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O brother, where art thou? Investment in siblings for inclusive fitness benefits, not father absence, predicts earlier age at menarche

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Numerous studies have indicated that father absence is associated with earlier age at menarche, with many evolutionary theories assuming that father absence is a causal factor that accelerates reproductive development. However, an alternative interpretation suggests that offspring may reproduce earlier in the presence of half- or step-siblings as the indirect fitness benefits to investing in them are lower, relative to delaying reproduction and investing in full siblings. From this perspective, father absence may perform no causal role in facilitating the onset of menarche. Using data from the Avon Longitudinal Study of Parents and Children, I find that individuals with only half- or step-siblings reach reproductive age earlier than those with only full siblings, with no independent effect of father absence. These results suggest that inclusive fitness benefits to investing in siblings, rather than father absence, may predict variation in age at menarche. These results provide a greater understanding of the adaptive mechanisms involved in reproductive decision-making, as well as potential implications for human life-history evolution and cooperative breeding more broadly.

1. Introduction

The onset of female reproductive potential—menarche—is an important stage in women’s development, resulting in profound biological and socio-cultural change [1], yet the underlying evolutionary reasons for variation in reproductive development remain unclear. A large body of research has indicated that father absence is associated with younger age at menarche [2–5]. These findings present an evolutionary puzzle, as decreased parental investment, such as resulting from an absent father, ought to negatively impact offspring fitness [6], meaning that delayed reproduction may instead be expected.

One set of adaptive explanations, grouped under a ‘predictive adaptive response’ paradigm [7], suggests that individuals adapt their reproductive strategy when their father is absent to maximize future reproductive success. These theories posit that father absence may cue for a future environment in which it may be fitness-enhancing to reproduce earlier. Several variations of this general theory exist, including father absence as a cue for increased adult mortality [8] and father absence as an indicator of increased early-life adversity, which may predict a harsher adult environment [9]. However, these predictive adaptive response theories require that early-life environments are highly correlated with future environments, which may not be a plausible assumption in many cases [10]. A further theory suggests that father absence may result in reduced parental investment, causing children to invest in earlier reproduction rather than continued growth [2,3].
However, an alternative adaptive theory based on inclusive fitness considerations [11] suggests that these effects may not be driven by father absence, but rather differential indirect fitness benefits to investing in siblings as a function of relatedness [6,12]. Individuals may be more likely to forego immediate reproduction and invest in siblings if these are full siblings \((r = 0.5)\) as the indirect fitness benefits are greater, relative to investing in half-siblings \((r = 0.25); r = 0\) in the case of step-siblings). Indeed, previous research has indicated that the presence of half- or step-brothers is associated with earlier age at menarche [13]. From this perspective, father absence performs no causal role in facilitating the onset of menarche, but rather alters the relatedness between an individual and their subsequent siblings [6].

I, therefore, aim to explore the relative merits of each of these adaptive theories for the observed accelerated reproductive timing associated with father absence. According to predictive adaptive response or parental investment theories in which father absence performs a causal role in accelerating menarche, effects of half- or step-siblings ought to be independent of father absence. By contrast, theories based on inclusive fitness predict that the presence of half- or step-siblings may mediate the impact of father absence on age at menarche as children invest more in their own reproduction rather than their siblings’ fitness. I find support for inclusive fitness considerations driving these results, as children with only full siblings reach menarche later than those with only half- or step-siblings, with no independent effect of father absence.

2. Material and methods

Data were obtained from the Avon Longitudinal Study of Parents and Children (ALSPAC) [14]. ALSPAC recruited 14 541 pregnant women resident in the former Avon Health Authority in southwest England with an estimated date of delivery between 1st April 1991 and 31st December 1992. When the oldest children were approximately 7 years of age an attempt was made to increase the initial sample with eligible cases who failed to join the original study. The total cohort is therefore 15 247 pregnancies, resulting in 15 468 fetuses, of which 14 701 were alive at 1 year of age (for more details see the cohort profile paper [14]).

Age at menarche was assessed from a series of nine questionnaires, completed approximately annually between the ages of eight and 17, and two research clinics attended at ages 13 and 16. First-reported age at onset of menarche was the dependent variable (for additional details, see [4]). Detailed family composition data obtained from a questionnaire completed by the child’s mother (when the child was age seven) were used to assess relatedness between the study child and their siblings. Reproductive histories for each of the mother’s relationships and those of their partner were ascertained, from which relatedness between the study child and siblings was determined. Four categories were constructed: only full siblings; only half- or step-siblings; both full and half/step-siblings; and no siblings. Half- and step-siblings were grouped together for practical reasons owing to small sample sizes (few individuals had only half- or step-siblings).

Father absence and the child’s age when the biological father left were queried in three maternal questionnaires when the study child was aged seven, eight and ten. Any children whose father left prior to their sixth birthday were coded as ‘father absent’, while all other cases were coded as ‘father present’ (even if the father left at an older age). This cut-off was chosen as previous research with this sample has indicated that age at menarche in children with an absent father after age five is no different from those with a father present [4]. Potentially confounding variables were also assessed, including: birthweight, mother’s highest education level, presence of severe financial problems, home ownership status (all of which may cue early-life adversity and socio-economic disadvantage), total number of siblings [15] and mother’s self-reported age at menarche. Other than total number of siblings, control variables were collected during the mother’s pregnancy. Descriptive statistics for all independent variables are displayed in electronic supplementary material, tables S1 and S2.

The total number of cases for which age at menarche, sibling relatedness and father absence data were available was 2921, which reduced to 2297 once other confounders were included. Please note that the study website contains details of all the data that are available through a fully searchable data dictionary (http://www.bristol.ac.uk/alspac/researchers/access/). Statistical analyses were conducted using multivariate linear regression models using the function regress in Stata v.14 (StataCorp., USA).

### Results

The average age at menarche in this sample was 12.62 (s.d. = 1.17), with notable differences between sibling categories (figure 1; electronic supplementary material, table S3). The average age at menarche for individuals with only half/step-siblings was 12.28 (s.d. = 1.33), while for those with only full siblings it was 12.7 (s.d. = 1.14). In a univariate model with ‘only full siblings’ as the reference group, there is strong evidence that age at menarche was lower in those with only half/step-siblings \((b = -0.42, 95\% \text{ CI}[-0.18; -0.67], p = 0.001, d = 0.37, r^2 = 0.033; \text{table 1, model 1})\). Consistent with previous research [4], in a univariate model containing just father absence, individuals with an absent father reached menarche at an earlier age \((b = -0.23, 95\% \text{ CI}[-0.12; -0.33], p < 0.001, d = 0.2, r^2 = 0.01; \text{table 1, model 2})\). In a model containing both ‘sibling relatedness’ and ‘father absence’, age at menarche was younger in those with only half/step-siblings \((b = -0.37, 95\% \text{ CI}[-0.11; -0.63], p = 0.005, d = 0.31, r^2 = 0.023; \text{table 1, model 3})\), with no independent effect of father absence \((b = -0.11, 95\% \text{ CI}[0.06; -0.27], p = 0.206)\). These patterns remain if potentially confounding variables are included (table 1, model 4), as well as in an optimized model with non-predictive variables \((p > 0.1)\) removed.
Table 1. Models exploring the association between age at menarche and sibling relatedness. Model 1 presents the univariate model between age at menarche and sibling relatedness. Model 2 presents a univariate analysis of father absence, sibling relatedness, and mother’s highest education level. Model 4 includes all potentially confounding variables. Model 3 presents an optimal version of the full model, resulting in increased relatedness between siblings, preceded by additional confounding variables in model: mother’s highest education level and mother’s age at menarche. Model 5 presents an optimized version of the full model, resulting in increased relatedness between siblings, preceded by additional confounding variables in model: mother’s highest education level and mother’s age at menarche.

| Model          | N   | Variable                      | Coefficient  | Standard Error | P-value |
|----------------|-----|-------------------------------|--------------|----------------|---------|
| Model 1 (n = 2545) |     | sibling relationship (ref: only full siblings) | 0.23 | 0.05 | 0.05 ** |
| Model 2 (n = 2397) |     | half/sib, and step-sib        | -0.12 | 0.03 | 0.02 |
| Model 3 (n = 3743) |     | only half/sib                 | -0.11 | 0.04 | 0.04 ** |
| Model 4 (n = 2297) |     | only full siblings            | 0.08 | 0.02 | 0.011 |
| Model 5 (n = 2921) |     | no siblings                   | 0.03 | 0.02 | 0.032 |

4. Discussion

These findings indicate that the inclusive fitness benefits to investing in siblings, rather than father absence, predict variation in age at menarche. Individuals with only half-step-siblings were found to reach reproductive age on average five months earlier than those with only full siblings (figure 1). This is consistent with individuals investing more in their siblings if they are full siblings for indirect fitness benefits, while individuals with half step-siblings are more likely to invest in their own reproduction as the inclusive fitness gains are lower [6,12]. One plausible mechanism driving these findings is ‘intergenerational reproductive conflict’ [17]. If there is reproductive competition between mothers and children (such that competing for reproductive resources damages the other’s inclusive fitness), children are more likely to invest in their mother’s reproduction (i.e. delay reproduction and invest in siblings) in the presence of full, rather than half-step siblings [6].

Controlling for the relationship between siblings, no independent effect of father absence was observed. Father absence may therefore play no causal role in accelerating the onset of reproductive potential. Although these results provide evidence against ‘father absence’ hypotheses, other forms of early-life adversity or high levels of extrinsic mortality may still influence reproductive decision-making, consistent with life-history theory [2,18]. Here, I only demonstrate that father absence may not accurately represent these adaptive challenges.

These results also have wider implications for understanding the evolution of human life history. They suggest that the evolution of extended childhood and cooperative breeding in humans [19,20] may in part be owing to long-term pair-bonding resulting in inclusive fitness gains to investing in full siblings. Ethnographic studies have indicated that a significant proportion of allomaternal care is from siblings [21] and that the presence of older siblings often increases offspring survival [22], suggesting that cooperation occurs between siblings and has important fitness consequences. These patterns are also found in industrial societies, where young siblings engage in repeated cooperative interactions [23], while among adults full siblings invest more in one another than half-siblings [24]. These findings are consistent with comparative phylogenetic analyses demonstrating that monogamous mating systems, resulting in increased relatedness between siblings, preceded the evolution of cooperative breeding in birds [25], mammals [26] and eusocial insects [27]. Although requiring additional research, these findings suggest that the evolution of extended childhood in humans may, in part, be owing to kin selected benefits of cooperating with full siblings.
References

1. Uskul AK. 2004 Women’s menarche stories from a multicultural sample. Soc. Sci. Med. 59, 667 – 679. (doi:10.1016/j.socscimed.2003.11.031)

2. Ellis BJ. 2004 Timing of pubertal maturation in girls: an integrated life history approach. Psychol. Bull. 130, 920 – 958. (doi:10.1037/0033-2909.130.6.920)

3. Quinlan RJ. 2003 Father absence, parental care, and female reproductive development. Evol. Hum. Behav. 24, 376 – 390. (doi:10.1016/S1090-5199(03)00039-4)

4. Culpin I, Heron J, Araya R, Melotti R, Lewis G, Joinson C. 2014 Father absence and timing of menarche in adolescent girls from a UK cohort: the mediating role of maternal depression and major financial problems. J. Adolesc. 37, 291 – 301. (doi:10.1016/j.jadopecol.2014.02.003)

5. Webster GD, Graber JA, Gesselman AN, Crosier BS, Schember TO. 2014 Life history theory of father absence and menarche: a meta-analysis. Evol. Psychol. 12, 273 – 294. (doi:10.1177/147470491401200202)

6. Moya C, Sear R. 2014 An intergenerational conflict model of age at first birth in humans. Peerj 2, e512. (doi:10.7717/peerj.512)

7. Gluckman PD, Hanson MA, Spencer HG. 2005 Predictive adaptive responses and human evolution. Trends Ecol. Evol. 20, 527 – 533. (doi:10.1016/j.tree.2005.08.001)

8. Chisholm JS. 1993 Death, hope, and sex: life-history theory and the development of reproductive strategies. Curr. Anthropol. 34, 1 – 12. (doi:10.1086/204131)

9. Belsky J, Steinberg L, Draper P. 1991 Childhood experience, interpersonal development, and reproductive strategy: an evolutionary theory of socialization. Child Dev. 62, 647 – 670. (doi:10.2307/1131166)

10. Nettle D, Frankenhuis WE, Rickard U. 2013 The evolution of predictive adaptive responses in human life history. Proc. R. Soc. B 280, 20131343. (doi:10.1098/rspb.2013.1343)

11. Hamilton WD. 1964 The genetical evolution of social behavior. J. Theor. Biol. 7, 17 – 52. (doi:10.1016/0022-5193(64)90059-6)

12. Emlen ST. 1995 An evolutionary theory of the family. Proc. Natl Acad. Sci. USA 92, 8092 – 8099. (doi:10.1073/pnas.92.18.8092)

13. Matchcock RL, Susman EJ. 2006 Family composition and menarcheal age: anti-inbreeding strategies. Am. J. Hum. Biol. 18, 481 – 491. (doi:10.1002/ajhb.20508)

14. Boyle A et al. 2013 Cohort profile: The ‘Children of the 90s’—The index offspring of the Avon longitudinal study of parents and children. Int. J. Epidemiol. 42, 111 – 127. (doi:10.1093/ije/dys064)

15. Bogaert AF. 2008 Menarche and father absence in a national probability sample. J. Biosoc. Sci. 40, 623 – 636. (doi:10.1017/S0021932007003286)

16. Zuur AF, Ieno EN, Elphick CS. 2010 A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3 – 14. (doi:10.1111/j.2041-210X.2009.00001.x)

17. Cant MA, Johnstone RA. 2008 Reproductive conflict and the separation of reproductive generations in humans. Proc. Natl Acad. Sci. USA 105, 5332 – 5336. (doi:10.1073/pnas.0711911105)

18. van Leeuwen AJ. 2016 Life history theory and the social clustering of adolescent behaviour. Doctoral Thesis, UCL.

19. Hedy SB. 2009 Mothers and others: the evolutionary origins of maternal understanding. Cambridge, MA: Harvard University Press.

20. Kaplan HS, Hill K, Lancaster J, Hurtado AM. 2000 A theory of human life history evolution: diet, intelligence, and longevity. Evol. Anthropol. 9, 156 – 185. (doi:10.1002/1520-6550(2000)9:4<156::AID-EVANS>3.0.CO;2-7)

21. Kramer KL. 2010 Cooperative breeding and its significance to the demographic success of humans. Annu. Rev. Anthropol. 39, 417 – 436. (doi:10.1146/annurev.anthro.012809.105054)

22. Sear R, Mace R. 2008 Who keeps children alive? A review of the effects of kin on child survival. Evol. Hum. Behav. 29, 1 – 18. (doi:10.1016/j.evolhumbehav.2007.10.001)

23. Abramovitch R, Peplar D, Corter C. 1982 Patterns of sibling interaction among preschool-age children. In Sibling relationships: their nature and significance across the lifespan (eds ME Lamb, B Sutton-Smith), pp. 61 – 86. Hillsdale, NJ: Erlbaum.

24. Pollett TV. 2007 Genetic relatedness and sibling relationship characteristics in a modern society. Evol. Hum. Behav. 28, 176 – 185. (doi:10.1016/j.evolhumbehav.2006.10.001)

25. Conwell CK, West SA, Davis KE, Griffin AS. 2010 Promiscuity and the evolutionary transition to complex societies. Nature 466, 969 – 972. (doi:10.1038/nature09333)

26. Lukas D, Clutton-Brock T. 2012 Cooperative breeding and monogamy in mammalian societies. Proc. R. Soc. B 279, 2151 – 2156. (doi:10.1098/rspb.2011.2468)

27. Hughes WOH, Oldroyd BP, Beekman M, Ratnieks FLW. 2008 Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science 320, 1213 – 1216. (doi:10.1126/science.1156108)