An evolutionary model of stature, age at first birth and reproductive success in Gambian women

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We have built a model to predict optimal age at first birth for women in a natural fertility population. The only existing fully evolutionary model, based on Ache hunter-gatherers, argues that as women gain weight, their fertility (rate of giving birth) increases—thus age at first birth represents a trade-off between time allocated to weight gain and greater fertility when mature. We identify the life-history implications of female age at first birth in a Gambian population, using uniquely detailed longitudinal data collected from 1950 to date. We use height rather than weight as an indicator of growth as it is more strongly correlated with age at first birth. Stature does not greatly influence fertility in this population but has a significant effect on offspring mortality. We model age at first reproduction as a trade-off between the time spent growing and reduced infant mortality after maturation. Parameters derived from this population are fitted to show that the predicted optimal mean age of first birth, which maximizes reproductive success, is 18 years, very close to that observed. The reaction norm associated with variation in growth rate during childhood also satisfactorily predicts the variation in age at first birth.

Keywords: life-history trade-off evolution; age at first birth; height; father absence; The Gambia

1. INTRODUCTION

We expect evolved trade-offs between life-history functions such as growth, reproduction and survival (Roff 1992; Stearns 1992). Natural fertility populations, i.e. those that have not undergone a demographic transition, provide valuable data to investigate reproductive scheduling from a Darwinian perspective (e.g. Hill & Hurtado 1996; Sear *et al.* 2000; Strassmann & Gillespie 2002). We use data from a rural Gambian population to examine the determinants of age at first birth, a key transition in each woman's life history. Empirically derived relationships between growth and determinants of future reproductive success are used to develop a model of optimal age at first birth that maximizes reproductive success.

Poorly nourished women draw on reserves accumulated throughout childhood when pregnant (Tracer 1991; Gibson & Mace 2002). But delaying the age of onset of reproduction reduces fitness (Käär *et al.* 1996), so women face a trade-off between spending a long time accumulating resources through childhood growth versus starting reproduction. This trade-off can be used to model the optimal age at first birth (Stearns & Koella 1986; Hill & Hurtado 1996). Hill & Hurtado (1996) find that heavier Ache women are more fertile and later first birth allows for a longer period of pubertal weight gain, which is correlated with higher birth rates. The optimal age at first birth they predicted for the Ache is 18 years, near the observed mean of 17.5 years. We develop a similar model, but it is based on height rather than weight and the key influence of height on fitness is via child mortality, not via the mother's fertility.

The timing of puberty in humans has a range of physical and social correlates. Some studies show that weight and obesity are good predictors of menarche (Kaplowitz *et al.* 2001; Mul *et al.* 2001). Others show that height, or skeletal maturation, is more important than weight (Qamra *et al.* 1991; Bogin 1999). Menarcheal age is influenced by early development and negatively correlated with preschool height-for-age (Simondon *et al.* 1998). Yet low-birth-weight girls mature earlier than 'normal' counterparts, especially if they experience extensive catch-up growth (Ibanez *et al.* 2000; Dos Santos Silva *et al.* 2002). In Western countries, father absence is linked to earlier sexual maturity (Belsky *et al.* 1991; Hulanicka *et al.* 2001; Ellis *et al.* 2003). However, Waynforth (2002) has found that father absence is correlated with later first births among Maya horticulturalists and Ache hunter-gatherers. Thus, paternal correlates of age at first birth vary between societies. Women whose menarche is early are shorter adults (Georgiadis *et al.* 1997; Okasha *et al.* 2001) and women rarely grow in stature at all after their first birth.

Adult height has important implications for future reproductive success. In Africa, young primipara (16 years or younger) are more likely to experience pregnancy complications than older primipara (20–24 years), because of physiological immaturity and lack of health awareness; they give birth to lighter infants suffering from higher mortality (Schwab Zabin & Kiragu 1998; Rush 2000). In a previous analysis of this Gambian database, we show that taller women have fewer stillbirths and reduced infant mortality (Sear *et al.* 2004). They have very slightly shorter birth intervals but this does not reach statistical significance in our sample (Sear *et al.* 2004); thus maternal stature has a bigger impact on offspring mortality than on fertility.

We assess the life-history implications of age at first birth from two different viewpoints. First, we use event

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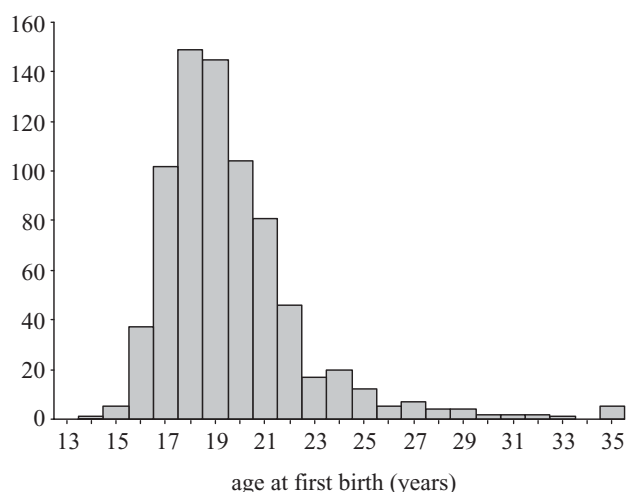465

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Figure 1. Histogram of age at first birth for women born between 1950 and 1974.

history analysis to determine the predictors of age at first birth. Second, we use the trade-off between adult height and future reproductive success to create a simple evolutionary model to predict optimal age at first birth in this population.

2. MATERIAL AND METHODS

(a) *Data*

The data were collected in four Gambian villages from 1950 to date. Literate villager elders recorded the dates of all births and deaths; from 1950 to 1980 this was supplemented by annual surveys measuring the weight, height and haemoglobin levels of all villagers. All three of these measures are likely to be related to nutritional status during childhood. Haemoglobin, in particular, is also likely to be related to the child's experience of disease, of which malaria was the most serious threat during childhood. From 1950 to 1975 there was high fertility and mortality, as well as seasonal variation in birth, death and growth patterns (Billewicz & McGregor 1981, 1982; Moore *et al.* 1997). In 1975 MRC opened a nutrition clinic providing free health care. Mortality dropped very quickly but fertility patterns are just starting to change (Sear 2001; personal observation). Food supplementation during lactation reduced postpartum amenorrhoea (Lunn *et al.* 1981), showing fecundity to be energetically constrained.

The Mandinka, a Muslim population, was originally composed of subsistence farmers (Thompson 1965). Today, many supplement their income with remittances from wage earners. Median age at first birth is 18 years (figure 1). Girls were traditionally married at menarche (Thompson 1965), but there are no individual data on marriage, menses, schooling or contraception; the latter remained rare until recently (personal observation). Contraception is not normally available before first birth, but is subsequently on offer. Reported current contraceptive use in 2001 was 13.8% among married, non-pregnant and non-menopausal women ($n = 253$); 29% of all ever-married women ($n = 395$) tried contraception at least once during their lifetime. Although it is unlikely that birth control is used to postpone age at first birth, it may influence completed family size.

Table 1. Sample selection for the event history analysis.

step	sample	n
1	whole database	10147
2	females	5111
3	born 1950–1974	1820
4	stayed in village	1544
5	alive at age 13 years	872
6	had at least one child	832
7	had first birth before age 25 years	815
8	no missing variables	427

An appropriate sub-sample was chosen from the database (table 1). First births postponed beyond age 25 years are presumably not due to delayed physical maturity, so by excluding late first births and infertile women we focus on the potential links between growth and reproduction. Event history analysis (EHA) identifies the predictors of age at first birth by modelling the duration of time until first birth occurs. Variable states at age *ca.* 13 years serve as a baseline. Anthropometric measurements are from the nearest annual survey; girls were aged 12.5–13.5 years when measured, but height at age *ca.* 13 years is corrected for age in months in a linear way. We chose to investigate height at age 13 years because this is before any first births and thus height is not yet being influenced by age at first birth. We also investigate whether the presence/absence of parents and sex of elder siblings help predict age at first birth. Preliminary investigations showed that missing sibling data created problems, therefore dummy variables were used, including dummies for missing data. We also included village, birth cohort and birth season in the analysis. Because some effects vary with age, we tested three separate models, one for the whole sample (13–25), one for younger women (13–19) and one for older women (19–25). Each is a single model with all variables entered simultaneously; categorical variables are tested as simple contrasts. The EHA was performed as a Cox regression in SPSS 10.1.

(b) *Model of optimal age at first birth*

We constructed a theoretical, deterministic model of optimal age at first birth using an Excel spreadsheet. The model calculates the number of children a woman has over her lifespan, which survive at least until age 5 years, depending upon her rate of growth and her age at first birth. Offspring mortality is related to adult height. Thus optimal age at first birth as a function of growth rate can be determined. Although stochastic, intergenerational models reflect reality more accurately, this simple approach nonetheless deciphers the effects of many parameters and allows us to test 'what if?' scenarios.

The model is as follows (definitions of parameters in table 2a).

(i) Adult height (ht_{ad}) and height at first birth are considered identical in the model and derived from height at age 10, average height velocity (g) and age at first birth (fb):

$$ht_{ad} = ((fb - 10) \times g) + ht_{10} \text{ (logical calculation),}$$

where

$$g = 3.5 + 0.12 \times (ht_{10} - 110) \text{ (empirically derived).}$$

(ii) Maternal height influences child survival (s) as follows:

$$s = 0.13 + (ht_{ad} - 110) \times 0.008\,33 \text{ (empirically derived).}$$

Table 2. Model details.

(*a*) glossary of terms used in model

c	number of children born in each period
fb	age at first birth (years)
g	growth rate/height velocity (cm yr^{-1})
ht_{10}	height at age 10 years (cm)
ht_{ad}	adult height (cm)
ibi_d	inter-birth interval after a dead child (month)
ibi_l	inter-birth interval after a live child (month)
lb	age at last birth (years)
m	proportion of children dying before age 5 years
n	total number of children born
p	period length (month)
s	proportion of children surviving to age 5 years

(*b*) inter-birth interval lengths for each 5 year period in model

mother's age (years)	interval length after live child (month)	interval length after dead child (month)
< 16	30	22
16–20	32	24
21–25	33	25
26–30	34	26
31–35	40	32
> 35	50	42

(iii) The number of children ever born is $n = ((lb - fb) \times 12/(ibi_l \times s + ibi_d \times m))$ (theoretical calculation). We adjust inter-birth interval (*ibi*) for maternal age as shown in table 2*b* and cumulatively add the number of children born across all periods of a woman's life: $\Sigma c(p/(ibi_l \times s + ibi_d \times m))$.

(iv) The number of surviving children is: $\Sigma c \times s$.

3. RESULTS

(*a*) *Statistical predictors of age at first birth*

Table 3 presents the EHA results, identifying the best predictors of age at first birth. All anthropometric variables are highly significant: better body condition leads to earlier first birth. The effects vary with age: height and weight have the strongest effect below age 19 years, whereas haemoglobin has a greater effect after age 19 years. There are apparent differences in age at first birth between villages, but these are not significant when the sibling data are removed from the regression and may be due to poorer data quality in two of the villages (Jali and Kanton Kunda). All villages are included, but village differences are controlled for. There is no secular trend in age at first birth, nor is there a strong effect of season of birth on age at first birth.

The presence of the father is associated with earlier age at first birth, although this does not reach statistical significance. Older brothers also increase the likelihood of first birth. The role of male kin in promoting female fertility
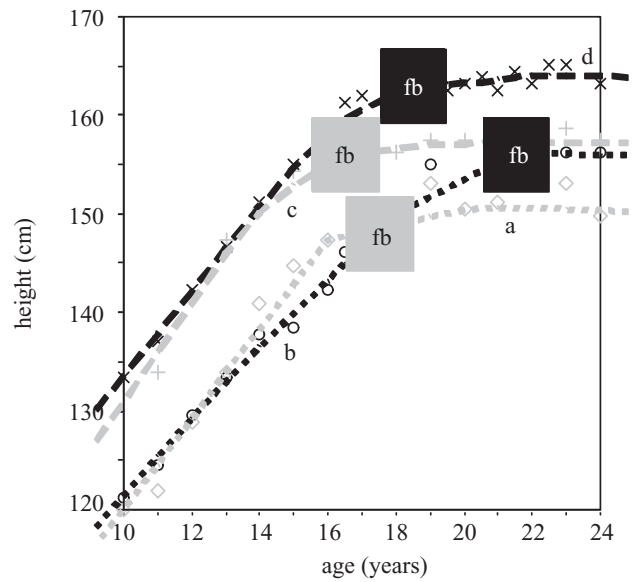
Figure 2. Four illustrative individual height-for-age curves showing alternative life-history strategies: a, short–early; b, short–late; c, tall–early; d, tall–late; *fb* flags symbolize first birth and lines are Lowess fit of data points.

at puberty is very interesting, given that in this population they have little if any effect on offspring survival, whereas female kin have little effect on fertility, but markedly improve offspring survival (Sear *et al.* 2000, 2003; Mace & Sear 2004).

The effect of height at age 13 years on age at first birth is by far the strongest of these effects. In a simple multiple regression using only those women that have given birth, height at age 13 years accounts for *ca.* 18% of the variance in age at first birth for those who gave birth younger than 19 years, whereas 24% of the variance can be explained if all parameters are included. Thus height is clearly a key parameter in determining the onset of puberty, and our life-history model (see below) is based around it.

(*b*) *Trade-off between age and height at first birth*

Table 4 shows that if a woman is tall at age 13 years, she will tend to be a tall adult. Controlling for height at age 13 years, later age at first birth also correlates with taller adult height. There is a trade-off between age and size at maturity, which is illustrated by four examples in figure 2. The difference between short and tall girls at age 13 years reflects genetic, developmental and environmental constraints, whereas having an early versus late first birth is an individual trade-off. Both early age at first birth and tall adult size are beneficial for reproductive success; but few girls can achieve both—trade-offs in resource allocation apply, and selection should find the optimal allocation between growth and length of reproductive span for girls growing at different rates.

As mentioned above, stature is not associated with fertility in this population; it is linked to child survival (Sear *et al.* 2004). Figure 3 shows the magnitude of the effect. Each centimetre of growth in maternal height is associated with a change in offspring mortality of *ca.* 2%. Having quantified this effect, it is possible to use the model described to predict when, depending on rate of growth, a girl should stop allocating energy to extending her

Table 3. Predictors of age at first birth for rural Gambian women.

(Overall model statistics: (a) $n = 437$, $\chi^2 = 79$, d.f. = 20, $p < 0.001$; (b) $n = 313$, $\chi^2 = 76$, d.f. = 20, $p < 0.001$; (c) $n = 124$, $\chi^2 = 35$, d.f. = 20, $p = 0.021$.)

variable	(a) first birth 13–25 years		(b) first birth 13–19 years		(c) first birth 19–25 years	
	odds ratio	p-value	odds ratio	p-value	odds ratio	p-value
height at age 13 years (cm)	1.039	< 0.001	1.053	< 0.001	1.012	0.487
BMI at age 13 years (kg m^{-2})	1.123	0.004	1.138	0.007	0.901	0.212
haemoglobin at age 13 years (g cm^{-3})	1.113	0.006	1.034	0.499	1.355	< 0.001
mother dead/absent at age 13 years	1		1		1	
mother alive at age 13 years	0.952	0.782	0.906	0.672	0.713	0.317
father dead/absent at age 13 years	1		1		1	
father alive at age 13 years	1.275	0.062	1.060	0.723	1.245	0.386
no older siblings	1		1		1	
more elder sisters than brothers	0.949	0.777	0.708	0.130	0.777	0.500
more elder brothers than sisters	1.478	0.032	0.867	0.520	1.953	0.079
same number of sisters and brothers	0.898	0.603	0.524	0.009	0.666	0.372
missing data on birth order	0.961	0.883	0.629	0.156	0.526	0.231
missing data on sibling sex	0.598	0.007	0.533	0.029	0.796	0.494
Keneba	1		1		1	
Manduar	1.171	0.290	1.450	0.034	1.119	0.736
Kanton Kunda	1.579	0.027	1.479	0.105	2.144	0.110
Jali	1.417	0.070	1.078	0.776	2.502	0.013
born 1950–54	1		1		1	
born 1955–59	1.206	0.206	1.466	0.027	0.726	0.327
born 1960–64	1.034	0.822	1.129	0.488	0.822	0.545
born 1965–68	1.001	0.995	1.135	0.568	0.533	0.176
born January–March	1		1		1	
born April–June	1.017	0.922	1.067	0.747	1.959	0.077
born July–September	0.991	0.958	1.278	0.192	1.146	0.733
born October–December	1.125	0.883	1.435	0.053	1.227	0.581
missing month of birth	0.917	0.637	1.120	0.600	0.819	0.642

Table 4. Linear regression analyses showing the impact of age at first birth on adult height.

(Dependent variable: adult height ($\geqslant 25$ years); $r^2 = 0.480$, $p < 0.001$, $n = 721$.)

variable	β-coefficient	s.e.	p-value
constant			< 0.001
height at age 13 years	0.75	0.063	< 0.001
age at first birth	0.33	0.017	< 0.001

growth and start the reproductive phase of her life history, to maximize her reproductive success.

The results of the parameterized optimality model are shown in figure 4. Using the empirical population mean for women's height and age-specific inter-birth intervals, and height-specific rates of child survival, the model accurately predicts the observed median age at first birth for this population (18 years). Figure 5 shows that the predicted reaction norm of mean age at first birth for girls of various growth rates is close to the observed reaction norm, although the model does slightly overestimate optimal age at first birth. Table 5 shows what happens when each model parameter is varied. Of particular note is that faster childhood growth, shorter reproductive spans and lower child mortality are all associated with earlier optimal ages at first birth. The latter is interesting given that high childhood mortality is not normally associated with later
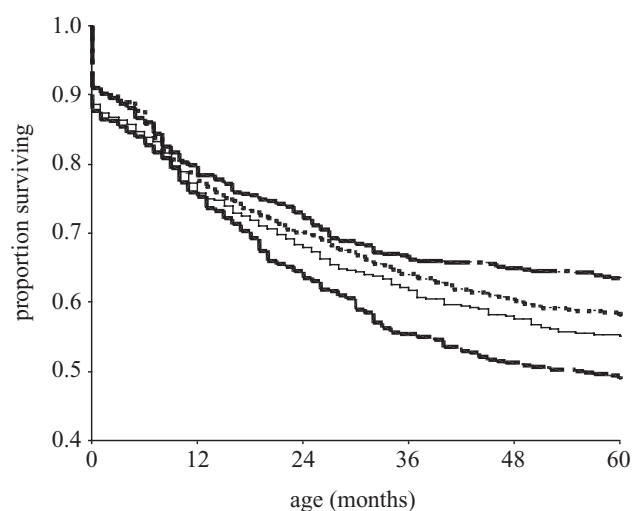

Figure 3. The proportion of births surviving (including stillbirths) over 5 years of women in the first, second, third and fourth quartiles for height (lines shown in that order, with the highest line representing the tallest quartile, etc.).

first birth. This occurs because the relative importance of the protective effects of maternal stature increases when offspring mortality is high.

4. DISCUSSION

The benefits of delayed first reproduction are experienced through the lower offspring mortality of taller

Table 5. Predictions of optimal age at first birth for population means and variations.

| model variables	Gambian dataset population mean	separate changes leading to earlier optimal age at first birth	separate changes leading to later optimal age at first birth
height at age 10 years	127 cm	127–150 cm	110–127 cm
mean inter-birth intervals	32 months after live child 24 months after dead child	shorter inter-birth intervals, i.e. higher overall fertility	longer inter-birth intervals, i.e. lower overall fertility
link between inter-birth interval and maternal age	mean *ibi* increases with age (see § 2).	*ibi* increases very rapidly with age	*ibi* increases very slowly with age or stays constant
age at last birth	39 years	35–38 years	40–45 years
mean child mortality	40% die before age 5 years	15–35% die before age 5 years	45–65% die before age 5 years
link between child mortality and maternal height	link to maternal height (see § 2).	child mortality weakly linked to maternal height	child mortality strongly linked to maternal height
optimal age at first birth	18 years	15–17 years	19–22 years
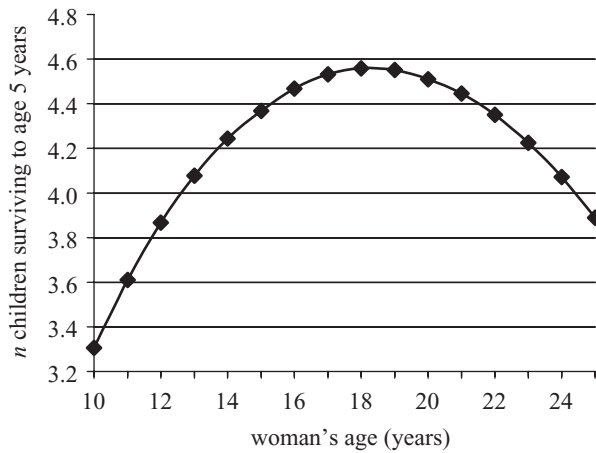
Figure 4. Fitness as a function of age at first birth modelled using population mean values of growth rate and age-specific fertility measures; and height-specific values for infant mortality for this population.
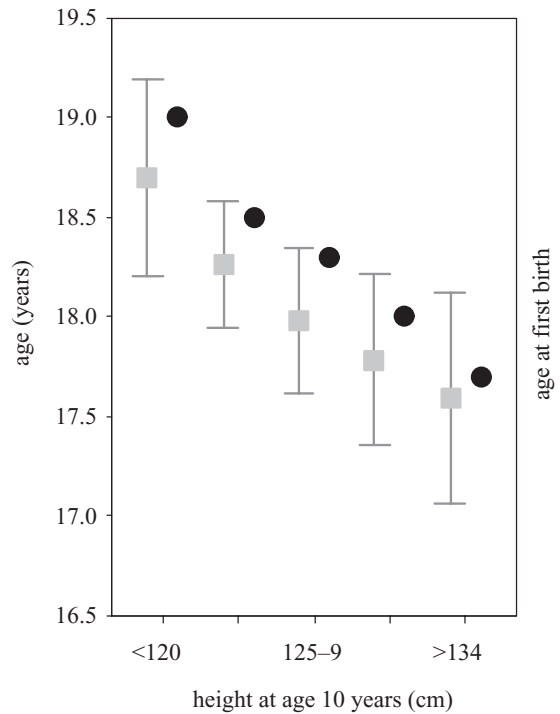

Figure 5. Modelled and observed reaction norm of age at first birth depending on height category at age 10 years. Vertical bars, 95% confidence interval; squares, observed mean; filled circles, optimal mean.

women. Trade-offs are usually difficult to demonstrate because of confounding phenotypic plasticity, but by controlling for height at age 13 years, we can reveal the trade-off between age at first birth and final adult height. Through optimality modelling we place the timing of puberty in an evolutionary context: we show that females start reproducing when the time they spend growing is balanced by the lifetime reduction in offspring mortality that the additional height will afford them. The modelled reaction norm is close to that observed, but it does predict slightly later than observed age at first birth. This is likely to be because our simple model does not capture intergenerational effects or adult mortality. Adding either of these effects would select for shorter generation times and earlier puberty. Sear *et al.* (2004) have also found a U-shaped relationship between adult height and adult mortality. A slight increase in adult mortality with above average stature could also select for earlier age at first birth, at least in tall women. However, it should be noted that female (non-maternity related) mortality in early adulthood is trivial (in our sample no female deaths *unrelated to maternity* in 18–25-year-olds were observed at all). Thus the absence of intergenerational effects may be a more important cause of this small discrepancy between observed and predicted age at first birth.

Hill and Hurtado's model is built around a relationship between weight and fertility, but in this population we find that relationship is not very important. Our model grew out of the observed link between height and offspring survival. It would be interesting to identify which human groups follow which set of trade-offs and whether populations exist that would benefit from analyses combining both approaches.

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