
Human parental age difference and offspring count: and we still do not know what men or women want

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Two recent studies (Fieder & Huber 2007; Helle *et al.* 2008) present data on optimal age differences of human couples and show a hump-shaped relationship between parental age difference and lifetime offspring count. Boyko (2008) thereafter correctly pointed out that sex-specific locations of the peak offspring count are a logical impossibility (except for sampling error, see also Fieder *et al.* 2008a). Boyko's contribution is a welcome reminder that sexual selection studies must take into account the Fisher condition: the fact that male and female reproductive success is logically intertwined because each offspring has precisely one genetic father and one genetic mother. This simple statement is surprisingly often overlooked. Corrective action is frequently needed because a failure to take the Fisher condition into account can dramatically change evolutionary predictions (see Kokko *et al.* (2006) and references therein).

Despite the laudable clarity of Boyko's short letter, its take-home message (expressed in the title as 'Optimal age difference cannot differ between monogamous males and females') may lead to the impression that the interests of men and women must logically coincide when forming monogamous partnerships. Such an interpretation is mistaken, as is the original assertion that the effects of parental age differences allow inferences about best male and female options separately (Fieder & Huber 2007; Fieder *et al.* 2008a,b). As a thought experiment, consider a case where a pair's offspring count (lifetime reproductive success, LRS), after lifelong monogamy, equals

$$\text{LRS} = M \left[\frac{x}{2a_x} \left(1 - \frac{x}{2a_x} \right) + \frac{y}{2a_y} \left(1 - \frac{y}{2a_y} \right) \right]. \quad (1)$$

Here, x and y denote female and male age (respectively) at the time of pairing; a_x and a_y indicate the ages at pairing that lead to the largest contribution to pair fitness; and M scales the LRS towards realistic values. This is a toy model, intentionally chosen so that male and female ages contribute independently to pair fitness. This makes it particularly easy to state the optimal mate choice rule. For a female of any age, the best choice is a mate of age a_y , likewise, for a male of any age it is ideal to find a female of age a_x .

The accompanying reply can be viewed on page 261 or at <http://dx.doi.org/doi:10.1098/rsbl.2008.0082>.

Figure 1a shows an example with $a_x=20$, $a_y=30$, together with the arbitrary assumption that age at pairing varies between 20 and 40 for females and between 20 and 50 for males. In this example, males should always seek partners as young as possible (figure 1b), while females maximize their fitness by finding a 30-year-old mate, regardless of their own age (figure 1c).

Could we discover these optimal mate choice rules if we did not know the underlying function (equation (1)), and only plotted LRS data against parental age difference? Effects of age differences depend on how often specific (x, y) pairs exist, because the LRS of a $x=20, y=30$ pair is likely to differ from a pair with $x=30, y=40$. Consider an example where all possible pairs are equally common. Mean LRS then has a double-humped shape that reaches its maximum with an age difference of 21 years (figure 1d). A statistical quadratic fit to the same data estimates the optimal difference as 14 years (figure 1d). Neither value is of much help for detecting the underlying optimal mate choice rules for each sex. 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. If the underlying mate choice rules were more complicated than in this hypothetical example, the task would get harder still.

Thus, optimal mate choice can differ between monogamous males and females despite the Fisher condition. It is difficult to distinguish between the effects of age *per se* and the age differences (Fieder *et al.* 2008b; Lindqvist *et al.* 2008). Here, estimating the original fitness surface (figure 1a) would be helpful. Mate-choice decisions can influence the age of one's mate but not one's own. Therefore, shifts along the x and y axes (figure 1a) differ dramatically in their feasibility for a focal individual. This asymmetry is unavoidably lost in all analyses based on parental age differences, which consequently should be interpreted with great caution.

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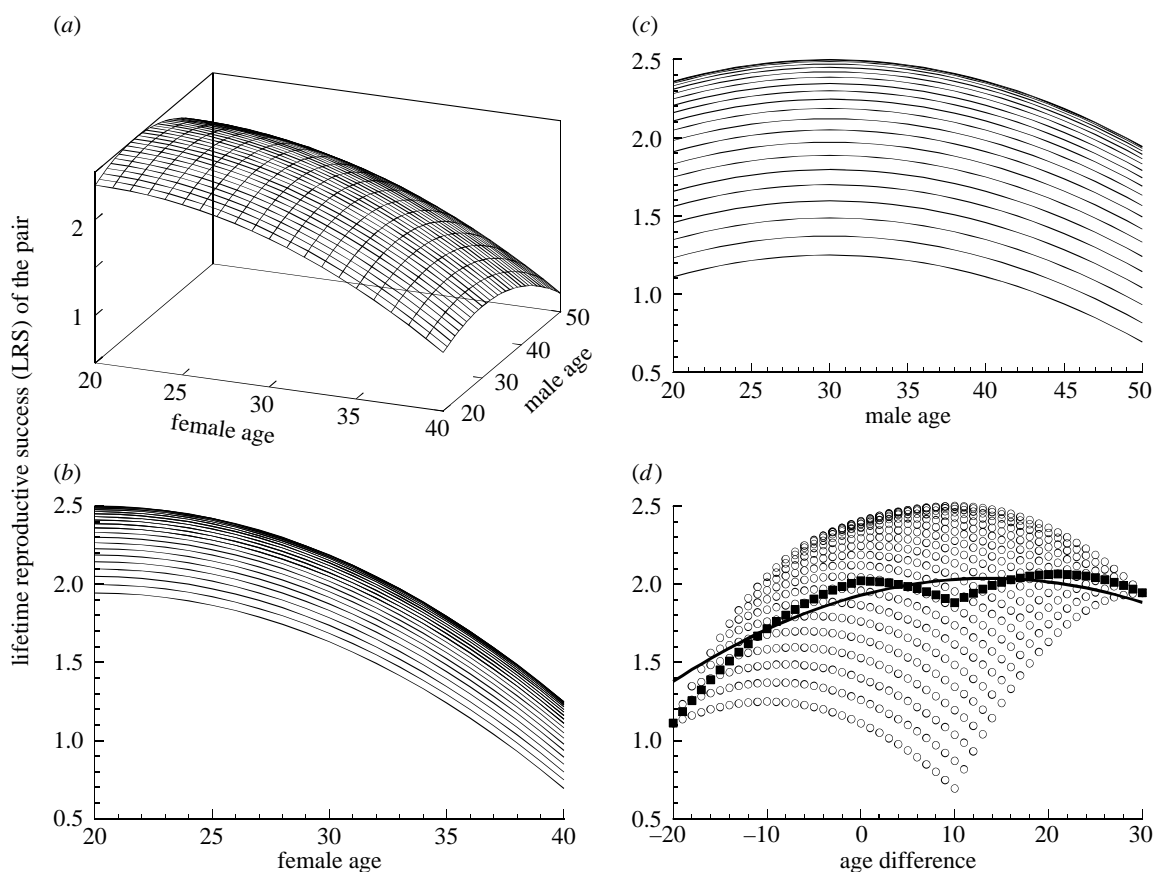


Figure 1. Consequences of equation (1) with $M=5$, $a_x=20$, $a_y=30$. (a) The complete fitness surface; (b) male fitness with respect to female age, different curves corresponding to different male ages; (c) female fitness with respect to male age, different curves corresponding to different female ages; (d) all combinations of parental age difference and the consequent LRS (open circles), the mean LRS for a specific age difference (filled squares), and a quadratic regression ($LRS = -0.0006d^2 + 0.0159d + 1.93$, where $d=y-x$) fitted to data assuming one data point for each possible age combination (x, y) and no sampling error.

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