Letter

Does Contraceptive Use Lead to Increased Affairs? A Response to Larmuseau *et al.*D. James Harris^{1,2,*}

Several recent studies using genetic tools have indicated that extra pair paternity (EPP) rates in humans appear, in various cultures, to be around 1% [1–3], a degree well below previously proposed levels of 10–30% [4]. Since these genetic studies enable EPP rates to be assessed over hundreds of years, rates can be estimated before the widespread use of contraceptives, which have been proposed to potentially impact female choice and EPP rates [5]. In a recent article in *TREE*, Larmuseau *et al.* [6] noted that the 1% EPP rates have stayed near constant over several human societies and over the past few hundred years. From this, they state ‘without the availability of modern contraceptives the historical EPP rates should have been much higher, in the range of 10–20%, based on present behavioural measures of EPCs [Extra pair copulations] and observed kin investments of matrilineal and patrilineal family members’. Furthermore, they conclude ‘it appears that people were more faithful in their relationships in the past, or – put differently – that the recent widespread adoption of modern contraceptives has sexually liberated women, resulting in a greater number of extra-marital affairs, but in EPP rates that have remained as low as they were before.’ It is worth reconsidering whether the data can support such strong statements.

Even given the difficulties in obtaining accurate EPC levels, Simmons *et al.* [7] note ‘a population wide rate of EPC of about 20% is expected to generate a population wide rate of EPP of about 0.6%.’ Thus, a historic EPP rate of 1% would in fact imply higher

EPC rates well above 20% and at the upper end of the range of 0.8–30% of women who report EPC in modern studies (reviewed in [8]). In other words, this evidence does not support an increase in EPC, or a link with contraceptives. Regarding matrilineal and patrilineal family member investments, studies show that investment is on average greater through matrilineal relatives, and this is typically assumed to reflect potential paternity uncertainty, caused by EPC [9]. Gaulin *et al.* [10] suggested a paternal uncertainty of 13–20%, estimated using an assumption of a linear relation with investment (as scored from 0–6 with interval properties), leading to the proposition that matrilineal aunts invest 25% more than do patrilineal ones. Given that EPP rates are in fact now known to be lower, this simply implies that the model overemphasizes the difference, or that matrilineal input is a lower percentage greater than patrilineal investment. While inferring that matrilineal relatives invest more in their relatives than do patrilineal ones is simple, categorizing this into a value (such as 10% more or 25% more) is difficult and requires many assumptions. The model itself fits any EPP rate above zero and, therefore, also cannot be used to support a hypothesized increase in female infidelity, or a link with contraceptive use.

I welcome the perspective of Larmuseau *et al.* [6] in highlighting the new data on EPP rates, which are certain to shed new light on avenues of research in human sexual behavior and even effective population sizes. Larmuseau *et al.* [6] do note that various factors will have a role in EPP rates and, indeed, recent studies have indicated that society group size and sexually transmitted diseases may have facilitated the emergence of socially imposed monogamy [11]. However, the data do not support a hypothesis that women are currently less faithful than they were in the past, or that this is linked to the use of modern contraceptives.

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Letter

Long-term Trends in Human Extra-Pair Paternity: Increased Infidelity or Adaptive Strategy? A Reply to Harris

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In a recent article we showed that human extra-pair paternity (EPP) rates did not substantially decline in contemporary

relative to historical Western societies over the past few hundred years [1]. In both cases, ~1–2% of all children appeared to be the product of cuckoldry. This came as a great surprise, given the known steady increase in the adoption rate and reliability of contraception over the past century [2]. We proposed several hypotheses to explain this paradox. One, which Harris [3] focused on, was that women may have become more sexually liberated, and now engage in relatively more extramarital affairs. Harris [3] counters our hypothesis by arguing that the low historic EPP rate of ~1% would in fact be consistent with very high rates of extra-pair copulation (EPC) that exceed the estimates in contemporary societies, and that the available data therefore do not support the idea that woman may have become less faithful. We show here that the implicit assumptions by which EPC rates were estimated by Harris [3] are erroneous. We then go on to review two explanations for the observed patterns: one being based on increased infidelity, and the other based on the idea that EPC could have rare adaptive benefits for woman in specific circumstances, such as when their husband is infertile.

The way in which Harris [3] infers the EPC rate from the EPP rate is based on a calculation first presented by Simmons *et al.* [4]. In this article the EPP rate was defined as the probability of conceiving a child derived from an EPC following a single act of intercourse, and was calculated as the probability for woman to engage in EPC multiplied by the probability of conception (3% if timing was random with respect to their menstrual cycle and if the woman were not to use contraception [5]). There are several issues with this calculation. First, the EPP rate as defined and used in this calculation does not correspond to the EPP rates as inferred from genetic studies, which are simply the proportion of children that are derived from EPC. Using the genetic EPP rate definition, it is clear that the EPC rate would in fact equal the EPP rate if the likelihood of

conception following an EPC act was the same as that following within-pair copulation. Another issue was that the cited EPC rates were not defined as the proportion of copulations that were extra-pair, but were merely inferred from questionnaires in which it was asked if woman had had sexual intercourse with a third party while in a relationship with their partner. Harris [3] then go on to cite very indirect estimates of EPP rates based on matrilineal versus patrilineal biases in kin investments [6], which had earlier already been shown to be unreliable [7], and which do not directly relate to the question of whether infidelity has increased or not.

Our rationale for inferring that infidelity might have increased in recent times was in fact very simple, and not reliant on highly uncertain inferences about the actual EPC rate. If EPP rates have remained stable over the past few hundred years, while the reliability and adoption rate of contraception have greatly increased over this period [2], the logical consequence is that woman must now be engaging in relatively more affairs, at least if seeking EPCs is primarily motivated by pleasure-seeking or acquiring possible social or material benefits from the extra-pair partner, and that rare pregnancies resulting from EPCs would in effect all be unplanned. We agree with Harris [3], however, that it is likely that the greater availability of more reliable contraception was certainly not the sole driver in this change in sexual attitudes. For example, in an analysis of all available data on EPP rates in high-income countries, we find that our claim of increased sexual liberation over the past few hundred years is well supported because EPP rates in fact have not merely remained stable but have significantly increased among children born between the 1940s and early 1960s (ca 2.5% [8]) compared to the EPP rates inferred for children born over the past 400 years in historical EPP studies (~0.8% [1]) (Figure 1). Nevertheless, as we noted before [9], it is clear that many factors could have contributed to this

Figure 1. Historical Evolution of Human Extra-Pair Paternity (EPP) Rates. EPP rates in Western high-income societies have risen significantly ($P = 0.0001$) from ~0.8% in historical EPP studies (which measured the mean EPP rate per child over the last ~400 years [1]) to ~2.5% for children born between approximately 1945 and 1962, but then significantly declined again ($P = 0.002$) to ~1.2% following the introduction of the birth control pill (ca 1965) [8]. Data are based on Anderson [12] and Voracek [8], subsetting to data from high-income Western societies, with the addition of some recently published studies and the exclusion of very small studies or studies deriving from paternity testing labs (which both show a strong upward bias [8]) (supplemental information online for details; N = number of studies, n = total number of children investigated, bars show means plus 95% confidence intervals).

pattern, including not only increased adoption rates of contraception but also changing social norms, increased urbanization, greater financial independence, and increased secularization. In addition, as first shown by Voracek *et al.* [8], it appears that the introduction of the birth control pill around 1965 has caused a significant decline in EPP rates based on available recent data, in line with the great increase in reliability of this specific contraceptive method [8]. Even so, EPP rates after the introduction of the pill still do not show a significant decrease compared to the historical EPP data (Figure 1), which suggests that over the time-span of several hundred years increased sexual liberalization is still obvious and well supported.

Another hypothesis, not discussed in our original paper, could be that EPP is a rare, adaptive strategy for women to achieve

reproductive benefits, for example if they have an partner who is infertile, a condition that affects an estimated 6% of all men [10]. Supporting evidence for this adaptive ‘fertility assurance’ hypothesis comes from a study on couples where the husband suffered from male infertility, where 29% of the conceptions following a fertility treatment were found to be derived from extra-pair sexual interactions [11]. If approximately one third of all women with an infertile partner would pursue EPCs as a specific strategy to become pregnant, we would expect this to result in an EPP rate of approximately $6\%/3 = 2\%$, which is in the ballpark of both contemporary and historical EPP rate estimates (Figure 1). Under this hypothesis, EPP rates would be expected to remain approximately constant, and would be largely independent of the reliability of available contraception because the intention of woman in this case would be to become pregnant of an extra-pair mate.

Overall, it is clear that further research will be necessary to conclusively decide between these alternative hypotheses for why EPCs occur in humans, and what the motivation and possible adaptive value could be behind their occurrence.

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Appendix A Supplemental Information

Supplemental Information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2016.06.012>.

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Letter

Pushing Past Boundaries for Trait Hypervolumes: A Response to Carmona *et al.*

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Functional diversity (FD) has a key role in community assembly [1], biodiversity conservation [2], and ecosystem functioning [3]. Carmona *et al.* [4] recently proposed an approach for quantifying FD across scales using a probability density function (PDF; the distribution of values

along one or more functional trait axes) to better measure functional redundancy, overlap, and dissimilarity. Their work is timely because it builds on a growing interest in making biological inferences from functional traits, and is useful because it unifies functional diversity concepts. However, their approach may lead to inaccurate inferences because of statistical issues around using PDFs to infer trait distribution boundaries, and around transforming data.

Carmona *et al.* propose a fully probabilistic interpretation of trait distributions – that is, one where distributions do not have boundaries (Figure 1A) [4]. However, their illustrations are drawn with boundaries (e.g., their Figure 2 [4]). In general, when using PDFs for statistical inference, distributions are better understood when edges are delineated at a certain probability thresholds (Figure 1B). These edges allow for proper quantification of space within the PDF and, as such, are crucial when using PDFs to estimate FD metrics, such as richness (total space occupied) and redundancy (number of species per unit space occupied). If a threshold is not used to delineate edges, and the probability density estimated with a Gaussian kernel or any other function with non-zero probability density everywhere, then hypervolumes will have infinite boundaries that are not useful for analysis. Thresholds can be chosen either by fixing a value [5] or by using an algorithm [6]. Importantly, the choice of threshold can change the size and shape of the trait distribution, leading to different values of FD metrics and different inferences (e.g., overlap or no overlap) (Figure 1B).

Another issue in working without boundaries via a fully probabilistic assumption is that trait distributions must integrate to one, potentially leading to the biologically unrealistic overlap of multiple traits. Traits with wide ranges are forced into distributions that take very low values over most of their ranges, even if biological performance is high over that range.