization models, in the sense that there is no empirical dependency that is opposite to that predicted by modelling. It would appear that the observed dependencies of human life-history traits on environmental conditions are generated, at least partly, by the process of evolutionary adaptation. In addition, this optimization can be ensured by means that are cultural (e.g. by changing the age at marriage) rather than biological (e.g. by changing the body size or the birth weight).

The general feature of the discrepancies between the data analysis and modelling is that the empirically observed dependencies of life-history traits on the availability of food supply predicted by the model are worse than the dependencies on environmental mortality. So an additional study is necessary to clear up the source of these discrepancies: whether they are due to inadequacies of the model or to disparities in the matching of modelled and observed variables.

ACKNOWLEDGEMENTS

The authors are grateful to P. Taylor for helpful comments. The work was supported by a CNRS senior research fellowship for A.T. and by grants from EGIDE (2001) to E.B. to visit CEPM and RFBR (01-04-48384) to E.B. and A.T.

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APPENDIX 1

An example of optimal life-history traits values (for $a = 1.7$ and $m = 0.9$)

t	u_t	v_t	w_t	z_t	E_t	L_t	X_{t+1}	Y_{t+1}
1	0	33	67	no	2.3	0.99	4.5	0.0
2	0	27	73	no	2.5	0.98	6.4	0.0
3	0	27	73	no	2.7	0.96	8.3	0.0
4	0	27	73	no	2.8	0.95	10.4	0.0
5	0	27	73	no	3.0	0.94	12.6	0.0
6	0	27	73	no	3.1	0.93	14.9	0.0
7	0	27	73	no	3.2	0.92	17.3	0.0
8	0	27	73	no	3.3	0.91	19.7	0.0
9	0	27	73	no	3.4	0.91	22.2	0.0
10	0	27	73	no	3.5	0.90	24.8	0.0
11	0	27	73	no	3.6	0.89	27.4	0.0
12	0	27	73	no	3.7	0.88	30.1	0.0
13	0	27	73	no	3.8	0.87	32.9	0.0
14	0	27	73	no	3.8	0.86	35.7	0.0
15	0	27	73	no	3.9	0.86	38.5	0.0
16	0	27	73	no	4.0	0.85	41.5	0.0
17	0	27	73	no	4.0	0.84	44.4	0.0
18	0	27	73	no	4.1	0.83	47.4	0.0
19	0	27	73	no	4.2	0.82	50.5	0.0
20	0	27	73	no	4.2	0.82	53.6	0.0
21	80	20	0	no	4.2	0.81	53.6	3.4
22	80	20	0	no	4.2	0.80	53.6	6.8
23	80	20	0	no	4.2	0.79	53.6	10.2
24	80	20	0	yes	4.2	0.78	53.6	13.6
25	80	20	0	no	4.2	0.78	53.6	3.4
26	80	20	0	no	4.2	0.77	53.6	6.8
27	80	20	0	no	4.2	0.76	53.6	10.2
28	80	20	0	yes	4.2	0.75	53.6	13.6
29	80	20	0	no	4.2	0.74	53.6	3.4
30	80	20	0	no	4.2	0.74	53.6	6.8
31	80	20	0	no	4.2	0.73	53.6	10.2
32	80	20	0	yes	4.2	0.72	53.6	13.6
33	80	20	0	no	4.2	0.71	53.6	3.4
34	80	20	0	no	4.2	0.71	53.6	6.8
35	80	20	0	no	4.2	0.70	53.6	10.2
36	80	20	0	yes	4.2	0.69	53.6	13.6
37	80	20	0	no	4.2	0.68	53.6	3.4
38	80	20	0	no	4.2	0.68	53.6	6.8
39	80	20	0	no	4.2	0.67	53.6	10.2
40	80	20	0	yes	4.2	0.66	53.6	13.6
41	80	20	0	no	4.2	0.66	53.6	3.4
42	80	20	0	no	4.2	0.65	53.6	6.8
43	80	20	0	no	4.2	0.64	53.6	10.2
44	80	20	0	yes	4.2	0.64	53.6	13.6
45	80	20	0	no	4.2	0.63	53.6	3.4
46	80	20	0	no	4.2	0.62	53.6	6.8
47	80	20	0	no	4.2	0.62	53.6	10.2
48	80	20	0	yes	4.2	0.61	53.6	13.6
49	80	20	0	no	4.2	0.60	53.6	3.4

50	80	20	0	no	4.2	0.60	53.6	6.8
51	80	20	0	no	4.2	0.59	53.6	10.2
52	80	20	0	yes	4.2	0.58	53.6	13.6
53	80	20	0	no	4.2	0.58	53.6	3.4
54	80	20	0	no	4.2	0.57	53.6	6.8
55	80	20	0	no	4.2	0.57	53.6	10.2
56	80	20	0	yes	4.2	0.56	53.6	13.6
57	80	20	0	no	4.2	0.55	53.6	3.4
58	80	20	0	no	4.2	0.55	53.6	6.8
59	80	20	0	no	4.2	0.54	53.6	10.2
60	80	20	0	yes	4.2	0.54	53.6	13.6
61	80	20	0	no	4.2	0.53	53.6	3.4
62	80	20	0	no	4.2	0.53	53.6	6.8
63	80	20	0	no	4.2	0.52	53.6	10.2
64	80	20	0	yes	4.2	0.52	53.6	13.6
65	80	20	0	no	4.2	0.51	53.6	3.4
66	80	20	0	no	4.2	0.51	53.6	6.8
67	80	20	0	no	4.2	0.50	53.6	10.2
68	80	20	0	yes	4.2	0.49	53.6	13.6
69	80	20	0	no	4.2	0.49	53.6	3.4
70	80	20	0	no	4.2	0.48	53.6	6.8
71	80	20	0	no	4.2	0.48	53.6	10.2
72	80	20	0	yes	4.2	0.47	53.6	13.6
73	80	20	0	no	4.2	0.47	53.6	3.4
74	80	20	0	no	4.2	0.46	53.6	6.8
75	80	20	0	no	4.2	0.46	53.6	10.2
76	80	20	0	yes	4.2	0.45	53.6	13.6
77	80	20	0	no	4.2	0.45	53.6	3.4
78	80	20	0	no	4.2	0.45	53.6	6.8
79	80	20	0	no	4.2	0.44	53.6	10.2
80	80	20	0	yes	4.2	0.44	53.6	13.6
81	87	13	0	no	4.2	0.43	53.6	3.7
82	87	13	0	no	4.2	0.42	53.6	7.4
83	87	13	0	no	4.2	0.42	53.6	11.0
84	87	13	0	yes	4.2	0.41	53.6	14.7
85	87	13	0	no	4.2	0.41	53.6	3.7
86	87	13	0	no	4.2	0.40	53.6	7.4
87	87	13	0	no	4.2	0.39	53.6	11.0
88	87	13	0	yes	4.2	0.39	53.6	14.7
89	87	13	0	no	4.2	0.38	53.6	3.7
90	87	13	0	no	4.2	0.38	53.6	7.4
91	87	13	0	no	4.2	0.37	53.6	11.0
92	87	13	0	yes	4.2	0.37	53.6	14.7
93	87	13	0	no	4.2	0.36	53.6	3.7
94	87	13	0	no	4.2	0.35	53.6	7.4
95	87	13	0	no	4.2	0.35	53.6	11.0
96	87	13	0	yes	4.2	0.34	53.6	14.7
97	87	13	0	no	4.2	0.34	53.6	3.7
98	87	13	0	yes	4.2	0.33	53.6	7.4
99	93	7	0	no	4.2	0.32	53.6	4.0
100	93	7	0	yes	4.2	0.31	53.6	7.9

APPENDIX 2

Two-letter codes for countries and autonomous areas (Internet codes are used)

Code	Country	Code	Country
ae	United Arab Emirates	hn	Honduras
ag	Antigua & Barbuda	ht	Haiti
an	Antilles (NL)	id	Indonesia
ar	Argentina	ie	Ireland
at	Austria	il	Israel
au	Australia	in	India
bb	Barbados	is	Iceland
bd	Bangladesh	it	Italy
bf	Burkina Faso	jm	Jamaica
bg	Bulgaria	jp	Japan
bi	Burundi	ke	Kenya
bj	Benin	ki	Kiribati
bn	Brunei	kn	St Kitts & Nevis
bo	Bolivia	kp	North Korea
br	Brazil	kr	South Korea
bw	Botswana	kw	Kuwait
bz	Belize	lc	St Lucia
ca	Canada	lk	Sri Lanka
cf	Central African Rep	lr	Liberia
cg	Congo Brazz	ls	Lesotho
ch	Switzerland	ly	Libya
ci	Cote d'Ivoire	ma	Morocco
cl	Chile	mg	Madagascar
cm	Cameroon	ml	Mali
cn	China	mm	Myanmar
co	Colombia	mn	Mongolia
cr	Costa Rica	mq	Martinique (FR)
cu	Cuba	mr	Mauritania
cz	Czech Rep	mw	Malawi
dm	Dominica	mx	Mexico
do	Dominican Rep	my	Malaysia
dz	Algeria	mz	Mozambique
ec	Ecuador	nc	New Caledonia (FR)
eg	Egypt	ne	Niger
es	Spain	ng	Nigeria
fi	Finland	nl	Netherlands
fj	Fiji	no	Norway
fr	France	np	Nepal
gd	Grenada	nz	New Zealand
gf	Guyana (FR)	pa	Panama
gh	Ghana	pe	Peru
gm	Gambia	pf	Polynesia (FR)
gn	Guinea	pg	Papua New Guinea
gp	Guadeloupe (FR)	ph	Philippines
gr	Greece	pk	Pakistan
gt	Guatemala	pl	Poland
gy	Guyana	pt	Portugal

py	Paraguay	to	Tonga
ro	Romania	tr	Turkey
ru	Russia	tt	Trinidad & Tobago
rw	Rwanda	tz	Tanzania
sa	Saudi Arabia	ug	Uganda
sb	Solomon Is	uk	United Kingdom
sd	Sudan	us	United States
se	Sweden	uy	Uruguay
sg	Singapore	vc	St Vincent & Grenadines
sl	Sierra Leone	ve	Venezuela
sn	Senegal	vu	Vanuatu
so	Somalia	ws	Western Samoa
sr	Suriname	ye	Yemen
st	Sao Tome & Principe	yu	Yugoslavia
sy	Syria	za	South Africa
sz	Swaziland	zm	Zambia
tg	Togo	zr	Congo Dem Rep
th	Thailand	zw	Zimbabwe
tn	Tunisia		