A probabilistic approach to the assessment of some life history pattern parameters in a Middle Pleistocene human population

A.I. Durand, S.L. Ipiña, J.M. Bermúdez de Castro

Abstract

Parameters of a Middle Pleistocene human population such as the expected length of the female reproductive period \(E(Y)\), the expected interbirth interval \(E(X)\), the survival rate \(\tau\) for females after the expected reproductive period, the rate \(\varphi_2\) of women who, given that they reach first birth, do not survive to the end of the expected reproductive period, and the female infant plus juvenile mortality rate \(\varphi_1\) have been assessed from a probabilistic standpoint provided that such a population were stationary. The hominid sample studied, the Sima de los Huesos (SH) cave site, Sierra de Atapuerca (Spain), is the most exhaustive human fossil sample currently available. Results suggest that the Atapuerca (SH) sample can derive from a stationary population. Further, in the case that the expected reproductive period ends between 37 and 40 yr of age, then \(24 \leq E(Y) \leq 27\) yr, \(E(X) = 3\) yr, \(0.224 \leq \tau \leq 0.246, 0.49 < \varphi_2 < 0.754\) and \(0 \leq \varphi_1 < 0.264\). When, however, the end of the expected reproductive period occurs after 40 yr of age, it turns out that \(24 \leq E(Y) \leq 30\) yr, \(E(X) = 3\) yr, \(0.204 \leq \tau \leq 0.246, 0.74 < \varphi_2 \leq 0.754\) and \(0 \leq \varphi_1 < 0.056\).

Keywords: Probabilistic approach; Atapuerca; Life history pattern

1. Introduction

There is a growing interest in understanding those aspects of the paleobiology of the Plio-Pleistocene hominids related to their life history patterns (see [1,2] for recent reviews). In fact, the appearance of new methods in the last 15 yr has allowed us to recognize remarkable differences between Plio-Pleistocene hominids and modern humans regarding rates and patterns of...
development [3–7]. The results of these studies suggest that all *Australopithecus* species and early *Homo* reached maturity nearly twice as fast as modern humans and therefore, they had periods of development similar to those of great apes. Furthermore, a recent study has showed that early *Homo erectus* probably had a life cycle which is intermediate between those of extant apes and modern humans [8]. All these results agree with predictions based on brain size [9] and lead us to examine the evidence from Sima de los Huesos [10] relevant to the evolution of hominid life history patterns. This site has provided near 2000 human fossil remains representing a minimum of 32 individuals [11], a detailed description of which can be seen by the interested reader in [12].

The observed mortality pattern present in this SH human sample aroused our interest in analyzing certain parameters of the aforementioned hominid life history niche. The purpose is to comparing them, when feasible, with the corresponding life history parameters in other human populations, particularly the Neanderthals. The analysis was carried out from a probabilistic standpoint and considering that paleo-anthropological data are the main source of information we can analyze concerning the life history pattern of Middle Pleistocene human populations. The main consequence of this analysis has been that the values for parameters such as the expected length of the female reproductive period, the expected interbirth interval, the survival rate for females after the expected reproductive period, the rate of women who reached but do not survive the end of the expected reproductive period and the female infant plus juvenile mortality rate, are assessed.

2. Material and estimation of the age at death

The human fossil material recovered from the SH site up until the 1995 season includes 17 important mandibular specimens, most of which preserve teeth in situ, as well as 24 smaller mandibular fragments [13]. The sample also includes five upper maxillary fragments preserving the premolars and/or molars in situ. One of these specimens (AT-405) belongs to Cranium 6, whereas the more complete Cranium 5 also preserves some maxillary teeth in situ [10]. A total of 202 teeth were catalogued as isolated specimens. This material was used to obtain the minimum number of individuals (MNI) represented in the SH hypodigm. The procedure and criteria followed in order to obtain the MNI is explained in detail elsewhere [11] and will not be repeated here. Table 1 of that paper includes information concerning the specimens which define each individual.

The age at death for the SH immature individuals was estimated based on modern human patterns of dental eruption/development; when necessary, observations on conventional radiographs of the SH specimens were made. As there is some evidence that European Middle and early Upper Pleistocene hominids had slightly accelerated dental formation schedules in relation to modern humans [14–17], such estimations may be biased. The tooth wear based procedure developed by Miles [18], which uses as a baseline group those individuals with incompletely developed dentitions to establishing criteria about rates of wear for particular teeth, has been employed. Following Miles’ method, it has been assumed that the lower M1 of the SH hominids comes into occlusion at 6 yr and the lower M2 at 12 yr.
Nowell [19], Wolpo/C128 [15] and Hillson [20] have pointed out that Miles’ procedure is debatable. Nowell, for instance, suggested that a minimum number of 20 individuals aged between 6 and 19 yr are required to establish rate of wear for particular teeth and to this effect, it is to be noticed that the number of the SH individuals having enough information is far from that number. Furthermore, because of the high variability of the time formation of M3 in modern humans and the possibility that the mean age for the emergence into occlusion of these teeth in the European Middle Pleistocene population was significantly lower than in most living populations [15], the application of the observed wear rates in the lower M1 and M2 to the M3 may be hazardous. The use of Miles method offers reasonable results only for the youngest adults but the greater the age the lesser the accuracy of this procedure to assign specific ages-at-death to the individuals; as a consequence, wide age intervals have been constructed (see also [21,22]).

<table>
<thead>
<tr>
<th>Individual</th>
<th>Age-at-death</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>IX</td>
<td>4–6</td>
<td>–</td>
</tr>
<tr>
<td>XXV</td>
<td>7–9</td>
<td>–</td>
</tr>
<tr>
<td>XVII</td>
<td>9–11</td>
<td>–</td>
</tr>
<tr>
<td>XXX</td>
<td>11.5–12.5</td>
<td>–</td>
</tr>
<tr>
<td>XXXII</td>
<td>11.5–12.5</td>
<td>–</td>
</tr>
<tr>
<td>XX</td>
<td>13.5–14.5</td>
<td>m</td>
</tr>
<tr>
<td>XVI</td>
<td>13.5–14.5</td>
<td>–</td>
</tr>
<tr>
<td>XXIX</td>
<td>13.5–14.5</td>
<td>–</td>
</tr>
<tr>
<td>II</td>
<td>14.5–15.5</td>
<td>m</td>
</tr>
<tr>
<td>XIV</td>
<td>14.5–15.5</td>
<td>–</td>
</tr>
<tr>
<td>XI</td>
<td>14.5–15.5</td>
<td>f</td>
</tr>
<tr>
<td>X</td>
<td>15.5–16.5</td>
<td>f</td>
</tr>
<tr>
<td>XXIII</td>
<td>16.5–17.5</td>
<td>f</td>
</tr>
<tr>
<td>XV</td>
<td>16.5–17.5</td>
<td>–</td>
</tr>
<tr>
<td>III</td>
<td>17.5–18.5</td>
<td>f</td>
</tr>
<tr>
<td>XXVI</td>
<td>17.5–18.5</td>
<td>–</td>
</tr>
<tr>
<td>XIX</td>
<td>17.5–18.5</td>
<td>f</td>
</tr>
<tr>
<td>XXVIII</td>
<td>17.5–18.5</td>
<td>–</td>
</tr>
<tr>
<td>I</td>
<td>18.5–19.5</td>
<td>f</td>
</tr>
<tr>
<td>XII</td>
<td>19.5–20.5</td>
<td>m</td>
</tr>
<tr>
<td>VI</td>
<td>21.5–22.5</td>
<td>f</td>
</tr>
<tr>
<td>XXIV</td>
<td>21.5–22.5</td>
<td>–</td>
</tr>
<tr>
<td>VIII</td>
<td>21.5–22.5</td>
<td>m</td>
</tr>
<tr>
<td>XXII</td>
<td>24.5–25.5</td>
<td>m</td>
</tr>
<tr>
<td>XXVII</td>
<td>26–30</td>
<td>m</td>
</tr>
<tr>
<td>VII</td>
<td>26–30</td>
<td>m</td>
</tr>
<tr>
<td>XVII</td>
<td>26–30</td>
<td>–</td>
</tr>
<tr>
<td>XIII</td>
<td>26–30</td>
<td>m</td>
</tr>
<tr>
<td>XXXI</td>
<td>26–30</td>
<td>f</td>
</tr>
<tr>
<td>IV</td>
<td>26–30</td>
<td>f</td>
</tr>
<tr>
<td>XXI</td>
<td>31–40</td>
<td>f</td>
</tr>
<tr>
<td>V</td>
<td>31–40</td>
<td>–</td>
</tr>
</tbody>
</table>
3. Probabilistic approach

It is our aim to analyze the relationship between the expected values of the two random variables *length of the female reproductive period* or *period of childbearing*, which has been denoted $Y$, and *interbirth interval*, symbolized $X$, on the one hand, and the percentage of women who survive to the end of the expected value of the reproductive period, on the other hand. The analysis is based on the assumption that the population is constant, that is the population has a rate of increase equal to 0. It is also assumed that women lived in a panmictic population and there was no impediment in becoming pregnant after sexual intercourse.

There are two factors that account for the rate of increase of a population; one of these is the so-called ‘net reproduction rate’, represented by $R_0$. This index is defined (see [23]) as

\[ \int_{a}^{\beta} l(a)m(a) \, da, \]

where $a$ is the youngest fertile age, $\beta$ the highest fertile age, $l(a)$ the probability of survivorship to age $a$, and $m(a) \, da$ is the probability that a woman who has reached age $a$ will give birth to a girl child before age $a + da$.

Generally speaking, the $l$ and $m$ probabilities are estimated from data taken from a life table, provided that in such a table there is enough data. It seems evident that when dealing with paleoanthropological data such as the ones here studied (note that there are only ten females and eight males in the Atapuerca-SH sample, see Table 1), to estimate or make conjectures on $l(a)$ and particularly $m(a)$ is a risky task. This was the reason why we thought of an alternative probabilistic approach which is not based on the estimation of probabilities such as $l$ or $m$. Nevertheless, the interested reader can refer to the works of Mode [24] and Gage and Mode [25] to consult some other models of human reproduction, constructed on the basis that probabilities such as the mentioned $l$ and $m$ can be estimated with a high degree of reliability.

In this manner, in paleoanthropological studies, it is customary to define the net reproduction rate $R_0$ (see, e.g. [26]) as

\[ R_0 = \omega \tau \mathcal{C}, \]

where $\omega$ is the sex ratio, $\tau$ the percentage of women who survive to the end of the expected period of childbearing and $\mathcal{C}$ is the expected value of the number of children per woman. If $R_0$ equals 1, the number of female children by which a female child will be replaced is 1. The population remains constant in size over time. If $R_0$ is less than, or greater than 1, then the population decreases, or increases, in size.

As much $\omega$ as $\tau$ are considered as constant; $\omega$ is always equal to 0.5 whereas $\tau$ has been left to take values depending upon corresponding mathematical expectations of both length of the female reproductive period and interbirth interval. For the sake of simplicity, the product $\omega \tau$ has been represented by $\psi$. As commented above, $\mathcal{C}$ is the expected value of the random variable, from now on denoted $\mathcal{C}$, *number of children per woman*, defined as

\[ \frac{1}{n} \sum_{i=1}^{n} C_i, \]
where \( C_i \) is the number of children of the \( i \)th woman. As a consequence, \( R_0 \) is the expected value of the random variable which we will designate \( R_0 \).

The number of children a woman may have, represented by \( C \), may be theoretically defined as the quotient
\[
\frac{Y}{X},
\]
given that \( Y \) represents the length of the female reproductive period and \( X \) is the interbirth interval. In probability, it is customary to use the gamma distribution \( \mathcal{G}(\rho, \zeta) \), \( \rho > 0, \zeta > 0 \) family in the modeling of waiting times until an event occurs \( \zeta \) times (see, e.g. [24,27]). Thus, let
\[
Y : \mathcal{G}(\lambda, 1), \quad \lambda > 0
\]
and
\[
X : \mathcal{G}(\alpha, 1), \quad \alpha > 0
\]
be two independent and exponentially distributed random variables, with capital letter \( \mathcal{G} \) denoting a gamma distribution and Greek letters \( \lambda \) and \( \alpha \) the parameters of such distributions; as is well known (see, e.g. [28]), the expected values of these variables are
\[
E(Y) = \frac{1}{\lambda}
\]
and
\[
E(X) = \frac{1}{\alpha}.
\]

We will, in the first place, localize the probability density function of the random variable \( C \). To this purpose, we will use the method that allows to find the distribution of a function of several random variables (see, e.g. [29]), so that let
\[
C = Y/X, \quad W = X,
\]
\[
X = W, \quad Y = CW
\]
be a transformation and its inverse which has Jacobian
\[
J = \begin{vmatrix} w & c \\ 0 & 1 \end{vmatrix} = w = |J|.
\]

Accordingly, the joint probability density function of the \( C \) and \( W \) random variables is
\[
h(c, w) = \lambda e^{-\lambda c} w e^{-\alpha w} = \lambda \alpha w e^{-(\lambda c + \alpha w)}, \quad c > 0, \ w > 0.
\]
The marginal density \( h_C \) of \( C \) can be then calculated as follows:
\[
h_C(c) = \lambda \alpha \int_0^\infty w e^{-(\lambda c + \alpha w)} dw = \lambda \alpha \int_0^\infty \frac{v e^{-v}}{\left(\lambda c + \alpha \right)^2} dv
\]
\[
= \frac{\lambda \alpha}{(\lambda c + \alpha)^2} \int_0^\infty v e^{-v} dv = \frac{\lambda \alpha}{(\lambda c + \alpha)^2} \Gamma(2),
\]
capital letter \( \Gamma \) being the gamma function.
Hence,

\[ h_C(c) = \begin{cases} \frac{\lambda}{(\lambda c + \alpha)^2}, & c > 0, \\ 0, & \text{elsewhere}. \end{cases} \]

It seemed advisable to us that this \( h_C \) density should be truncated at \( M \), the maximum number of children a woman may have, since this way the resultant density will more satisfactorily approximate, from a practical standpoint, the behavior of the random variable \( C \). Thus,

\[
1 = k\lambda \int_0^M \frac{1}{(\lambda c + \alpha)^2} \, dc = k\lambda \int_0^M \frac{1}{(\lambda c + \alpha)^2} \, dc
\]

\[
= k\lambda \left[ -\frac{1}{\lambda c + \alpha} \right]_0^M = \frac{k\lambda M}{\lambda M + \alpha} \Rightarrow k = \frac{\lambda M + \alpha}{\lambda M}.
\]

Summarizing, the probability density function of \( C \) is

\[
h_C(c) = \begin{cases} \frac{\alpha(\lambda M + \alpha)}{M(\lambda c + \alpha)^2}, & 0 < c < M \\ 0, & \text{elsewhere}, \end{cases}
\]

and its distribution function

\[
H_C(c) = \frac{\alpha(\lambda M + \alpha)}{M} \int_0^c \frac{1}{(\lambda v + \alpha)^2} \, dv = 1 + \frac{\alpha}{\lambda M} - \frac{\alpha(\lambda M + \alpha)}{\lambda M(\lambda c + \alpha)}
\]

that is,

\[
H_C(c) = \begin{cases} 0, & c \leq 0, \\ 1 + \frac{\alpha}{\lambda M} - \frac{\alpha(\lambda M + \alpha)}{\lambda M(\lambda c + \alpha)}, & 0 < c < M, \\ 1, & c \geq M. \end{cases}
\]

\( E(C) \), the mathematical expectation of \( C \), is defined as

\[
E(C) = \frac{\alpha(\lambda M + \alpha)}{M} \int_0^M \frac{c}{(\lambda c + \alpha)^2} \, dc.
\]

This integral may be solved by parts as follows:

\[
u = c, \quad du = dc, \quad dv = (\lambda c + \alpha)^{-2} \, dc, \quad v = -\frac{1}{\lambda(\lambda c + \alpha)},
\]

so,

\[
E(C) = \frac{\alpha(\lambda M + \alpha)}{M} \left\{ -\frac{1}{\lambda(\lambda c + \alpha)} \right\}_0^M + \frac{1}{\lambda} \int_0^M \frac{dc}{\lambda c + \alpha}
\]

\[
= \frac{\alpha(\lambda M + \alpha)}{M} \left\{ -\frac{M}{\lambda(\lambda M + \alpha)} + \frac{1}{\lambda^2} \ln(\lambda c + \alpha) \right\}_0^M
\]

\[
= -\frac{\alpha}{\lambda} + \frac{\alpha(\lambda M + \alpha)}{\lambda^2 M} \ln \left( \frac{\lambda M + \alpha}{\alpha} \right).
\]
On the other hand, because of

\[ R_0 = \psi C, \]

it follows that

\[ E(R_0) = R_0 = \psi E(C) = \psi C = \psi E(C). \]

Assuming that either \( R_0 \) is normally distributed or the observed number of women, \( n \), is large enough, as is well known by the central limit theorem (see, e.g. [30]), the random variable \( R_0 \) has a limiting distribution which is normal with parameters:

\[ R_0 \sim \mathcal{N}(\mu, \text{var}(C)/n). \]

Now, by letting

\[ E(R_0) = R_0 = \psi E(C) = 1 \]

the relationship between parameters \( \lambda \) and \( \alpha \), hence between expected values of period of childbearing and time interval between births, can be disclosed in a situation in which, on one hand, the population is constant in size and, on the other hand, is an optimal situation because, as is well known, the maximum value of the normal probability density function is attained at the mathematical expectation of this type of distribution. Thus,

\[ R_0 = E(R_0) = 1 \Rightarrow \psi \left[ -\frac{\alpha}{\lambda} + \frac{\alpha(\lambda M + \alpha)}{\lambda^2 M} \ln \left( \frac{\lambda M + \alpha}{\alpha} \right) \right] = 1 \]

\[ \Rightarrow -\frac{\alpha}{\lambda} + \frac{\alpha(\lambda M + \alpha)}{\lambda^2 M} \ln \left( \frac{\lambda M + \alpha}{\alpha} \right) = \frac{1}{\psi} \Rightarrow \frac{1}{\psi} = -\frac{(\lambda M + \alpha)}{\alpha} + \left( \frac{\lambda M}{\alpha} + 1 \right) \ln \left( \frac{\lambda M}{\alpha} + 1 \right) = \frac{\lambda^2 M}{\psi \alpha^2} \]

\[ \Rightarrow -tM + (tM + 1) \ln(tM + 1) = \frac{\lambda^2 M}{\psi} \Rightarrow (tM + 1) \ln(tM + 1) = \frac{tM(t + \psi)}{\psi}, \]

\[ 0 < t = \frac{\lambda}{\alpha} \leq 1, \quad M > 0. \]

This implicit equation was subject to the constraint

\[ P(M - 1 \leq C \leq M) = 10^{-2}, \]

for we assumed that the event ‘one woman out of one hundred women who has either \( M - 1 \) or \( M \) children’ is a rare event. Such a choice for the value of this probability will be commented in Section 5. This way

\[ 10^{-2} = H_C(M) - H_C(M - 1) = 1 - H_C(M - 1) \]

\[ = 1 - \left( 1 + \frac{1}{tM} - \frac{tM + 1}{tM(tM - t + 1)} \right) \]

\[ = \frac{1}{tM^2 - (1-t)M}, \quad 0 < t = \frac{\lambda}{\alpha} \leq 1, \]

so that the following system of two equations was solved (Maple V, rel. 5 package [31]) for different values of \( \psi \).
\[ tM^2 - (1 - t)M = 10^2, \]
\[ (tM + 1) \ln(tM + 1) = \frac{tM(t + \psi)}{\psi}, \quad 0 < t = \frac{\lambda}{z} \leq 1, \quad M > 0. \]  

(1)

### 4. Hypothesis tests concerning \( \tau \) and results

Table 1 shows the estimated age-at-death of the 32 individuals identified in the SH hypodigm. The estimated sex, based on dental [32] and mandibular [33] evidence, for 19 individuals is also presented in this table. The mortality pattern observed in the Atapuerca-SH sample is characterized by a low representation of individuals under the age of 10 yr, a higher mortality among the adolescents and prime-age adults and a lower older adult mortality.

Since
\[ t = \frac{\lambda}{z}, \]

it follows that
\[ \frac{1}{\lambda} = \frac{1}{z} \] if and only if
\[ E(Y) = \frac{1}{t} E(X). \]

Table 2 gives some solutions for the proposed (1) system of equations. If, for example, one assumes that the expected length of the female reproductive period \( (E(Y)) \) is around 27 yr and likewise, that the expected interbirth interval \( (E(X)) \) is 4 yr, then the percentage of women who survive the end of the expected period of childbearing is 0.28 (or 28%).

If first birth, denoted \( \eta \), occurs at 13 yr and the expected value for the length of the female reproductive period is 24 yr then a woman would be 37 yr of age at the end of her reproductive period.

Let \( S_c \) be the random variable number of women in the SH sample who survive to \( E(Y) + \eta \) when \( 37 \leq E(Y) + \eta \leq 40 \) yr and let \( S_d \) be the random variable number of women in the SH sample who survive to \( E(Y) + \eta \) when \( E(Y) + \eta > 40 \) yr. These two variables are distributed according to binomial laws, that is, \( S_c: B(10, \tau_c) \) and \( S_d: B(10, \tau_d) \), where \( \tau_c \) is the percentage of women who survive to \( E(Y) + \eta \) with \( 37 \leq E(Y) + \eta \leq 40 \) yr, and \( \tau_d \) is the percentage of women who survive to \( E(Y) + \eta \) with \( E(Y) + \eta > 40 \) yr.

<table>
<thead>
<tr>
<th>( E(Y) )</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>( E(X) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>24.242</td>
<td>0.246</td>
<td>0.305</td>
<td>0.360</td>
<td></td>
</tr>
<tr>
<td>25.316</td>
<td>0.236</td>
<td>0.295</td>
<td>0.348</td>
<td></td>
</tr>
<tr>
<td>26.490</td>
<td>0.228</td>
<td>0.285</td>
<td>0.338</td>
<td></td>
</tr>
<tr>
<td>27.211</td>
<td>0.224</td>
<td>0.280</td>
<td>0.330</td>
<td></td>
</tr>
<tr>
<td>28.571</td>
<td>0.216</td>
<td>0.270</td>
<td>0.318</td>
<td></td>
</tr>
<tr>
<td>29.197</td>
<td>0.214</td>
<td>0.265</td>
<td>0.312</td>
<td></td>
</tr>
<tr>
<td>30.769</td>
<td>0.204</td>
<td>0.260</td>
<td>0.300</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>( \tau )</th>
<th>0.28</th>
</tr>
</thead>
</table>
Next, let
\[ H_0 : \tau_c = \tau_0, \quad H_1 : \tau_c < \tau_0 \]
be a hypothesis test for this parameter, and let the size of the critical region be \( \gamma = 0.05 \). Based on the fact that in the SH sample there is one woman aged between 31 and 40 yr, we look for a \( \tau_0 \) value which leads to the rejection of \( H_0 \). Since \( F_{Sd}(1) = 0.046 \) for \( \tau_0 = 0.4 \) (Table 3), where \( F_{Sd} \) is the distribution function of \( S_d \), it is concluded that the \( \tau_0 \) value we are searching out is 0.4.

Likewise, let
\[ H_0 : \tau_d = \tau_0, \quad H_1 : \tau_d < \tau_0 \]
be a hypothesis test for \( \tau_d \), being \( \gamma = 0.05 \) as well. As in the SH sample there is no woman who exceeds 40 yr, we search out the value of \( \tau_0 \) which leads to the rejection of \( H_0 \). Now, \( F_{Sd}(0) = 0.049 \) for \( \tau_0 = 0.26 \) (Table 3), \( F_{Sd} \) being the distribution function of \( S_d \).

It is obvious that in the SH sample the two above mentioned events are observed, that is, there is one woman aged between 31 and 40 yr and no woman aged over 40 yr. As a consequence, we should consider the two above hypothesis tests at a time so that the percentage of women who survive to \( E(Y) + \eta \) would be less than 0.26 (Table 3) if both null hypotheses are accepted as true. This is an important result because the range of values for \( \tau \) which are solutions for the system of two equations proposed (Table 2) is constrained to the values of \( \tau \) in the column \( E(X) = 3 \) since (see Table 2) \( \tau \geq 0.26 \) for \( E(X) = 4, 5 \). In addition, it is pointed out that such a result means that the SH sample can derive from a population which was stationary as, otherwise, we ought to have obtained a value for \( \tau \) that would not be present in Table 2.

Tables 4 and 5 have been constructed on the assumption that first birth is reached at different ages and that \( 37 \leq E(Y) + \eta \leq 40 \) (Table 4) or \( E(Y) + \eta > 40 \) (Table 5). In Table 4, for instance, if first birth starts at 14 yr, the expected length of the reproductive period would vary between approximately 24 and 26 yr because \( E(Y) + \eta \leq 40 \). That \( 24 \leq E(Y) \leq 26 \), in turn, implies that \( 0.228 \leq \tau_c \leq 0.246 \) (see Table 2).

On the other hand, given the definition of \( \tau_c \), the percentage of women who do not survive to \( E(Y) + \eta \), when \( 37 \leq E(Y) + \eta \leq 40 \), is represented by \( 1 - \tau_c \). If \( \varphi_{1c} \) is the percentage of female children who do not survive to first birth and \( \varphi_{2c} \) is the percentage of women who, given that they reach first birth, do not survive to \( E(Y) + \eta \), then
\[
1 - \tau_c = \varphi_{1c} + \varphi_{2c}.
\]

### Table 3
<table>
<thead>
<tr>
<th>( \tau_0 )</th>
<th>( F_{Sc}(1) )</th>
<th>( F_{Sd}(0) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.736</td>
<td>0.348</td>
</tr>
<tr>
<td>0.2</td>
<td>0.375</td>
<td>0.107</td>
</tr>
<tr>
<td>0.25</td>
<td>0.244</td>
<td>0.056</td>
</tr>
<tr>
<td>0.26</td>
<td>0.222</td>
<td>0.049</td>
</tr>
<tr>
<td>0.3</td>
<td>0.149</td>
<td>0.028</td>
</tr>
<tr>
<td>0.4</td>
<td>0.046</td>
<td>0.006</td>
</tr>
</tbody>
</table>
In view of the fact that the observed number of women who survive to first birth among the 10 women of the SH sample depends on the age at which first birth occurs, two distinctive cases can be explored.

In the first case, suppose $g_{13}^{14}, 14, 15$. In this instance, $0.224 \leq \tau_e \leq 0.246$ (Table 4), so if we consider the maximum endpoint of this interval

$$\tau_e = 0.246 \iff 1 - \tau_e = 0.754 \iff \varphi_{1c} + \varphi_{2c} = 0.754 \Rightarrow \varphi_{2c} \leq 0.754.$$

Let $V_c$ be the random variable defined as the number of women who, given that they reach first birth, do not survive to $E(Y) + \eta$, when $37 \leq E(Y) + \eta \leq 40$, out of the 10 women found in the SH
sample. This variable is distributed according to a binomial model with parameters 10 and \( \varphi_{2c} \). Now, let

\[
\begin{align*}
H_0 & : \ varphi_{2c} \leq 0.754, & H_1 & : \ varphi_{2c} > 0.754
\end{align*}
\]

be the corresponding hypothesis test for the parameter \( \varphi_{2c} \) with size for the critical region \( \gamma = 0.05 \). Since, according to data in Table 1,

\[
P(V \geq 9 \mid \varphi_{2c} = 0.754) = 0.253156 > \gamma = 0.05,
\]

it can be concluded that the SH sample can derive from a population with \( \varphi_{2c} \leq 0.754 \).

Additionally, paying attention to the minimum endpoint of the above interval for \( \tau_{c} \),

\[
\tau_c = 0.224 \Rightarrow \varphi_{2c} \leq 0.776,
\]

so if, as before, the test

\[
\begin{align*}
H_0 & : \ varphi_{2c} \leq 0.776, & H_1 & : \ varphi_{2c} > 0.776
\end{align*}
\]

is constructed, it is obvious that \( H_0 \) is again not rejected. Accordingly, the rate \( \varphi_{2c} \) of women who do not survive to \( E(Y) + \eta \), having reached first birth, is less than or equal to 0.754. By simply setting that

\[
P(V \geq 9 \mid \varphi_{2c} = \varphi_{2c_0}) > \gamma = 0.05,
\]

a lower bound for \( \varphi_{2c} \) can be found. Thus, after calculations, \( \varphi_{2c_0} > 0.605 \).

Lastly, as

\[
0.754 \leq 1 - \tau_c \leq 0.776 \iff 0.754 \leq \varphi_{1c} + \varphi_{2c} \leq 0.776
\]

\[
\Rightarrow 0.754 - \varphi_{2c} \leq \varphi_{1c} \leq 0.776 - \varphi_{2c},
\]

and

\[
0.605 < \varphi_{2c} \leq 0.754,
\]

it can be concluded that

\[
0 \leq \varphi_{1c} < 0.171.
\]

In the second case, suppose \( \eta = 16 \). Now, \( \tau_c = 0.246 \) as can be seen in Table 4 which means that

\[
1 - \tau_c = \varphi_{1c} + \varphi_{2c} = 0.754 \Rightarrow \varphi_{2c} \leq 0.754.
\]

As before,

\[
\begin{align*}
H_0 & : \ varphi_{2c} \leq 0.754, & H_1 & : \ varphi_{2c} > 0.754
\end{align*}
\]

is a test for the \( \varphi_{2c} \) parameter with \( \gamma = 0.05 \). Because of

\[
P(V \geq 8 \mid \varphi_{2c} = 0.754) = 0.537637 > \gamma = 0.05,
\]

according to data in Table 1, the null hypothesis is accepted. Also, by setting

\[
P(V \geq 8 \mid \varphi_{2c} = \varphi_{2c_0}) > \gamma = 0.05,
\]
it turns out that, in this instance, \( \varphi_{2c_0} > 0.49 \), that is to say
\[
0.49 < \varphi_{2c} \leq 0.754.
\]

Finally,
\[
\tau_c = 0.246 \iff 1 - \tau_c = \varphi_{1c} + \varphi_{2c} = 0.754 \Rightarrow \varphi_{1c} = 0.754 - \varphi_{2c},
\]
or, what is the same,
\[
0 \leq \varphi_{1c} < 0.264.
\]
All these results are summarized in Table 4.

Results for \( \tau_d, \varphi_{1d}, \) and \( \varphi_{2d} \) in Table 5 have been obtained through a procedure which is analogous to the one just described and the definition of the random variable \( \mathcal{V}_d \), that is, number of women who, given that they reach first birth, do not survive to \( E(Y) + \eta \), when \( E(Y) + \eta > 40 \), out of the 10 women found in the SH sample. It is to be noticed that in this instance solutions for \( \eta = 17 \) are the same as the ones for \( \eta = 16 \).

5. Discussion

As described in Section 3, it was set that
\[
p = P(M - 1 \leq C \leq M)
\]
is equal to \( 10^{-2} \). In an attempt to investigate which \( p \) value is the best option to choose, some values for this \( p \) probability were tested against demographic data corresponding to a population of East African hunter–gatherers, a forager population which has been held to present the best available model of Pleistocene forager adaptations [34].

Table 3 from [35] on Hazda demography offers mortality data for women grouped in different age intervals; 26\% of women were older than 45 yr. When our proposed (1) system of equations, given that \( p = 10^{-2} \), is tested against these data, it turns out that if \( \tau = 0.26 \) and \( E(X) = 4 \), then \( E(Y) \) will equal 30.7 (Table 2). This is in accordance with the mean age at childbearing calculated by these authors.

These results were, when \( p = 10^{-3} \) and \( \tau = 0.26 \), \( E(Y) \leq 15 \) with \( E(X) = 4 \), and \( E(Y) \leq 11 \) with \( E(X) = 3 \). Also, in the case that \( p = 5 \times 10^{-2} \) and \( \tau = 0.26 \), then \( E(Y) \leq 17 \) with \( E(X) = 4 \) and \( E(Y) \geq 13 \) being \( E(X) = 3 \). As can be seen, the results for \( E(Y) \) are different enough from the ones shown in [35] to conclude that \( p = 10^{-2} \) is the more reasonable alternative.

Some authors such as Hassan [26] have stated that the average period between successful births is a basic factor in determining fertility in human populations. An average between 27 and 29 months has been estimated through different methods for the birth interval in modern populations (Barret: quoted in [36], [26,37]). This average seems to be longer in the hunting-gathering groups; in effect, successful births in these groups are spaced 3–4 and even 5 yr apart [38–40]. Since there is evidence that lactation inhibits ovulation [41], such a wide interval is in agreement with the prolonged nursing period reported for these human groups [39].

The fossil record offers some evidence to estimate the mean of the length of the nursing period. Dental enamel hypoplasias are considered as indicators of increased exposures to health risk at
the time of weaning [42]. Peak age for hypoplasias between 2 and 4 yr has been observed in certain pre-industrial populations [43,44]. Based on the study of a sample of Neanderthal specimens, Ogilvie et al. [45] have reported a peak around 4 yr for the European early Upper Pleistocene population. Similarly, Bermúdez de Castro and Pérez [46] have observed a peak age for hypoplasias between 3 and 4 yr in the SH human dental sample, thus suggesting a weaning period for these hominids similar to that of recent hunter–gatherers.

In women, the length of the reproductive period depends on the age at which they are able to give birth for the first time. However, there is no evidence in the paleontological record in relation to the age of first birth or the length of the reproductive period. We have then no recourse but to specify some plausible intervals within which we are confident of the values for the length of the reproductive period and first birth. Thus, the expected length of the reproductive period has been assumed to be between those of the chimpanzee $E(Y)$ (around 24 yr [2]) and the modern human $E(Y)$ (around 30 yr). On the other hand, the mean age at menarche for modern human populations ranges from 12 to 18 yr according to 116 samples published by Eveleth and Tanner [47]. According to these authors, this variation depends basically on socioeconomic, climatic and genetic factors, though a 82.7% of the samples listed have mean ages at menarche between 12 and 13.8 yr. A period of adolescent sterility which ranges from 1 to 3 yr in both chimpanzees [48] and humans [49] follows the first ovulation, so that women of at least some modern populations could give birth for the first time at an average age of 13–16.8 yr.

There are some differences between the mortality pattern observed in the Atapuerca SH sample in relation to the pattern of some recent foraging human populations such as Dobe !Kung, Hazda or Ache [22]. The percentage of infants and children in the SH hominid sample could be explained by differential taphonomic preservation. Nevertheless, the preservation of bones and teeth of some infants as well as the most fragile bone elements of the adults suggest to us that differential preservation has not been the factor responsible for the more frequent presence of permanent teeth with respect to the deciduous teeth in the current SH hypodigm. Furthermore, the careful excavation procedures of the SH site include the washing and screening of the sediments to obtain micromammal fossil remains, as well as careful microscope examination of the resultant fractions by means of binocular lens. These procedures exclude the problem of recognition of small anatomical elements during excavation which may have affected many other excavations in the past [22]. Finally, it is also plausible to consider that the pre-adolescent mortality in the Middle Pleistocene could be lesser than the corresponding mortality distribution of recent foraging groups [22].

Based on the assumption that first birth occurred between 13 and 16 yr of age, the expected length of the period of childbearing would be between 24 and 27 yr, the expected interbirth interval would equal 3 yr and the percentage of women who survive to $E(Y) + \eta$ would vary between 22.4% and 24.6%, in the case that $37 \leq E(Y) + \eta \leq 40$ (see Table 4). Likewise, when $E(Y) + \eta > 40$, then $24 \leq E(X) \leq 30$, $E(X) = 3$ and $0.204 \leq \tau_d \leq 0.246$, see Table 5. This result concerning the survivorship of women beyond 35–40 yr is roughly in accordance with the corresponding survivorship proposed by Trinkaus [22] for the Neanderthal population, who assumes that approximately 20% of people, hence men and women, survived beyond 40 yr.

The values obtained for the percentage of women who having surpassed nubility do not survive to the expected end of the childbearing period, and the percentage of female children who do not
survive nubility, are in the intervals (49%, 75.4%) and [0%, 26.4%), respectively, when $37 \leq E(Y) + \eta \leq 40$ (see Table 4). Such values for the endpoints of these intervals are a consequence of the assumption that nubility begins when the female child is either 13, 14, 15 yr old or is 16 yr old. By taking into consideration that the XX individual of the SH sample (Table 1) was a 14 year old male, hence secondary sexual characters have already appeared at that age, it seems a reasonable alternative to think that the beginning of nubility tends towards 13 yr rather than 16 yr. In the event that this were the case, the intervals become (60.5%, 75.4%) for the percentage of women who surviving nubility do not reach the expected age of the childbearing period end, and [0%, 17.1%) for the percentage of female children who do not survive nubility. As a consequence, the mortality of female children before nubility in the Atapuerca-SH population was different from the corresponding mortality proposed by Trinkaus [22] whose data for the Neanderthals suggest that 33.6% of the children would not survive beyond 10 yr of age.

On the other hand, when $E(Y) + \eta > 40$, the resultant intervals for $\varphi_{2d}$ and $\varphi_{1d}$ were (74%, 75.4%) and [0%, 5.6%), respectively (see Table 5). In this instance, therefore, there exists an appreciable difference between Trinkaus' proposal concerning children survivorship beyond 10 yr of age and our results.

In brief, the Atapuerca-SH infant mortality is at most half the Neanderthal infant mortality. If, as some authors (see, e.g. [26]) maintain, the major age-group that would influence on the population growth is that of prereproductive females – it seems that throughout prehistoric times, human populations were afflicted by a high depletion of that age-group – then one can conclude that the group of Neanderthals studied by Trinkaus [22] would be a declining population (remember that in this work we obtain results provided that the net reproduction rate is equal to 1). In fact, this same conclusion was drawn by Trinkaus [22] based on his analysis of the prime-age adult mortality.

The percentage $\tau$ of women who survive to the end of the reproductive period that has been used here in the definition of the index $R_0$ of net reproduction, presupposes that our $R_0$ underestimates the actual $R_0$ of the population, that is, our $R_0$ is less than or equal to the actual $R_0$. This is a consequence of not having considered in the $R_0$ definition those women who have reached the beginning of the reproductive period, and who die before reaching the end of the reproductive period. In other words, from a reproductive point of view, our $R_0$ implies that there is the same number of women at both the beginning and end of the reproductive period. On the other hand, if, instead of the $\tau$ here used, $R_0$ is defined by taking into account the percentage of women who survive to the beginning of the reproductive period, it is clear that the resultant $R_0$ would overestimate the actual $R_0$ of the population, so, in this case, the resultant $R_0$ would be greater than or equal to the actual $R_0$. Since our probabilistic approach is based on the fact that $R_0$ is equal to 1, the actual $R_0$ of the population is, in the first case, greater than or equal to 1, and, in the second case, less than or equal to 1.

As mentioned in Section 3, when dealing with paleoanthropological data, to make conjectures on what could happen in the reproductive period of the women of a specific population, is a risky task, so that one can legitimately ask is it better to choose the underestimation or overestimation alternative? We have thought that it would be better to underestimate $R_0$ since in this way the population is stationary or growing. In other words, by underestimating $R_0$ we can guarantee the population survival and growth. To us it seemed less informative to overestimate $R_0$ since now the population would be stationary or become endangered by extinction.
Acknowledgements

This work has been supported by Dirección General de Investigación Científica y Técnica del MEC, Proyecto no. PB93-066-C03-03. We would like to thank the anonymous reviewers for their comments on the paper.

References