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Comment

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Parental age differences in humans and their relationship to male and female reproductive success (Fieder & Huber 2007; Helle *et al.* 2008) have recently provoked a flurry of papers that question whether all data have been appropriately analysed and interpreted (Fieder & Huber 2007; Boyko 2008; Fieder *et al.* 2008*a*,*b*; Lindqvist *et al.* 2008). Fieder & Huber (2007), for instance, correctly recognized that both relative age differences and absolute age can matter in this context. However, these are not easy to disentangle. It is even more difficult to determine whether the two sexes can separately achieve what is 'optimal' for them by choosing a specific age difference between themselves and a partner (Boyko 2008; Kokko 2008).

In response to concerns that male and female interests might be erroneously represented as equal when they are not (Kokko 2008), Bookstein *et al.* (2008) find 'toy models' irrelevant because they do not capture all aspects of real data. Dismissal of toy models owing to the lack of fit is, however, not only misguided, but also dangerous if it leads to a false belief that logical errors cannot have crept into more advanced ways of treating data. Toy models are never meant to improve the fit to any dataset. They provide thought-provoking scenarios that illustrate a general problem that would be easy to miss in more complicated scenarios, despite being present there too.

In the case of human reproduction, a toy model can explain why male and female interests may differ despite equal reproductive rates for both members of the pair (Kokko 2008). I agree with Bookstein *et al.* (2008) that it remains important to see whether the same conceptual issues arise in more complicated scenarios. They discuss (i) assortative mating such that similar-aged pairs are more common, and (ii) interactions between pairs such that male and female age combine in nonlinear ways to produce pair fitness. While criticizing the assumptions of an intentionally simplified model, they emphasize that results will differ if certain assumptions are relaxed. This is undoubtedly true. They, unfortunately, fail to address the crux of the issue: whether new results, e.g. adding interaction terms, could avoid problems that the thought experiment intended to highlight—in this case, whether an analysis based on parental age difference allows separate inferences on male and female reproductive options and mate-choice rules.

Will relaxing simplistic assumptions, using more realistic models, help? Kokko (2008) discussed the very points raised by Bookstein *et al.* (2008), by stating (i) 'changing the relative frequency of different pairs in the data will change the estimated location of the optimum, but never in a way that helps disentangling the different mate-choice optima of the two sexes', and (ii) 'if the underlying mate-choice rules were more complicated than in this hypothetical example, the task would get harder still'. Point (i) deals with the issue of similar-aged pairs being more common, and (ii) applies whenever male and female age interact to yield total offspring number (since this naturally necessitates more complicated underlying mate-choice rules). Thus, far from different models using 'incompatible algebra' (Bookstein *et al.* 2008), the issue of whether simple and more complex scenarios yield conceptually different outcomes had already been dealt with, albeit briefly (Kokko 2008).

It is a more serious claim that models combine age data in illogical ways. It is legitimate to count all offspring produced during a monogamous partnership from pair formation until one partner dies, and quantify the expected success of such pairs by graphing the obtained data against the ages of the two members at pairing. Nothing in this procedure assumes that spouses age at a different rate. The suggested comparisons (Kokko 2008) refer to mate-choice situations, not ageing. A 20-year-old female who rejects a 22-year-old suitor in favour of a 20-year-old has not suddenly aged 2 years, even though the analysed age difference has diminished by this amount. Any interpretations of data must be made keeping this in mind—an issue surprisingly easily clouded in statistical detail.

Differences between a spouse's age and one's own very probably have a significant impact on fitness (e.g. Fieder & Huber 2007; Helle *et al.* 2008). The lively debate surrounding this issue shows, however, that the analysis of such effects has surprisingly many pitfalls. The suggested approach i.e. fitting a three-dimensional fitness surface against age-at-pairing of both spouses, avoids some of them (Kokko 2008), but it might also highlight a scarcity of data that yield reliable information on the consequences of unusual age combinations. This is an unavoidable consequence of the fact that humans pair assortatively with respect to age (Bookstein *et al.* 2008). Nevertheless, given that human datasets tend to be rather large, this approach appears worth trying. Otherwise, it will remain very difficult to evaluate claims that age preferences for partners yield fitness benefits for both men and women (Fieder & Huber 2007). To sum up, I fully agree with Bookstein *et al.* (2008) that sexual selection is far more complicated in systems with biparental care (Kokko & Jennions 2008) than, for example, on leks, and that this necessitates great care when building arguments and analysing data.

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Bookstein, F. L., Fieder, M. & Huber, S. 2008 Spouses age at the same rate: reply to H. Kokko, 'Human parental age difference and offspring count: a comment on Fieder *et al.*' *Biol. Lett.* **4**, 261. (doi:10.1098/rsbl.2008.0082)

Boyko, A. R. 2008 Optimal age difference cannot differ between monogamous males and females: a comment on Fieder and Huber. *Biol. Lett.* **4**, 82. (doi:10.1098/rsbl.2007.0456)

Fieder, M. & Huber, S. 2007 Parental age difference and offspring count in humans. *Biol. Lett.* **3**, 689–691. (doi:10.1098/rsbl.2007.0324)

Fieder, M., Huber, S. & Bookstein, F. L. 2008*a* Reply to Adam R. Boyko 'Optimal age difference cannot differ between monogamous males and females: a comment on Fieder and Huber'. *Biol. Lett.* **4**, 83. (doi:10.1098/rsbl.2007.0548)

Fieder, M., Huber, S. & Bookstein, F. L. 2008*b* Reply to Lindqvist *et al.* 'Does parental age difference affect offspring count in humans: comment on Fieder and Huber'. *Biol. Lett.* **4**, 80–81. (doi:10.1098/rsbl.2007.0567)

Helle, S., Lummaa, V. & Jokela, J. 2008 Marrying women 15 years younger maximized men's evolutionary fitness in historical Sami. *Biol. Lett.* **4**, 75–77. (doi:10.1098/rsbl.2007.0538)

Kokko, H. 2008 Human parental age difference and offspring count: and we still don't know what men or women want. *Biol. Lett.* **4**, 259–260. (doi:10.1098/rsbl.2007.0619)

Kokko, H. & Jennions, M. D. 2008 Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**, 919–948. (doi:10.1111/j.1420-9101.2008.01540.x)

Lindqvist, E., Cesarini, D. & Wallace, B. 2008 Does parental age difference affect offspring count in humans? Comment on Fieder and Huber. *Biol. Lett.* **4**, 78–79. (doi:10.1098/rsbl.2007.0514)

NOTE FROM THE EDITOR

I thank all the authors for their valuable discussions on this topic. After careful reflection, I deem the issue has now been thoroughly considered and we will consider no further comments on the article.

Brian Charlesworth.