

contradicts the above statement violates the constraints of formal logic, and thus produces incorrect probabilities. Templeton uses the study of Fagundes *et al.* as an example for an incorrect analysis, where  $q$  represents the rate of interbreeding between modern and archaic human populations [5].

To re-evaluate Templeton's argument in a simpler setting, let us consider a coin tossing experiment where  $q$  is the probability of observing a Head. Suppose that we want to test the null hypothesis ( $H_0$ ) that the coin is fair  $q = 0.5$ . Under the alternative hypothesis ( $H_1$ ), we assume that  $q$  can take any random values between 0 and 1. In a Bayesian framework,  $H_0$  and  $H_1$  represent non-overlapping events and our assumptions about the distribution of  $q$  are formulated conditionally on these separate events. Let us now calculate the posterior probabilities of the two hypotheses. We give equal prior weights to  $H_0$  and  $H_1$ . The coin is flipped 20 times, and we observe 9 'heads'. A short computation shows that the posterior probability of  $H_0$  is 3.3637 times greater than the posterior probability of  $H_1$ . The above exact calculation of probabilities highlights that Templeton's criticism of ABC is, in fact, a criticism of the general rules of Bayesian inference. According to Templeton,  $H_0$  and  $H_1$  would be nested events. However, in a proper Bayesian framework, such as the one we used in the above coin tossing experiment, the two hypotheses represent non-nested events.

Templeton's letter also includes a "coherent correction" to ABC. He suggests that data should be simulated only under the general model to obtain the posterior distribution of the parameter. Then, he constructs a hypothesis test using the 95% credible interval for the parameter. In the coin tossing example, his suggestion amounts to testing if the 95% credible interval of  $q$  contains 0.5. This simple alternative to a Bayesian model choice was proposed earlier by Lindley [8]. An example of the application of Lindley's method is given in Beaumont and Balding [9], who

developed a Bayesian algorithm to scan genomes for signatures of natural selection. More generally, Lindley's method is often applied by statisticians to alleviate the computational burden of Markov chain Monte Carlo algorithms, even though it is not fully Bayesian. Nevertheless, the Bayes factor is often preferred in the literature [10]. In the context of ABC, Csilléry *et al.* [7] suggested the use of methods based on posterior predictive distributions because Bayes factors are not properly defined when regression-based algorithms are used. One point where Csilléry *et al.* [6] and Templeton could agree is that computing model complexity and evaluating alternative models still require further research.

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## Letters Response

# Response to Carere *et al.* Human mate preference: inconsistency between data and interpretations

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We would first like to thank Carere *et al.* [1] for their interest and for providing us with an opportunity to discuss our paper [2], since further debate on this topic with scientists from different fields, such as behavioural physiology, will have a strong benefit for future research. Additionally, we assume their comments could be representative of a community generally sceptical about evol-

utionary psychology, and it is therefore crucial to correct misleading points if we are to attract scientists from all fields to solve the question we raised.

First, Carere *et al.*'s title 'Human mate preference: inconsistency between data and interpretations' is not correct. To date, there is no evidence against the hypothesis that hormonal contraceptives affect mate preferences in humans, and the fact that all ten previous studies point in the same direction deserves interest, given the

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potentially important outcomes for women if the effect of the pill on mate preferences is strong enough to affect mate choice. We also would like to point out that nowhere in the paper do we make the statement that this is confirmed to be the case, but rather call for more studies.

Second, and importantly, we do not assume women's behaviour to be related only to variation in hormones affected by the pill. As for any complex trait, many environmental and genetic factors interact, and this is obviously true for mate preferences. It is important to note that most of the previous studies on mate choice both in animal behaviour and human psychology have been based on controlled experiments (i.e. fixing all parameters except the one of interest to assess the effect of that particular parameter independently of others), which in turn explains why the link between hormonal contraceptive use and mate preferences has generally not been investigated along with other important factors, such as personality. As we stated in our paper, pill-induced change in mate preference in such experiments might not translate into actual mate choice. Yet the effect associated with hormonal contraceptive use appears to be strong enough to significantly reduce the amount of tips received by lap-dancers [3], which suggests that the link between contraceptive use and women's attractiveness might not be negligible in real life situations. Nevertheless, we acknowledge that it is pivotal to address the magnitude of the link between pill use and mate preferences relative to other factors, as this would be useful in assessing the likelihood that the use of the pill affects mate choice.

Third, from their comment, it appears that the term "mimicking pregnancy" to describe the hormonal state of a pill user is misleading. Actually, we did not mean that pregnant women and pill users were quantitatively similar relative to their hormonal levels. Indeed, there is evidence that pill users have very low levels of both progesterone and oestrogen as compared to pregnant women [4]. However, neither pill users nor pregnant women show ovulation (and hormonal fluctuations associated with it), which makes them qualitatively similar in that they cannot reproduce. We welcome future efforts to establish the detailed hormonal mechanisms leading to differential behaviour displayed by pill users compared to non-users.

Fourth, we do not fully agree with the authors' statements about the sample size. Although the total number of individuals (~1200) is obviously limited (as our paper clearly states in a call for more studies), the presented sample size lies in the upper half of the current behavioural studies. Furthermore, rather than the sample size itself, what is really intriguing is that all previous studies independently point in the same direction. The take-home message of our paper was not an answer, but rather a refined question, based on 10 studies with similar results, and we felt it was enough to start seriously considering the possibility that the pill might affect mate choice. From that perspective, further studies aiming at solving several under-

lying questions are now warranted, in particular (1) how individual characteristics (e.g. age, personality and attractiveness) interact with cycling mate preferences and pill uptake, (2) identifying the molecular correlates of cycling mate preferences and how they interact with hormone based contraceptives, (3) determining the cross-cultural validity of cycling mate preferences, and (4) to what extent cycling mate preferences translate into actual mate choice for extra-pair copulation and long-term relationships.

Fifth, we are not "brilliantly resolving the dual sexuality dilemma" nor presenting men as "pollinator wasps". The reasoning behind men's and women's mate preferences can be applied to any mammal species where males and females differ in their level of obligatory parental investment. In such species, indeed, males might increase their reproductive success and chance to contribute to the next generation by increasing their number of sexual partners. Females however, are left with the maximization of offspring quality and paternal investment. Since getting both resources in the same man is not always possible, and given that women have not always been able to choose their partners (see Box 1 of Ref. [2]), the evolution of a mechanism allowing women paired with a suboptimal partner to prefer high-quality men when fertile is not unlikely. Reproductive benefits associated with extra-pair copulation in females have been extensively documented in non-human species, and it appears that extra-pair offspring are on average of better quality than in-pair offspring [5]. To date, there is no clear reason for the role of extra-pair paternity to be different in humans, where female infidelity is observed in all societies despite the strong costs associated with its discovery [6].

The final point of Carere *et al.* is based on the question whether "it does not count that men have plenty of sex with non-ovulating women as well". Men obviously also have plenty of sex with non-ovulating women, other men, or even toys. The real biologically relevant question to resolve is whether men prefer ovulating women to non ovulating women for sexual intercourse and whether pill-use changes the pool of men a woman chooses from.

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