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Developmental plasticity of human reproductive development: Effects of early family environment in modern-day France

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ABSTRACT

In a first study, we investigated how the absence of a father and the presence of a stepfather during early childhood affected physiological and behavioral traits related to reproductive development (such as age of menarche, age of first sexual intercourse and number of sexual partners) in a large sample set of male and female French university students. We evaluated which ages were sensitive to modifications in the family composition and found that menarche occurred earlier when the father was absent, particularly when the child was between 0 and 5 years of age. Father absence during early adolescence was associated with a younger age at first sexual intercourse and an increased number of sexual partners, for both sexes. The presence of a stepfather during this period further advanced the age of first sexual intercourse. We also measured testosterone levels in both sexes and analyzed their association with parental separation, and found that young women with separated parents had significantly higher afternoon levels of testosterone. In a second study, we analyzed direct fitness measures (such as number of children and grandchildren) in a large sample of French workers and found that parental separation during childhood was not associated with fitness variation. We discuss whether the reproductive outcomes of individuals having experienced modifications in the early family environment are the expression of costs or adaptive strategies.

1. Introduction

Humans acquire physical, social and cognitive competencies during an extended juvenile period [1,2], which is highly dependent on adult caregiving [3,4]. When the caretaking environment is modified, e.g., when one parent leaves and a stepparent arrives, child development may be affected. Associations between family conflict or the absence of a father with reproductive traits in children have been widely documented. In Western industrial societies, the absence of a father has been considered a risk factor for earlier onset of puberty, sexual activity, teen pregnancy and unstable marriages [5–7,57]. Additionally, parental conflict during childhood is associated with earlier onset of puberty, earlier age of heterosexual dating and higher number of sexual partners [6,8,9].

Marital conflicts appear to be a key indicator for reproductive traits in children, although both the absence of a parent and the presence of a stepparent may account for these observations. Often following parental division is the arrival of a stepparent. Remarriage occurs more often in pre-industrial societies than in industrial societies because of higher mortality risks [10,11], but the frequency is currently increasing in industrial societies as well. Children raised in a stepfamily often receive less general investment [12], both educational and financial [13–17] than children raised by both of their biological parents. Stepchildren express more physiological [18] and psychosocial stress [19], and tragically, are at higher risks for infanticide [20,21] and sexual abuse [22–24].

The presence of a stepfather may be associated with a reduced investment, and is therefore expected to increase costs associated with the absence of a father. A brief review of studies comparing these two effects is presented in Table 1. Studies testing the effects of the absence of a father vs. the presence of a stepfather has led to contradicting results concerning the age of puberty onset: three studies have claimed that the presence of a stepfather has an effect on the age of puberty onset [25,26,58], while another study shows no effect [27] (Table 1). Unexpected or unusual results require replication, such as the observation that the presence of a stepfather is associated with an earlier age of first sexual intercourse in women but not with a higher number of sexual partners compared to when a father is absent [26]. As most studies focus only on women, the effect of a stepfather on male reproductive development has not been extensively studied. Even if women are more sensitive to the trade-off between allocations of resources for physical growth vs. production of offspring [28], there may also be important family context effects on male reproductive developmental outcomes. Finally, the developmental outcomes of children from various parental environments have not been studied in a broad range of cultures, limiting the general applicability of the results (Table 1). Thus, we first aimed to clarify the specific effects of the absence of a father and the presence of a stepfather, investigating the details of timing sensitivity to these two factors.

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Table 1
Overview of studies on the effects of the absence of a father vs. the presence of a stepfather on reproductive traits in children

	Reference	N	Country	Father absence	Stepfather presence
Age of puberty	Bogaert [25]	1921 women 1511 men	USA	At age 14: associated with early puberty in both men and women	No effect
	Quinlan [26]	10,847 women	USA	Before age 5: associated with earlier menarche	No effect
	Ellis & Garber [58]	87 women	USA	Associated with earlier menarche	Associated with earlier menarche (supplementary effect of absence of a father)
Age of first sexual intercourse	Quinlan [26]	10,847 women	USA	Before age 5: associated with earlier first sexual intercourse	Associated with earlier first sexual intercourse
Number of sexual partners	Quinlan [26]	10,847 women	USA	In adolescence: associated with higher number of sexual partners	No effect

Sample size (*N*), country of study and results obtained are indicated.

Flinn and England have shown that the absence of a father, and to a further extent the presence of a stepfather, leads to a rise of cortisol levels in children [29]. Cortisol is a key hormone produced in response to physical and psychosocial stressors and modulates a wide range of somatic functions including energy release, immune activity, mental activity, growth, and reproductive function [30]. To our knowledge, the effects of the absence of a father and the presence of a stepfather on reproductive hormones have not been investigated. The levels of circulating testosterone in both men and women are associated with responses to competitive situations and social dominance, facilitating direct competitive behaviors such as aggression [31–34]. Testosterone levels can be considered as a proxy for the capacity to compete for access to mates [32,35].

However, sex differences are observed in endocrine patterns. Women produce one-fifth to one-seventh the levels of testosterone in men, and the link between competition and testosterone is contingent on the perception of losing or winning for men, but not for women [32]. Sex differences could be better understood in the context of life history strategies. For men, testosterone levels reflect the investment between parenting and mating, with higher testosterone levels associated with a higher investment in seeking copulations. The endocrine pattern in males is sensitive to social context: Marriage and fatherhood are associated with a decrease in testosterone levels in men [36–38]. According to Belsky's hypothesis, men who experience a rearing environment where the father is absent would shift to a mating strategy, leading to an increase in testosterone levels [39]. Additionally, in response to competition with other males, such as stepfathers, males are predicted to show an increase in testosterone levels. The second aim of this paper is to investigate whether parental separation is related to changes in testosterone levels of offspring.

Although previous studies have established a clear link between familial environment and traits potentially associated with reproductive success, none have actually measured fitness outcomes resulting from such family configurations. The challenge here is to understand the nature of these changes: are these changes plastic and adaptive responses to a change in the family environment or merely an expression of the costs of developmental perturbations?

Among current theories, some hypothesize that the observed changes are adaptive responses and consider them constrained and costly. Draper and Harpending posit that early experiences concerning fathering and marital relationships influence the reproductive strategy that individuals develop in adulthood [40]. As the expression of paternal investment is variable, it is in the child's interest to use environmental cues to assess the potential for paternal investment and adjust their future reproductive strategies accordingly. In particular, the absence of a father causes girls to advance sexual maturation and express higher sexual interests, which would be advantageous in an environment with low paternal investment. Belsky, Steinberg, and Draper state that children respond adaptively to many aspects of their rearing environments (e.g., poverty, the absence of a father, divorce) and are especially sensitive to events occurring during the first years of life [39]. They propose that early experience allows assessment of various environmental components (i.e., predictability and availability of resources, trustworthiness of others), which, in turn, affects reproductive strategy. From these foundations, Ellis focused on the influence of fathering and raised questions about the possible mechanisms by which fathers (either their physical presence or the quality of their investment) influence the onset of puberty in girls [5,28]. Note that these theories rely on the assumption that variations in paternal investment are sufficiently low among fathers within a population and that the level of paternal investment is sufficiently stable, and therefore predictable, in a given population.

Parental separation could also result in a reduction of parental investment. This would lead to those individuals who suffered the costs of a reduced investment to start reproducing earlier, in order to lengthen their reproductive life and therefore increase their total number of offspring [41]. Indeed, several reproductive strategies in humans, as in other animals, are based on the allocation of resources between quantity and quality of one's offspring [59,42]. The third aim of the present study is to clarify this situation and directly measure fitness outcomes using the best available estimators, number of children and grandchildren.

We first analyzed the effects of the absence of a father and the presence of a stepfather at various stages during childhood using a large panel of reproductive traits, including behavioral and physiological traits. We then tested whether family changes were associated with a decrease in fitness, and determined if the costs were compensated by plastic adaptive responses. We have thus investigated the influence of family changes on several reproductive traits and fitness measures using a retrospective study of childhood experiences.

In the first study (Study A), we surveyed a French student population comprised of young adults raised in three types of families: two biological parents, mother alone, or mother and stepfather. The age of menarche and age of first sexual intercourse (both related to length of reproductive period), as well as the number of sexual partners were reported. Additionally, the timing sensitivity to the absence of a father and the presence of a stepfather on the child's developmental traits was controlled. In a subsample of the same student population, we used saliva samples to assess physiological data on testosterone levels.

In the second study (Study B), the long-term effects of parental separation on the number of children and grandchildren were tested on a large sample of middle-aged adults participating in a longitudinal study on adult health.

2. Methods

2.1. Description of questionnaires and participants

2.1.1. Study A

In December 2004, anonymous questionnaires were completed by 1200 arts or sciences students from all academic levels at the University of Montpellier. Participation was voluntary, and all subjects were informed about the confidentiality and general aim of the study (effect of familial environment on various reproductive traits). Data on family characteristics and reproductive traits were recorded. Students were asked to detail their family compositions between 0 and 15 years of age, including with whom they were reared during childhood during three specific periods (from age 0 to 5 years, 5 to 10 years and 10 to 15 years). The six possible rearing choices were by either biological parent, by a mother and a stepfather, by a father and a stepmother, by a mother only, by a father only or by individuals other than parents. Each student was also asked about the father's socioeconomic status, number of full siblings and maternal birth order. Moreover, students were asked to provide age of menarche, age of first sexual intercourse and number of heterosexual partners. From the 1088 questionnaires, 978 were complete. Two familial categories ("raised by father only" and "raised by father and stepmother") were removed due to their low frequencies (under 1% from 0 to 10 years of age, and between 0.9 and 1.4% from 10 to 15 years of age), giving a final sample of 978 subjects that consisted of 708 women and 270 men.

Ages varied between 18 and 30 years of age, with a mean age of 20.9 ± 1.8 years for women and 22.0 ± 2.0 years for men. Data from students with parents living together (women = 536, men = 202) and students with separated parents (women = 172, men = 68) gave a frequency of 24.5% parental separation in the total student sample. Among students whose parents were separated, 194 were living or had lived with a stepparent(s) (women = 140, men = 54), while 46 had not (women = 32, men = 14). Among children with separated parents, the prevalence of stepparent presence was 80.8%.

Students who completed the questionnaire were also asked to provide saliva samples. However, only 75 volunteers provided samples for hormonal tests. Ages varied between 19 and 30 years, with a mean of 22.0 years for women and 22.3 years for men. Among them, 42 had been raised by two biological parents (women = 26, men = 16), while 18 had not (women = 5, men = 13). Among the 18 individuals with separated parents, only 2 women did not have a stepfather. Thus, for individuals who provided saliva samples, the effect of parental separation could not be differentiated from the effect of stepfather presence.

2.1.2. Study B

Data previously collected on 2000 adult volunteers in a medical research program (GAZEL cohort, see [43]) were used. This program is a large longitudinal follow-up started in 1989, which originally had 20,624 subjects working at Electricité de France-Gaz de France (EDF-GDF) comprised of 15,010 men between the ages of 40–50 years and 5614 women between the ages of 35–50 years. The GAZEL cohort was officially approved by the French National Committee for Data Processing and Liberty (CNIL). For each individual in this sample set, data on the number of children and grandchildren were available in addition to maternal birth order and socioeconomic status. By mail, we specifically asked individuals to describe their parental situation when they were between the ages of 0 to 15 years: reared by two biological parents, by a mother and stepfather (s), by a father and stepmother(s) or by others. Individuals with deceased parents as well as those belonging to the "raised by others" familial category were eliminated. The "raised by father and stepmother(s)" category was underrepresented (1.8%) and was also removed from the analysis. The data set was thus composed of 1255 individuals (women = 199, men = 1,056) varying between 55 and 65 years of age, with a mean age of 59.5 years (±2.8) for women and 59.7 years (±2.8) for men. Among them, 1155 individuals were reared by two biological parents (women = 183, men = 972) and 100 were reared by mothers and one or several stepfathers (women = 16, men = 84).

2.2. Testosterone measurements

2.2.1. Testosterone collection

Saliva samples were collected during a period of 1 month in March 2005. Participants were given kits for saliva collection that included labelled Salicaps tubes and straws (IBL, Hamburg). Each student was asked to provide saliva samples 8 times a day at specific times: upon wake-up, 60 min after wake-up, 90 min after wake-up, noon, 3 PM, 6 PM, 8 PM and 10 PM. Collection instructions were to rinse the mouth with fresh water and wait 5 min before providing saliva samples. Subjects were instructed not to eat, brush their teeth or smoke during the 30 min prior to collection, and immediately refrigerate each sample after collection. Saliva samples were brought back to the lab and immediately stored at −20 °C. Each subject who collected saliva had previously filled out the self-report questionnaire mentioned above. Each kit was returned with information on the subject's usual wake-up time, exact times of collection and other detailed remarks (e.g., illness or sporting activities of the day). Among the 75 saliva kits returned to the lab, 60 were suitable for analysis.

2.2.2. Testosterone analysis

Testosterone levels from saliva samples were determined using Luminescence Immunoassay (LIA) kits [44] (IBL, Hamburg). Briefly, saliva tubes were defrosted and centrifuged at 2400 rpm for 10 min. Standards, controls and samples were pipetted in duplicate into wells of a microtiter plate. Freshly prepared enzyme conjugate and testosterone antiserum were then added into each well. The plate was incubated for 4 h, the incubation solution was discarded and the plate was washed 4 times with diluted wash buffer. After removing excess solution, the AP

Table 2
Descriptive statistics for Study A and Study B

Study A	Men			Women		
	Lived with both parents (Mean ± SD)	Lived with mother alone (Mean ± SD)	Lived with mother and stepfather (Mean ± SD)	Lived with both parents (Mean ± SD)	Lived with mother alone (Mean ± SD)	Lived with mother and stepfather (Mean ± SD)
Age of menarche (yrs)				12.9 ± 0.1	12.5 ± 0.08	12.6 ± 0.1
Age of first sexual intercourse (yrs)	16.7 ± 0.1	16.6 ± 0.1	16.6 ± 0.1	17.0 ± 0.1	16.3 ± 0.1	16.4 ± 0.1
Number of sexual partners	5.3 ± 0.8	6.9 ± 0.8	4.9 ± 0.8	2.3 ± 0.2	5.2 ± 0.4	3.3 ± 0.2
Female PM testosterone levels (pg/ml)	74.4 ± 9.7	N/A	70.9 ± 7.5	10.6 ± 2.5	N/A	26.8 ± 4.3

Study B	Men		Women	
	Parents were separated (Mean ± SD)	Parents lived together (Mean ± SD)	Parents were separated (Mean ± SD)	Parents lived together (Mean ± SD)
Number of children	2.0 ± 0.1	1.9 ± 0.1	1.6 ± 0.1	1.5 ± 0.1
Number of grandchildren	1.6 ± 0.1	1.8 ± 0.1	1.7 ± 0.1	1.1 ± 0.1

N/A, data not available. Mean and standard deviation (SD) of reproductive traits for both men and women, according to household composition during childhood.

Table 3
Statistical models on the effects of family composition for Study A and Study B

Study A	Parental separation	Family composition between 0 to 5 years of age	Family composition between 5 to 10 years of age	Family composition between 10 to 15 years of age
Age of menarche (yrs)	Not tested	$\mathbf{F_{2,598}=4.55,\ P=0.01}$	$\mathbf{F_{2,598}=7.55,\ P<0.001}$	$\mathbf{F_{2,598}=6.55,\ P<0.01}$
Age of first sexual intercourse (yrs)	Not tested	$F_{2,721}=0.28$, $P=0.76$	$F_{2,721}=0.46$, $P=0.63$	$\mathbf{F_{2,721}=3.72,\ P=0.02}$
Number of sexual partners	Not tested	$F_{2,792}=0.73$, $P=0.48$	$F_{2,792}=0.43$, $P=0.54$	$\mathbf{F_{2,792}=2.23,\ P=0.03}$
Female PM testosterone levels	$\mathbf{F_{1,32}=4.50,\ P=0.04}$	Not tested	Not tested	Not tested
Study B			Parental separation	
Number of children			$F_{1,1075}=0.006$, $P=0.93$	
Number of grandchildren			$F_{1,1075}=0.73$, $P=0.39$	

Statistical values (F) and degrees of freedom are indicated. Significant results are in bold. Parental separation is a binary variable. For Study B, separated parents refer to both the mother alone and the mother with a stepfather.

chemiluminescence reagent was introduced into each well, and relative luminescence units (RLU) were measured with a luminometer 10 min later. A total of six standards (0 to 760 pg/mL) were used to obtain RLU of the standards and plotted against their concentrations, allowing the calculation of sample concentration directly from the standard curve (Microwin software). Samples with an inter-assay covariance between replicates higher than 7% were removed from the dataset. Testosterone release displays a circadian rhythm in both men and women with the highest concentrations in the morning and the lowest in the evening [45]. We have thus considered three variables: average testosterone level (average of all 8 samples), morning testosterone level (average of the first 4 samples) and afternoon testosterone level (average of the last 4 samples).

2.3. Statistical analysis

Data were analyzed using general linear models, allowing us to seek the best prediction of a dependent variable given the effects of independent ones. Analysis was conducted separately for the students' core sample (questionnaire), the students' subsample (saliva) and for the GAZEL cohort. For the students' core sample, the dependent variables included number of sexual partners (continuous), age of first sexual intercourse (continuous) and age of menarche (continuous). The independent variables of interest were family composition from ages 0 to 5 years (categorical), 5 to 10 years (categorical) and 10 to 15 years old (categorical). Potentially confounding variables were the child's gender (categorical), age (continuous), socioeconomic status of the father (categorical) and birth order (categorical). For the students' saliva samples, the dependent variables included mean testosterone levels (continuous), morning testosterone levels (continuous) and afternoon testosterone levels (continuous). The independent variable of interest was parental separation (binary). Confounding variables were student age (continuous), student gender (binary) and difference between usual wake-up time and sample wake-up time (continuous). For the GAZEL cohort, the dependent variables included number of children (integer) and

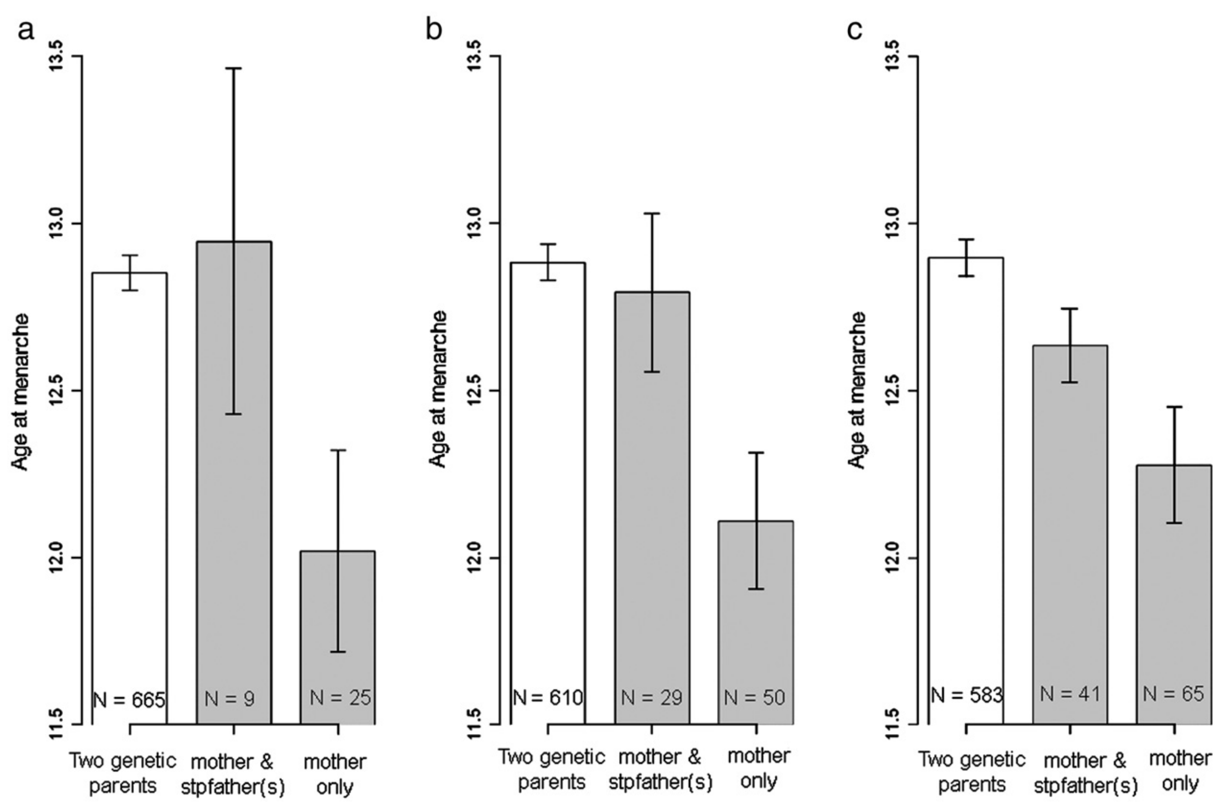

Fig. 1. Study A. Mean age of menarche reported by female students in relation to their parental family structure during the ages of 0 to 5 years (a), 5 to 10 years (b) and 10 to 15 years (c). Error bars indicate SEM. Sample size is indicated at the bottom of the bars.

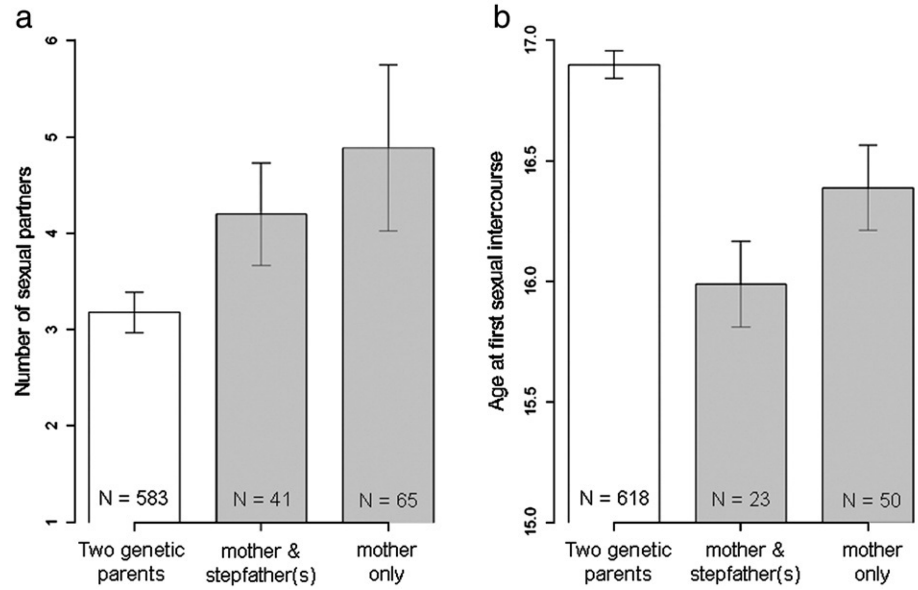

Fig. 2. Study A. Number of sexual partners (a) and age at first sexual intercourse (yrs) (b) reported by students of both sexes in relation to their parental family structure during early adolescence (10–15 years). Error bars indicate SEM. Sample size is indicated at the bottom of the bars.

number of grandchildren (integer). The independent variable of interest was parental separation (binary). Potentially confounding variables included gender (categorical), age (continuous), present socioeconomic status (qualitative) and birth order (categorical). For each analysis, a complete model was first considered with all independent variables, in addition to all biologically meaningful two-way interactions. When correlations between variables were higher than 0.30, only one of the two variables was considered in the model. The complete model was simplified using the AIC criterion [46], then the smallest AIC was chosen and simplified by eliminating the remaining non-significant variables (described by [47]). Higher-order terms were first tested and the least significant and non-significant terms (P>0.05) removed. The significance of the removed terms was evaluated by F-tests, and all statistical analyses were performed using R software [48].

3. Results

Descriptive data and statistical models on the relationship between family composition and reproductive traits in children are shown in Tables 2 and 3, respectively.

3.1. Family structure, sensitive periods and developmental traits (Study A, core sample)

Family composition when children were between the ages of 0 to 5 years was not associated with age of first sexual intercourse or number of sexual partners (P=0.76 and P=0.48, respectively; Table 3A). However, family composition at ages 0 to 5 was significantly related to age of menarche (P=0.01), as the absence of a father resulting from parental separation was associated with a reduction of almost 1 year in the age of menarche (Fig. 1a) compared to a situation with both parents present. Similarly, the absence of a father between the ages of 5 to 10 was not associated with either age of first sexual intercourse (P=0.63) or number of sexual partners (P=0.54), but was significantly associated with age of menarche (P<0.001, Fig. 1b).

When children were between the ages of 10 to 15 years, both the absence of a father and the presence of a stepfather were significantly associated with the age of menarche (P<0.01), age of first sexual intercourse (P=0.02) and number of sexual partners (P=0.03). However, being raised by the mother alone at this stage was associated with a larger reduction in the age of menarche (5.4 months) than the presence of a stepfather (3.8 months), as compared to the situation with two biological parents (Fig. 1c).

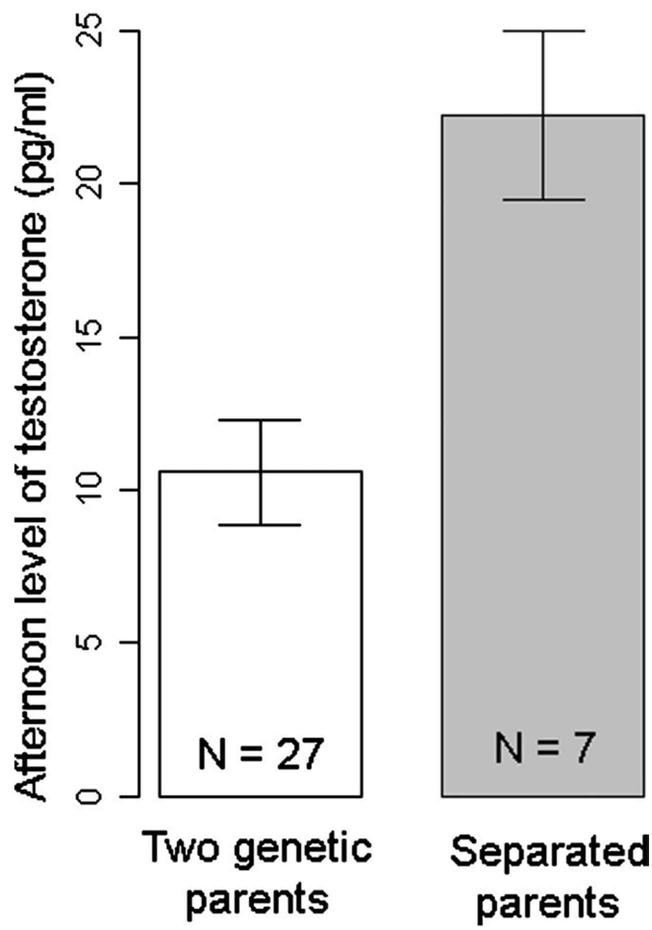

Fig. 3. Study A. Mean levels of afternoon testosterone levels measured in female students in relation to the separation status of their parents (separated vs. not separated). Error bars indicate SEM. Sample size is indicated at the bottom of the bars.

Conversely, the presence of a stepfather at this stage was associated with a larger reduction in the age of first sexual intercourse (1 year) than the absence of a father alone (6 months) (Fig. 2b). Finally, we did not observe any differences between children raised by their mother alone and children raised with a stepfather between the ages of 10 and 15 years on the number of sexual partners: a similar increase in the number of sexual partners was observed, in both sexes (Fig. 2a).

3.2. Parental separation and hormonal correlate (Study A, subsample)

Parental separation was not significantly related to male testosterone levels (mean level P=0.35, morning level P=0.24, afternoon level P>0.63), but an effect was detected for afternoon levels of testosterone in females (P=0.03). Parental separation was associated with a two-fold increase in female testosterone levels (Table 3A and Fig. 3) and controlled with a range of potentially confounding variables. In particular, the age ($F_{1,27}$=0.26, P=0.61), social status ($F_{1,27}$=3.11, P=0.09) and number of sexual partners ($F_{1,27}$=0.18, P=0.67) were not associated with PM testosterone levels in girls. One can note that the phase in the ovarian cycle is not controlled here, as this information was not available. However, the two groups compared are unlikely to differ for this trait as they were recruited from the same population, under the same settings.

3.3. Parental separation and reproductive success (Study B)

In the GAZEL cohort, parental separation was not related to number of children (P=0.93) or number of grandchildren (P=0.39). Volunteers who experienced separation early on (mother alone vs. mother and stepfather) did not report a higher number of either children or grandchildren (Fig. 4a & b).

4. Discussion

4.1. What are the relative effects of the absence of a father and the presence of a stepfather at different stages during childhood on reproductive traits?

This study examined the link between modifications of family structure and parental separation. In particular, we investigated the role that the absence of a father and the presence of a stepfather played on reproductive development, behavior and physiological traits of the offspring.

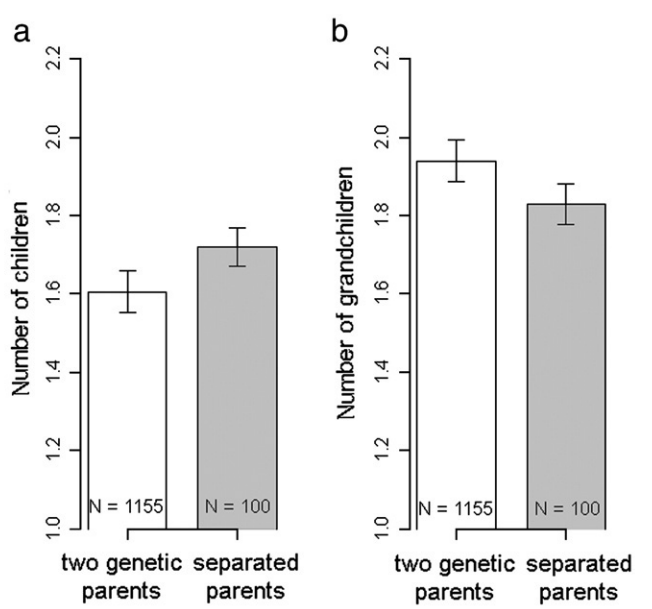

Fig. 4. Study B. Mean number of children (a) and grandchildren (b) reported by members of the GAZEL cohort according to the separation status of their parents. Error bars indicate SEM. Sample size is indicated at the bottom of the bars.

4.1.1. Mother alone compared with two parents

Although consistent with the effects observed from the absence of a father on reproductive traits described in the literature, we found that these effects seemed to depend on timing of occurrence in the child's life. In Study A, age of menarche was decreased by almost 1 year when the father was absent in the first 5 years of the child's life (Fig. 1). This decrease in the age of menarche associated with the absence of a father has been repeatedly found in previous studies as well (review in [49]). Our results are consistent with both Belsky's theory, which proposed that early experiences during the first 5–7 years of life would shape later outcomes, and Quinlan's empirical study, which controlled for the timing of sensitivity to family composition [26]. A second life stage sensitive to the absence of a father was between the ages of 10 to 15 years, concomitant with sexual maturation. Indeed, the age of first sexual intercourse was reduced by almost 6 months (Fig. 2b) and the number of sexual partners increased in both sexes (Fig. 2a). The effects of the absence of a father on the age of first sexual intercourse and number of sexual partners have also been described in previous studies [6,8,9,26].

4.1.2. Stepfather presence

Replacement of a father with a stepfather did not influence reproductive traits in children until the age of 10. However, the presence of a stepfather when children were 10 to 15 years old was associated with an earlier age of menarche (3.6 months earlier), although this trait was more sensitive to the absence of a father (Fig. 1c). The presence of a stepfather during this life stage was also associated with an earlier age of first intercourse for both sexes (1 year earlier, as compared to the situation with two parents, and 0.5 year earlier than the absence of a father) (Fig. 2b). This result is consistent with those of previous studies in women only [26].

4.2. Are family changes associated with fitness changes?

In Study B, we did not find any evidence for a change in the number of children or grandchildren. This effect is not likely to be due to contraceptive behaviors, as the proportion of women who took birth control pills at least once in their lives is low in this sample (~20%) and women with separated parents were as likely to have taken birth control pills as those in intact families. The absence of any fitness variation between these women suggests that parental separation does not lead to any decrease in fitness outcomes. However, several costs of parental separation have been identified and are related to loss of both of paternal and maternal care [50]. Several authors have proposed that the presence of a stepfather is associated with a diversion of maternal care, leading to less parental control [51]. In particular, early adolescence, which precedes the average age of first sexual intercourse (Table 2A), corresponds to a period of intense parent–offspring conflict. The presence of a stepfather most likely reinforces such conflicts and instability [52].

Reproductive traits of children associated with the absence of a father may, in part, be an expression of costs. Therefore, to compensate these costs, our results suggest that offspring acquire plastic adaptive responses and develop alternative reproductive strategies in response to family changes.

4.3. Evolutionary explanations

The intriguing and constant association between the absence of a father and reproductive traits has led to evolutionary explanations.

4.3.1. Conditional adaptation hypothesis

The psychosocial evolutionary hypothesis posits that future environments can be predicted from early environments, allowing children to develop optimal reproductive strategies [39]. More precisely, individuals who experienced stable early environment would perceive others as trustworthy, relationships as stable and resources predictable, leading to the development of a parenting strategy (delayed maturation, late sexuality and stable relationships). In contrast, individuals who experienced the absence of a father would perceive others as untrustworthy, relationships as opportunistic and resources unpredictable, leading to the development of a mating strategy (such as early maturation, precocious sexuality and short-term partners). The paternal investment theory represents a specific aspect of the psychosocial evolutionary hypothesis and focuses on the role of the father and other familial males in female development. Young girls would absorb information about paternal investment during their infancy and adjust their reproductive developments accordingly. Another theory also suggests that early experiences act as cues to predict future reproductive environments, and posits that the absence of a father would be an indicator of the degree of polygyny in the society. Polygyny would create a shortage of women at a reproductive age, producing an increased advantage for those who reproduced earlier. Indeed, comparative data indicate that the degree of polygyny is associated with a decrease in the mean age of menarche [53]. Much like most studies on the subject, the latter two theories are limited to females. Nevertheless, we found that males were affected by the absence of a father concerning their reproductive traits, through a decrease in age at first sexual intercourse and an increase in the number of sexual partners. Additionally, conditional adaptation models do not include effects associated with father's death. Indeed, father absence tend to induce quite different symptoms when resulting from either parental separation or father' death: in the latter case, father absence is unrelated with earlier age of menarche [54]. This observation also suggests that the quality of marital relationships and conflicts associated with separation from the father may be relevant to the onset of puberty. Most importantly, these theories rely on the assumption that ecological settings during infancy persist into adulthood and imply that variations within a population are sufficiently low to build an "optimal reproductive strategy." Therefore, an important limitation to consider is that behavior will be maladaptive if ecological settings change from one generation to the next.

4.3.2. Biosocial hypothesis

Ellis suggested that the presence of a father delays female reproductive development through the action of pheromones, primarily functioning to prevent inbreeding [27]. However, inhibitory signals from the father are unlikely because young girls who live with their fathers after parental separation do not show differences in age of menarche compared to girls who live with their mothers [26]. Another prediction of this hypothesis is that the presence of unrelated males, such as stepfathers, would accelerate the onset of puberty. However, our results do not show any additional effect of the presence of a stepfather on the age of menarche in the first 10 years of life. Finally, this hypothesis does explain effects on male children.

4.4. Genetic mechanisms

There is evidence that a variant X-linked androgen receptor (AR) gene is associated with predisposition to family abandonment and an increased number of sexual partners in men, as well as with the absence of a father and early age of menarche in women [55]. The authors propose that this gene is passed from fathers to daughters, causing earlier onset of puberty in girls whose father was absent. An intriguing result of Study A is that women with separated parents had twice as much testosterone. Although the small size of our sample makes us unable to differentiate the effect of the presence of a stepfather from the effect of the absence of a father, this result supports a testosterone-related genetic hypothesis. However, an empirical study conducted on two community surveys reported that polymorphisms of the androgen receptor gene was not related to adverse fathering behaviors, although was later found to be related to earlier age of menarche [56].

Although this hypothesis is interesting due to its genetic implication in the understanding of child development, several obvious limitations exist. First, it does not account for the results observed in men. Second, it does not exclude those genes associated with reproductive traits present in mothers who also transmit genetic information to their daughters. Additionally, other genes linked to male behavior would be transmitted from the fathers to their sons. Indeed, genetic variations might confound environmental effects on reproductive development and behavior. Human heritability estimate is 0.40 for pubertal timing, 0.28 for number of mates and range from 0.15 to 0.72 for age of first sexual intercourse (review in [26]). However, further support for the X-linked androgen receptor hypothesis must consider more than one generation, as a daughter receiving this X-linked gene from her father will then transmit that gene to both her male and female offspring. Population genetic modelling is required in this case. Moreover, information on parental reproductive behavior in our sample would be necessary for our understanding of the importance of genetics on reproductive traits in both sexes.

5. Conclusion

Our results suggest that the relationship between changes in family composition and reproductive traits of children are likely to result from a combination of environmental and genetic factors. Reproductive outcomes of individuals partly or completely raised in the absence of a father may be only due to a genetic correlation between the father's behavior and the children's reproductive traits, possibly misunderstood if considered *a priori* as costs. However, some effects are surely due to a loss of paternal care, especially those accentuated by the presence of a stepfather (diversion of maternal investment), and may be considered as costs suffered by developing individuals. Whether the modifications of reproductive traits are adaptive in the evolutionary sense requires the identification of fitness benefits associated with the absence of a father. The genetic link between child development and behavior of the father may be relevant in order to further investigate and understand the adaptive significance of certain responses to the family environment. Proximate causes of changes in developmental traits in children have not yet been fully deciphered. Understanding these mechanisms may help confirm or disprove evolutionary hypotheses concerning responses to modifications to the familial environment.

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References

[1] Mayr E. Behavior programs and evolutionary strategies. American Scientist 1974;62:650–9.
[2] Geary DC, Bjorklund DF. Evolutionary developmental psychology. Child Development 2000;71(1):57–65.
[3] Bogin B. Evolutionary hypotheses for human childhood. Yearbook of Physical Anthropology, 40. Allyn and Bacon; 1999. p. 63–89.
Buss DM. Evolutionary Psychology, The new science of the mind. Boston; 1997.

[4] McHenry HM. Behavioral ecological implications of early hominid body size. Journal of Human Evolution 1994;27:77–87.
[5] Ellis BJ. Does father absence place daughters at special risk for early sexual activity and teenage pregnancy. Child Development 2003;74(3):801–21.
[6] Kim K, Smith PK. Childhood stress, behavioural symptoms and mother–daughter pubertal development. Journal of Adolescence 1998;21:231–40.
[7] Maestripieri D, Roney JR, Debias N, Durante KM, Spaepen GM. Father absence, menarche and interest in infants among adolescent girls. Developmental science 2004;7(5):560–6.
[8] Kim K, Smith PK. Retrospective survey of parental marital relations and child reproductive development. International journal of behavioral development 1998;22(4):729–51.
[9] Kim K, Smith PK. Family relations in early childhood and reproductive development. Journal of reproductive and infant psychology 1999;17(2):133–47.
[10] Hewlett B. Demography and childcare in preindustrial societies. Journal of Anthropological Research 1991;47(1):1–37.
[11] Marlowe F. Showoffs or providers? The parenting effort of Hadza men. Evolution and Human Behavior 1999;20(6):391–404.
[12] Marlowe F. Male care and mating effort among Hadza foragers. Behavioral Ecology and Sociobiology 1999;46(1):57–64.
[13] Anderson KG, Kaplan H, Lam D, Lancaster J. Paternal care by genetic fathers and stepfathers II: reports by Xhosa high school students. Evolution and Human Behavior 1999;20(6):433–51.
[14] Anderson KG, Kaplan H, Lancaster J. Paternal care by genetic fathers and stepfathers I: reports from Albuquerque men. Evolution and Human Behavior 1999;20(6):405–31.
[15] Case A. Educational attainment of siblings in stepfamilies. Evolution and Human Behavior 2001;22:269–89.
[16] Lancaster JB, Kaplan HS. Parenting other men's children. Costs, benefits, and consequences. In: Cronk L, Chagnon N, Irons W, editors. Adaptation and human behavior. An anthropological perspective. New York: Aldine de Gruyter; 2000. p. 179–201.
[17] Zvoch K. Family type and investment in education: a comparison of genetic and stepparent families. Evolution and Human Behavior 1999;20(6):453–64.
[18] Flinn MV, Quinlan RJ, Decker SA, Turner MT, England BG. Male–female differences in effects of parental absence on glucocorticoid stress response. Human Nature 1996;7(2):125–62.
[19] Flouri E, Buchanan A. The role of father involvement in children's later mental health. Journal of Adolescence 2003;26:63–78.
[20] Daly M. Some differential attributes of lethal assaults on small children by stepfathers versus genetic fathers. Ethology and sociobiology 1994;15:207–17.
[21] Daly M, Wilson M. New York: Homicide; 1988.
[22] Klevens J. Risk factors and context of men who physically abuse in Bogota, Colombia. Child Abuse & Neglect 2000;24:323–32.
[23] Russel DEH. The prevalence and seriousness of incestuous abuse: stepfathers vs. biological fathers. Child Abuse & Neglect 1984;8:15–22.
[24] Sariola HU. The prevalence and context of incest abuse in Finland. Child Abuse & Neglect 1996;20:843–50.
[25] Bogaert AF. Age at puberty and father absence in a national probability sample. Journal of adolescence 2005;28:541–6.
[26] Quinlan RJ. Father absence, parental care, and female reproductive development. Evolution and Human Behavior 2003;24(6):376–90.
[27] Ellis BJ. Psychosocial antecedents of variation in girl's pubertal timing: maternal depression, stepfather presence, and marital and family stress. Child Development 2000;71(2):485–501.
[28] Ellis BJ. Timing of pubertal maturation in girls: an integrated life history approach. Psychological Bulletin 2004;130(6):920–58.
[29] Flinn MV, England BG. Social economics of childhood glucocorticoid stress response and health. American Journal of Physical Anthropology, 102. London: Routledge press; 2003. p. 33–53.
Flinn MV, England BG. Childhood stress: endocrine and immune responses to psychosocial events. In: Wilce JM, editor. Social & Cultural Lives of Immune Systems; 1997. p. 107–47.
[30] Quinlan RJ, Flinn MV. Parental investment and age at weaning in a Caribbean village. Evolution and Human Behavior 2003;24:1–16.
[31] Archer J. Testosterone and human aggression: an evaluation of the challenge hypothesis. Neuroscience and Biobehavioral Reviews 2006;30(3):319–45.
[32] Bateup B. Testosterone, cortisol, and women's competition. Evolution and Human Behavior 2002;23:181–92.
[33] Grant VJ, France JT. Dominance and testosterone in women. Biological Psychology 2001;58:41–7.
[34] Wagner JD, Flinn MV, England BG. Hormonal response to competition among male coalitions. Evolution and Human Behavior 2002;23:437–42.
[35] Gray PB, Chapman JF, Burnham TC, McIntyre MH, Lipson SF, Ellison PT. Human male pair bonding and testosterone. Human Nature 2004;15(2).
[36] Gray PB. Marriage and fatherhood are associated with lower testosterone in males. Evolution and Human Behavior 2002;23:193–201.
[37] Gray PB, Yang CJ, Pope HG. Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. Proceeding of the Royal society of London B 2006;273(7):333–9.
[38] Gray PB, Parkin JC, Samms-Vaughan ME. Hormonal correlates of human paternal interactions: a hospital-based investigation in urban Jamaica. Hormones and Behavior 2007;52:499–507.
[39] Belsky J, Steinberg L, Draper P. Childhood experience, interpersonal development, and reproductive strategy: an evolutionary theory of socialization. Child Development 1991;62(4):647–70.
[40] Draper P, Harpending H. Father absence and reproductive strategy: an evolutionary perspective. Journal of Anthropological Research 1982;38(3):255–73.
[41] Pettay JE, Helle S, Jokela J, Lummaa V. Natural selection on female life-history traits in relation to socio–economic class in pre-industrial human populations. Plos one 2007;2(7).
[42] Gillepsie D, Russell AF, Lummaa V. When fecundity does not equal fitness: evidence of an offspring quantity–quality trade-off in pre-industrial humans. Proceeding of the Royal society of London B 2008;22:713–22.
[43] Goldberg M, Leclerc A, Bonenfant S, Chastang JF, Schmaus A, Kaniewski N. Cohort profile: the GAZEL cohort study. International Journal of Epidemiology 2007;36:32–9.
[44] Westermann. Determination of cortisol in saliva and serum by a luminescence-enhanced enzyme immunoassay. Clinical labotary 2004;50:11–24.
[45] Dabbs JM. Salivary testosterone measurement: reliability across hours, days, and weeks. Physiology and Behavior 1990;48:83–6.
[46] Akaike H. A new look at the statistical model identification. Institute of Electrical and Electronics Engineers Transactions on Automatic Control 1974;19:716–23.
[47] Crawley MJ. Statistical computing: an introduction to data analysis using S-Plus. Chichester; 2003.
[48] R.2.0.1. The R development core team; 2005.
[49] Matchock RL, Susman EJ. Family composition and menarcheal age: anti-inbreeding strategies. American Journal of Human Biology 2006;18:481–91.
[50] Daly M, Wilson M. The truth about Cinderella: a Darwinian view of parental love. London; 1998.
[51] Flinn MV. Step- and genetic parent/offspring relationships in a Caribbean village. Ethology and Sociobiology 1988;9:335–69.
[52] Weisfeld GE. Parent–adolescent relations. Evolutionary principles of human adolescence, vol. 1. New York: Basis books; 1999.
[53] Kanazawa. Why father absence might precipitate early menarche. The role of polygyny. Evolution and Human Behavior 2001;22:329–34.
[54] Agid O, Shapira B, Zislin J, Ritsner M, Hanin B, Murad H. Environment and vulnerability to major psychiatric illness: a case control study of early parental loss in major depression, bipolar disorder and schizophrenia. Molecular Psychiatry 1999;4:163–72.
[55] Comings DE, Muhleman D, Johnson JP, MacMurray JP. Parent–daughter transmission of the androgen receptor gene as an explanation of the effect of father absence on age at menarche. Child Development 2002;73(4):1046–51.
[56] Jorm AF, Christensen H, Rodgers B, Jacomb PA, Easteal S. Association of adverse childhood experiences, age of menarche, and adult reproductive behavior: does the androgen receptor gene play a role? American Journal of Medical Genetics part B-neuropsychoatric genetics 2004;125B(1):105–11.
[57] Surbey MK. Family composition, stress, and the timing of human menarche. Socioendocrinology of Primate Reproduction. New York: Wiley-Liss; 1990. p. 11–32.
[58] Ellis BJ, Garber J. Psychosocial antecedents of variation in girl's pubertal timing: maternal depression, stepfather presence, and marital and family stress. Child Development 2000;71:485–501.
[59] Borgerhoff Mulder M. Optimizing offspring: the quantity±quality tradeoff in agropastoral Kipsigis. Evolution and Human Behavior 2000;21:391–410.

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